

Thesis
365 2


**An Analysis of Landscape Diversity on the Floodplain of a
Scottish Wandering Gravel-bed River.**

Helena Parsons B.Sc (Hons) M. Sc.

Department of Environmental Science,
University of Stirling.

September 2000
Submitted for the Degree of Doctor of Philosophy.

The contents of this thesis are original
and all of the work was undertaken
by the author. The results presented herein
are not taken from any other thesis
written by the author.

Signed..........

Abstract

This thesis examines landscape diversity within alluvial valley floors using the case study of a Scottish wandering gravel-bed river. The thesis aims are two-fold; firstly to investigate the spatial and temporal patterns of valley floor landscape diversity within semi-natural environments, and secondly to develop a methodology for quantifying alluvial valley floor landscape diversity in space and time. The diversity analysis involves quantifying the spatial patterns of geo-, pedo- and biodiversity (flora) within floodplain zones which have been exposed to approximately 100 years of recovery since flood embankment abandonment along the most active reaches of the river. In addition historical records including aerial photographs, maps and narrative accounts were used to assess the temporal patterns of the diversity of landscape patches and how they have changed through time using a series of landscape indices. The analysis thus accounts for the role of river channel change in producing a complex mosaic of land cover types within alluvial valley floors.

The spatial analysis revealed that landscape diversity tends to be greater in the perpendicular orientation to the main channel, i.e. along an aquatic-to-terrestrial environmental gradient. The temporal analysis results revealed that the landscape over the last 50 years has changed from being dominated by few relatively large isodiametric patches to a landscape dominated by small irregular shaped patches. Thus although landscape patch richness has increased along with an increase in land cover types through time, the landscape patches have also become more fragmented.

The major outcomes of the research are the deriving of quantitative results of the spatial and temporal patterns of floodplain landscape diversity, an evaluation of the role of channel dynamics in creating the diverse mosaic of land cover types, the identification of the environmental controls and supporting floodplain habitats of a number of rare species and a proposed methodology for assessing landscape diversity to be validated on other river systems.

Acknowledgements.

I would like to express my thanks to the Department of Environmental Science and the University of Stirling for funding this Ph.D research. Special thanks go to my supervisors, Dave, Donald and Ian, and to all the staff and students who have helped along the way. This research was also made possible by kind permission from Dr Ross Smith, Chris Langton and Graeme Morrison to work on the floodplain of the River Tummel. I would also like to thank Dr Ross Smith and the Royal Commission for supplying me with historical data of the river system. Thanks also to David Long and Douglas McKean at the Royal Botanic Gardens, Edinburgh for helping me with moss and willow identification.

Special thanks go to all who volunteered wilfully or by force with my field work, and for your tolerance, hard work and patience whilst scrambling through the undergrowth. I would also like to extend my gratitude especially to Stuart for always being keen to soldier on when things went wrong, and for never complaining about the weather. Special thanks also to two complete strangers, who subsequently became friends, David and Martin, for their hard work and enthusiasm.

Many thanks to all who funded my conference expenses, particularly to the Faculty of Natural Sciences, the BGRG, and the IALE for funding my attendance to the AGU Fall Meeting in San Francisco.

Personal thanks go to those in 4B108 whose lively and entertaining conversation has certainly played a vital role in helping us all maintain our sanity when the going gets tough, and to my family for always supporting me in everything I choose to do. All apologies go to those who I have failed to mention, I've not forgotten you I've just run out of room..... And Blair Urquhart.

Contents.

	<u>Page</u>
List of Figures	ix
List of Plates	xvi
List of Tables	xvii
List of Appendices	xxiii
Chapter 1: Introduction	
1.1. The ecological importance of riparian and floodplain landscapes	1
1.2. Rationale: aims and objectives	3
1.2.1. <i>Hypotheses</i>	6
1.3. Study area, River Tummel, Perthshire, Scotland	6
1.4. Wandering gravel-bed rivers	13
1.5. Thesis structure	14
Chapter 2: Literature review	
2.1. Landscape diversity	16
2.1.1. The landscape diversity concept	16
2.1.2. Landscape ecology approach: theory and application	21
2.1.3. Landscape patterns	23
2.1.4. Hierarchically structured landscapes: the nested hierarchy approach	24
2.1.5. Human impact on floodplains	25
2.2. Floodplains	28
2.2.1. Historical perspective	28
2.3. Geodiversity on floodplains	30
2.3.1. Geomorphic processes	30
2.3.2. Floodplain classification	33
2.4. Pedodiversity on floodplains	35
2.4.1. Geomorphology and soils	35
2.4.2. Soil flooding and its effects	37
2.4.3. Classification of alluvial soils	39
2.5. Botanical diversity on floodplains	39
2.5.1. Riparian landscapes	39

2.5.2.	Successional sequences in floodplain environments	40
2.5.3.	Geomorphic, soil, and vegetation relationships	43
2.5.4.	Botanical diversity	45
2.6.	Landscape indices	47
2.6.1.	Analysing landscape diversity	47
2.6.2.	Indices for measuring diversity	49
2.7.	Spatial analysis	52
2.7.1.	Geostatistics: semivariance and kriging	52

Chapter 3: The development of a methodology for interrogating floodplain landscape diversity: Tomdachoille Island SSSI, case study.

3.1.	Introduction	54
3.2.	Methodology	54
3.2.1.	Criteria for the selection of study areas	54
3.2.2.	Historical analysis and aerial photograph interpretation	56
3.2.3.	Field sampling strategy	56
3.2.3a.	<i>Sampling strategy</i>	56
3.2.3b.	<i>Vegetation survey</i>	58
3.2.3c.	<i>Soil sampling</i>	59
3.2.3d.	<i>Topographic survey</i>	60
3.2.4.	Field data handling and processing	60
3.2.4a.	<i>Vegetation data</i>	60
3.2.4b.	<i>Soil and substrate data</i>	64
3.2.4c.	<i>Elevation data</i>	65
3.2.5.	Statistical analysis: examination of heterogeneity and relationships	66
3.2.5a.	<i>Diversity indices</i>	66
3.2.5b.	<i>Exploratory data analysis (EDA)</i>	69
3.2.5c.	<i>Hypothesis testing</i>	69
3.2.5d.	<i>Geostatistics (semivariance and kriging)</i>	70
3.3.	Results	74
3.3.1.	Historical data interpretation	74
3.3.2.	Vegetation classification and description	74

3.3.2a.	<i>TWINSPAN interpretation</i>	76
3.3.2b.	<i>Community classification</i>	80
3.3.3.	Floristic relationships with environmental variables	82
3.3.4.	Soil classification and description	86
3.3.5.	Landform classification and description	91
3.3.6.	Diversity analysis	91
3.3.6a.	<i>Data grouped by plant community</i>	91
3.3.6ai.	<i>Richness</i>	91
3.3.6aii.	<i>Shannon index H' and J</i>	94
3.3.6aiii .	<i>Pedodiversity within the plant communities</i>	96
3.3.6aiv .	<i>Geodiversity within the plant communities</i>	98
3.3.6b.	<i>Data grouped by soil/substrate classes</i>	98
3.3.6bi.	<i>Biodiversity within the soil/substrate groups</i>	98
3.3.6bii.	<i>Geodiversity within the soil/substrate groups</i>	100
3.3.6c.	<i>Data grouped by landform</i>	101
3.3.6ci.	<i>Biodiversity within the landform classes</i>	101
3.3.6cii.	<i>Pedodiversity within the landform classes</i>	101
3.3.6d.	<i>Diversity variation perpendicular and parallel to the main channel</i>	103
3.3.6di.	<i>Habitat diversity</i>	103
3.3.6dii	<i>Pedodiversity</i>	105
3.3.6diii.	<i>Geodiversity</i>	105
3.3.6e.	<i>Landscape diversity</i>	108
3.3.6ei.	<i>Species unique to landform classes</i>	108
3.3.6eii.	<i>Landscape diversity evaluation</i>	110
3.3.7.	Results of exploratory data analysis	111
3.3.8.	Relationships between variables: correlation and regression	115
3.3.8a.	<i>Correlation</i>	115
3.3.8b.	<i>Regression</i>	128
3.3.9.	ANOVA	133
3.3.10.	Spatial variance analysis: geostatistics	137
3.3.10a.	<i>Semivariance and spatial dependence</i>	137
3.3.10b.	<i>Kriging</i>	143
3.4.	Discussion	151

3.4.1. Spatial patterns of succession on Tomdachoille	151
3.4.2. Spatial patterns and relationships between the landscape components	159
3.4.3. Spatial patterns of landscape diversity within the Tomdachoille study area	163
3.5. Summary	168

Chapter 4: Validation of the relationships between the components of landscape diversity along other reaches of the River Tummel.

4.1. Introduction	170
4.2. Methodology	170
4.2.1. Criteria for the selection of study areas	170
4.2.2. Field sampling strategy	173
4.3. Results	174
4.3.1. Historical data interpretation	174
4.3.2. Vegetation classification and description	174
4.3.2a. <i>TWINSPAN interpretation</i>	175
4.3.2b. <i>Community classification</i>	177
4.3.3. Floristic relationships with environmental variables	178
4.3.4. Soil classification and description	185
4.3.5. Landform classification and description	186
4.3.6. Diversity analysis	187
4.3.6a. <i>Data grouped by plant community</i>	187
4.3.6ai. <i>Richness</i>	187
4.3.6aaii. <i>Shannon index H' and J</i>	189
4.3.6aiii. <i>Pedodiversity within the plant communities</i>	191
4.3.6aiv. <i>Geodiversity within the plant communities</i>	193
4.3.6b. <i>Data grouped by soil/substrate group</i>	193
4.3.6bi. <i>Biodiversity within the soil groups</i>	193
4.3.6bii. <i>Geodiversity within the soil groups</i>	195
4.3.6c. <i>Data grouped by landform</i>	195
4.3.6ci. <i>Biodiversity within the landform classes</i>	195
4.3.6cii. <i>Pedodiversity within the landform classes</i>	197

4.3.6d.	<i>Diversity variation perpendicular and parallel to the main channel</i>	198
4.3.6di.	<i>Habitat diversity</i>	198
4.3.6dii.	<i>Pedodiversity</i>	200
4.3.6diii.	<i>Geodiversity</i>	201
4.3.7.	Species unique to landform units and vegetation types	202
4.3.8.	Relationships between variables- correlation and regression	205
4.3.8i.	<i>Correlation</i>	205
4.3.8ii.	<i>Regression</i>	215
4.3.9.	ANOVA	222
4.4.	Discussion	228
4.4.1.	Spatial patterns of succession within the Ballinluig dataset	228
4.4.2.	Spatial patterns and relationships between the landscape components	230
4.4.3.	Spatial patterns of landscape diversity within the Ballinluig dataset	232
4.5.	Summary	238

Chapter 5: Temporal analysis of landscape patterns.

5.1.	Introduction	240
5.2.	Methodology	240
5.2.1.	Digitising aerial photographs	240
5.2.2.	Classification and analysis of polygon coverages	242
5.3.	Results	247
5.3.1.	Temporal change in landscape patterns within the Tomdachoille reach	247
5.3.1a.	<i>1946 coverage</i>	247
5.3.1b.	<i>1968 coverage</i>	250
5.3.1c.	<i>1971 coverage</i>	250
5.3.1d.	<i>1988 coverage</i>	251
5.3.1e.	<i>1994 coverage</i>	251
5.3.2.	Temporal change in diversity indices within the Tomdachoille reach	252

5.3.3.	Temporal change in total area of each land cover class within the Tomdachoille reach	258
5.3.4.	Temporal change in landscape patterns within the River Tummel study area	262
5.3.4a.	<i>1946 coverage</i>	268
5.3.4b.	<i>1968 coverage</i>	268
5.3.4c.	<i>1988 coverage</i>	269
5.3.4d.	<i>1994 coverage</i>	269
5.3.5.	Temporal change in diversity indices within the River Tummel study area	270
5.3.6.	Temporal change in the area of each land unit within the River Tummel study area	272
5.3.7.	Temporal change in geomorphic landform patterns within the River Tummel floodplain	277
5.3.7a.	<i>1946 coverage</i>	277
5.3.7b.	<i>1968 coverage</i>	283
5.3.7c.	<i>1988 coverage</i>	283
5.3.7d.	<i>1994 coverage</i>	284
5.3.8.	Temporal change in diversity indices within the River Tummel floodplain	284
5.3.9.	Temporal change in the area of each land unit within the River Tummel study area	288
5.3.10.	Temporal change in landscape diversity within the River Tummel study area	292
5.3.11.	Long-term variation in habitat features on the River Tummel	293
5.4.	Discussion	295
5.5.	Summary	309
Chapter 6: Summary		
6.1.	Major outcomes of the research	310
6.1.1.	Landscape diversity on a wandering gravel-bed river; the case of the River Tummel	310
6.2.	Wider implications and major outcomes of the research	314
6.2.1.	Evidence for accepting or rejecting the null hypotheses	314

6.2.1a.	<i>Hypothesis 1a: Geomorphic landform heterogeneity is a major control on the botanical and pedological diversity within semi-natural zones within alluvial valley floors</i>	314
6.2.1b.	<i>Hypothesis 1b: Plant community type, vegetation composition and species diversity respond to an environmental gradient of elevation, substrate particle size and soil depth within alluvial valley floors</i>	314
6.2.1c.	<i>Hypothesis 2: The scale and pattern of botanical and pedological variation mirrors the scale and pattern of geomorphic landforms within alluvial valley floors</i>	315
6.2.1d.	<i>Hypothesis 3: Partial stabilisation of the floodplain land units as a result of river regulation increases landscape and botanical diversity within alluvial floodplain environments</i>	315
6.3.	Relationships of the findings to the scientific literature	316
6.3.1.	<i>Channel change</i>	316
6.3.2.	<i>Substrate particle size and inundation</i>	317
6.3.3.	<i>Elevation and inundation</i>	318
6.3.4.	<i>Timescales of change and development</i>	320
6.4.	Floodplain management and nature conservation	320
6.5.	Methodological development for assessing floodplain landscape diversity	322
6.6.	Further research	327
	References	330
	Appendix 1	355
	Appendix 2	357
	Appendix 3	360
	Appendix 4	387
	Appendix 5	388
	Appendix 6	395
	Appendix 7	396
	Appendix 8	402
	Appendix 9	406

Appendix 10	411
Appendix 11	419
Appendix 12	422
Appendix 13	425
Appendix 14	431
Appendix 15	435

List of Figures

	<u>Page</u>
Chapter 1:	
1.1. Location map of the River Tummel showing a) catchment area and b) the study reach.	4
1.2. Flow diagram detailing the aims of the thesis and how they are achieved by addressing the various components of the objectives to arrive at the overall aim to propose a protocol for floodplain landscape diversity assessment.	5
Chapter 3:	
3.1. NVC Phase 1 Habitat Survey map of Tomdachoille Island SSSI study area.	75
3.2. Dendrogram showing the sample divisions by species from TWINSPAN analysis. Eigenvalues indicate the strength of split at each level, the figures in brackets indicate the number of samples in each group. The negative branches are split to the left and the positive branches are to the right.	77
3.3. Ordination diagram of species and environmental variables on Tomdachoille Island SSSI. Environmental variables are denoted by arrows and red squares; the species carrying a high weight for its species score are marked on the diagram.	84
3.4. Total species richness and TSR within the plant communities on Tomdachoille Island SSSI.	92
3.5. Summary statistics for plant species richness on Tomdachoille Island SSSI calculated per quadrat.	92
3.6. Summary statistics for TSR within each plant community on Tomdachoille Island SSSI calculated per quadrat.	92
3.7. Summary statistics showing species diversity in terms of richness, H' (a) and evenness, J (b) measured by the Shannon index on Tomdachoille Island SSSI.	95

3.8.	Pedodiversity variation (a) and geodiversity variation (b) within the plant communities on Tomdachoille Island SSSI. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index.	97
3.9.	Biodiversity variation (a) and geodiversity variation (b) within the soil/substrate groups on Tomdachoille Island SSSI. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index.	99
3.10.	Biodiversity variation (a) and pedodiveristy variation (b) within the landform classes on Tomdachoille Island SSSI. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index.	102
3.11.	Habitat diversity across the floodplain perpendicular (a) and parallel (b) to the main channel. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index.	104
3.12.	Pedodiveristy variation across the floodplain perpendicular (a) and parallel (b) to the main channel. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index.	106
3.13.	Geodiversity variation across the floodplain perpendicular (a) and parallel (b) to the main channel. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index.	107
3.14.	Variation in mean values of environmental variables within the landform classes on Tomdachoille Island SSSI.	136
3.15.	Isotropic and anisotropic semivariograms for elevation and biodiversity indices holding a significant correlation with elevation on Tomdachoille Island SSSI. Separation distance (m).	139
3.16.	Isotropic and anisotropic semivariograms for pedological variables and indices holding a significant correlation with biodiversity indices on Tomdachoille Island SSSI. Separation distance (m)	140

3.17.	Block kriging maps of elevation (m) calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.	144
3.18.	Block kriging maps of species richness count (S) calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.	145
3.19.	Block kriging maps of the Shannon index (H') calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of Interpolated values.	146
3.20.	Block kriging maps of equitability (J) calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.	147
3.21.	Block kriging maps of soil depth (cm) calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.	148
3.22.	Block kriging maps of particle size range calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of Interpolated values.	149
3.23.	Kriging maps of particle size heterogeneity calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of Interpolated values.	150
3.24:	Conceptual model of the stages of vegetation succession in relation to elevation and particles size gradients within the Tomdacheuille Island SSSI study area.	152

Chapter 4:

- 4.1. NVC Phase 1 Habitat Survey map of Ballinluig Island study areas. 172
- 4.2. Dendrogram showing the sample divisions by species from TWINSpan analysis. Eigenvalues indicate the strength of the split at each level, the figures in brackets indicate the number of samples in each group. The negative branches are split to the left and the positive branches are to the right. 176
- 4.3. Ordination diagram of species and environmental variables within the additional study areas. Environmental variables are denoted by arrows and red squares, the species carrying a high weight for its species score are marked on the diagram. 182
- 4.4. Summary statistics of a) total species richness and b) TSR within the plant communities within the Ballinluig dataset. 188
- 4.5: Summary statistics showing species diversity in terms of a) Shannon index H' and b) equitability index J within the plant communities within the Ballinluig dataset. 190
- 4.6. Pedodiversity variation (a) and geodiversity variation (b) within the plant communities within the Ballinluig dataset.
 S = species richness; H'_{\max} = maximum negentropy;
 H' = Shannon index; J = equitability index. 192
- 4.7. Biodiversity variation (a) and geodiversity variation (b) within the soil/substrate groups within the Ballinluig dataset. S = species richness; H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index. 194
- 4.8: Biodiversity variation (a) and pedodiversity variation (b) within the landform classes within the Ballinluig dataset.
 S = species richness; H'_{\max} = maximum negentropy;
 H' = Shannon index; J = equitability index. 196
- 4.9. Predicted values from regression models plotted against actual values for the dependent variables H' , J and soil/substrate type within the Ballinluig dataset, a) Shannon index (H'), b) equitability index (J) and c) soil/substrate type. 216

4.10.	Predicted values plotted against actual values for the dependent variable H' within the point bar landform opposite Tomdachoille Island SSSI.	220
4.11.	Predicted values from the regression model plotted against actual values for the dependent variables species richness (S) within the Ballinluig dataset.	223

Chapter 5:

5.1.	Temporal variation in the botanical habitat types within the Tomdachoille reach of the River Tummel between 1946-1999.	248
5.2.	Temporal variation in the number of land cover types and total number of patches (a) and change in the mean area of the land cover types (b) within the Tomdachoille reach of the River Tummel between 1946-1994.	249
5.3.	Temporal variation in diversity indices for plant community types within the Tomdachoille reach of the River Tummel between 1946-1994. A) Shannon index; b) equitability index; c) dominance index; d) reciprocal of Simpson's index.	253
5.4.	Patterns of species richness within the plant communities on Tomdachoille Island and Ballinluig Island on the River Tummel.	255
5.5.	Temporal variations in shape indices <i>SI</i> (a) and <i>S2</i> (b) within the plant community types at the Tomdachoille reach of the River Tummel between 1946-1994.	257
5.6.	Temporal variations in the total area of each land cover type measured by the change index (C) within the Tomdachoille reach of the River Tummel between 1946-1994.	259
5.7.	Temporal variations in the number (a) and proportion (b) of each land cover type within the Tomdachoille reach of the River Tummel between 1946-1994.	260
5.8a.	Classified image of the botanical habitat types within the River Tummel floodplain, May 1946.	263

5.8b.	Classified image of the botanical habitat types within the River Tummel floodplain, August 1968.	264
5.8c.	Classified image of the botanical habitat types within the River Tummel floodplain, 1988.	265
5.8d.	Classified image of the botanical habitat types within the River Tummel floodplain, May 1994.	266
5.9.	Temporal variation in the number of land cover types and total number of patches (a) and the mean area of each land cover type (b) within the botanical habitat types within the River Tummel study area between 1946-1994 (excluding 1971).	267
5.10.	Temporal variation in botanical habitat diversity indices within the River Tummel study area between 1946-1994 (excluding 1971). A) Shannon index; b) equitability index; c) dominance index; d) reciprocal of Simpson's index.	271
5.11.	Temporal variation in shape indices $S1$ (a) and $S2$ (b) within the River Tummel study area between 1946-1994 (excluding 1971).	273
5.12.	Temporal variation in total area of each land cover measured by the change index (C) within the River Tummel study area between 1946-1994 (excluding 1971).	274
5.13.	Temporal variation in the number, N (a) and proportion, pi (b) of each land cover type within the River Tummel floodplain between 1946-1994 (excluding 1971).	276
5.14a.	Classified image of the geomorphic landforms within the River Tummel floodplain, May 1946.	278
5.14b.	Classified image of the geomorphic landforms within the River Tummel floodplain, August 1968.	279
5.14c.	Classified image of the geomorphic landforms within the River Tummel floodplain, 1988.	280
5.14d.	Classified image of the geomorphic landforms within the River Tummel floodplain, May 1994.	281

5.15.	Temporal variation in the number of land cover types and total number of patches (a) and the mean area (b) of the geomorphic landforms within the River Tummel study area between 1946-1994.	282
5.16.	Temporal variation in the diversity of geomorphic landforms within the River Tummel floodplain between 1946-1994 (excluding 1971). A) Shannon index; b) equitability index; c) dominance index; d) reciprocal of Simpson's index.	285
5.17.	Temporal variation in shape indices <i>SI</i> (a) and <i>S2</i> (b) within the geomorphic landforms within the River Tummel study area between 1946-1994.	287
5.18.	Temporal variation in the total area of each landform type measured by the change index (C) within the River Tummel study area between 1946-1994.	289
5.19.	Temporal variation in the number (a) and the proportion (b) of the land cover types within the River Tummel study area between 1946-1994.	291
5.20.	Temporal variation in physical features of the River Tummel between 1867-1994.	294

Chapter 6

6.1.	Simplified flow diagram of the relationships between geomorphic and pedological heterogeneity in creating biodiversity within alluvial valley floors.	319
6.2.	Protocol for the assessment of floodplain landscape diversity within alluvial valley floors based on aerial photograph examination and landscape patch analysis.	324
6.3.	Conceptual model of the role of varying degrees of channel stability/instability on the patterns of landscape diversity within alluvial valley floors based on the assumption that the intermediate disturbance hypothesis holds true.	325

List of Plates.

	<u>Page</u>
Chapter 1:	
1.1. Aerial photographs of the Tomdachoille reach of the River Tummel in a) 1946, b) 1968, c) 1971, d) 1988, and e) 1994.	7
1.2. Aerial photographs of the Ballinluig reach of the River Tummel in a) 1946, b) 1968, c) 1988, and d) 1994.	8
Chapter 3:	
3.1. Tomdachoille Island SSSI study area incorporating a diverse mosaic of semi-natural habitat types.	57
3.2. Vegetation communities within various landform features on Tomdachoille Island SSSI study area.	153

List of Tables

Page

Chapter 2:

- 2.1. Key references detailing the controls on diversity in floodplain environments. 18

Chapter 3:

- 3.1. The 'best fitting' British Plant Communities allocated to the vegetation types on Tomdachoille Island SSSI. 81
- 3.2. Forward selection of significant environmental variables ($p < 0.05$) in CANOCO. Total variance describes the cumulative variance each property explains when added to the model. The variables are presented in the order they were included into the model. 83
- 3.3. Summary statistics of the CANOCO results for the first 4 ordination axes. 83
- 3.4. Sample heterogeneity expressed by N_2 . Showing (a) samples with low N_2 (species poor) and (b) high N_2 (species rich). 87
- 3.5. Summary of the CANOCO output of species with (a) low tolerance ($N_2 < 3$) and (b) high tolerance ($N_2 > 60$). 88
- 3.6. Count of species unique to the landform classes. Showing (a) the number of species encountered in all landform classes through to the number of species unique to one landform class; (b) the number of species unique to only one or two landform classes; and (c) the count of the number of rare species nationally, locally and the total number of species occurring within each landform class within Tomdachoille Island SSSI study area. 109
- 3.7. Mean diversity (H') values calculated along transects within the study area showing variation in diversity between the landscape components and an average score for overall landscape diversity. 111

3.8.	Mean and standard deviation of diversity indices and key geomorphic and pedological variables within each landform on Tomdachoille Island SSSI.	112
3.9.	Mean and standard deviation of diversity indices and key geomorphic and pedological variables within the whole data set on Tomdachoille Island SSSI.	114
3.10.	Variance in diversity indices measured by the mean and the standard deviation (a) perpendicular and (b) parallel to the main channel on Tomdachoille Island SSSI.	114
3.11.	Correlations between diversity indices parallel to the channel on Tomdachoille Island SSSI. n = 10 (two-tailed test); critical Value = 0.5760; * p<0.05; ** p<0.01; *** p<0.001; - = not significant.	115
3.12.	Significant Pearson correlations (p<0.05) between environmental variables and indices within the whole data set for Tomdachoille Island SSSI. n = 142 (two-tail test); critical value = 0.1593; * p<0.05; ** p<0.01; *** p<0.001; - = not significant.	117
3.13.	Significant Pearson correlations (p<0.05) between environmental variables and indices within the backwater on Tomdachoille Island SSSI. n = 5 (two-tailed test); critical value = 0.7545; * p<0.05; ** p<0.01; *** p<0.001; - = not significant.	119
3.14.	Significant Pearson correlations (p<0.05) between environmental variables and indices within the abandoned channel on Tomdachoille Island SSSI. n = 15 (two-tail test); critical value = 0.4821; * p<0.05; ** p<0.01; *** p<0.001; - = not significant.	120
3.15.	Significant Pearson correlations (p<0.05) between environmental variables and indices within the point bar landform on Tomdachoille Island SSSI. n = 40 (two-tail test); critical value = 0.3044; * p<0.05; ** p<0.01; *** p<0.001; - = not significant.	122
3.16.	Significant Pearson correlations (p<0.05) between environmental variables and indices within the abandoned point bar on Tomdachoille Island SSSI. n = 17 (two-tail test); critical value = 0.4555; * p<0.05; ** p<0.01; *** p<0.001; - = not significant.	124

- 3.17. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the floodplain landform on Tomdachoille Island SSSI. $n = 53$ (two-tail test); critical value = 0.2732; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 126
- 3.18. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the embankment on Tomdachoille Island SSSI. $n = 15$ (two-tail test); critical value = 0.1593; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 127
- 3.19. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the whole data set. 129
- 3.20. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the backwater landform. 130
- 3.21. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the abandoned channel landform. 131
- 3.22. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the point bar landform. 131
- 3.23. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the abandoned point bar landform. 132
- 3.24. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the floodplain landform. 132
- 3.25. Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the embankment landform. 133
- 3.26. Results of analysis of variance (ANOVA) of environmental variables between the landform classes on Tomdachoille Island SSSI. 134
- 3.27. Nugget, sill, tange, regression coefficient (R^2) and reduced sum of squares (RSS) for the isotropic (a) and anisotropic (b) semivariogram models computed using the whole data set from Tomdachoille Island SSSI. * = log normal transformation; active lag = 196.66; uniform interval = 19.66. 138
- 3.28. Summary of species present in abundance at Tomdachoille that are undergoing a decline in abundance in the UK context (taken from Grime *et al.*, 1990). 167

Chapter 4:

- 4.1. The 'best fitting' British Plant Communities allocated to the vegetation types on Ballinluig Island SSSI. 179
- 4.2. Forward selection of significant environmental variables ($p < 0.05$) in CANOCO. The total variance describes the cumulative variance each property explains when added to the model. The variables are presented in the order they were included into the model. 180
- 4.3. Summary statistics of the CANOCO results for the first 4 ordination axes. 180
- 4.4. Sample heterogeneity expressed by N_2 . Showing (a) samples with low N_2 (species poor) and (b) samples with high N_2 (species rich). 184
- 4.5. Summary of the CANOCO output of species with (a) low tolerance ($N_2 < 3$) and (b) high tolerance ($N_2 > 25$). 184
- 4.6. Biodiversity parallel and perpendicular to the main channel within the a) W11c b) U4b c) MG5b d) W7 and e) SHpc community. N = number of observations; S = species richness (number of soil types); H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index. 199
- 4.7. Pedodiversity parallel and perpendicular to the main channel within the a) W11c b) U4b c) MG5b d) W7 and e) SHpc community. N = number of observations; S = species richness (number of soil types); H'_{\max} = maximum negentropy; H' = Shannon index; J = equitability index. 201
- 4.8. Count of species unique to the landform classes. Showing a) the number of species encountered in all landform classes through to the number of species unique to one landform class; b) the number of species unique to only one or two landform classes and c) the count of the number of rare species nationally, locally and the total number of species occurring within each landform class within the Ballinluig dataset. 203

- 4.9. Count of species unique to the plant community types. Showing a) the number of species encountered in all plant communities through to the number of species unique to one plant community; b) the number of species unique to only one or two plant communities and c) the count of the number of rare species nationally, locally and the total number of species occurring within each plant community within the Ballinluig dataset. 204
- 4.10. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the Ballinluig data set. $n = 49$ (two-tail test); critical value = 0.2732; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 206
- 4.11. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the backwater landform on Ballinluig Island SSSI. $n = 4$ (two-tail test); critical value = 0.8114; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 209
- 4.12. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the abandoned channel landform on Ballinluig Island SSSI. $n = 3$; critical value = 0.8783; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 211
- 4.13. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the point bar landform. $n = 8$ (two-tail test); critical value = 0.6319; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 212
- 4.14. Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the floodplain on Ballinluig Island SSSI. $n = 28$ (two-tail test); critical value = 0.3610; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant. 214

- 4.15. Paired t-test for the predictive capacity of the regression model for determining the Shannon index of diversity within the W11c sub-set of data from the Ballinluig Island database. Critical value = 2.26, 95% significance Level. 217
- 4.16. Paired t-test for the predictive capacity of the regression model for determining a) species richness, b) Shannon index, c) tree cover and d) tall herb cover within the abandoned channel on Ballinluig Island. Critical value = 2.78, 95% significance level. 219
- 4.17. Paired t-test for the predictive capacity of the regression model for determining a) Shannon index and b) soil/substrate type within the point bar opposite Tomdachoille Island. Critical value = 2.26, 95% significance level. 220
- 4.18. Paired t-test for the predictive capacity of the regression model for determining a) plant community type, b) species richness and c) soil/substrate type within the floodplain landform zones on Ballinluig Island. Critical value = 2.05, 95% significance level. 223
- 4.19. Results of analysis of variance (ANOVA) of elevation and species diversity indices between the landform types within the Ballinluig dataset. 225
- 4.20. Results of analysis of variance (ANOVA) of pedological properties between the landform types within the Ballinluig dataset. 226

Chapter 5:

- 5.1. Landscape diversity calculated as the average of the biodiversity and geodiversity results for the study area. 292

List of Appendices.

	<u>Page</u>
Appendix 1: Definitions of key words used in this thesis	355
Appendix 2: Criteria for the selection of study areas	357
Appendix 3: Floristic tables of species data from Tomdachoille Island SSSI	360
Appendix 4: Species scores derived from CANOCO carrying a high weight ($N_2 > 65$) for interpreting the ordination diagram of axes 1 and 2	387
Appendix 5: Soil/substrate classification, Tomdachoille	388
Appendix 6: Geomorphic landform classification	395
Appendix 7: Diversity analysis, Tomdachoille	396
Appendix 8: Species unique to landform units on Tomdachoille Island SSSI	402
Appendix 9: Best sub-sets regression analysis for the Tomdachoille dataset	406
Appendix 10: Floristic tables of species data from the Ballinluig dataset	411
Appendix 11: Soil/substrate classification, Ballinluig	419
Appendix 12: Diversity analysis, Ballinluig	422
Appendix 13: Species unique to landform units and plant community types within the Ballinluig dataset	425
Appendix 14: Bonferroni post-hoc tests results for ANOVA	431
Appendix 15: Summary statistics of temporal analysis of landscape patches along the River Tummel between 1946-1994	435

Chapter 1: Introduction

1.1. The ecological importance of riparian and floodplain landscapes

Riparian and floodplain landscapes have been reported to be one of the most species rich habitats in temperate climates (Gregory *et al.*, 1991; Malanson, 1993; Naiman and Décamps, 1990; Peterson *et al.*, 1987). Riparian zones have also been recognised for their importance in maintaining the ecological integrity and diversity of aquatic systems (Decamps and Tabacchi, 1993; Hynes, 1975; Peterson *et al.*, 1987; Salo, 1990; Ward, 1998). However, despite diversity being a key ecological issue at present, little is known about the spatial patterns of plant community diversity within floodplains and riparian zones, or the processes creating and maintaining these habitats (Décamps and Tabacchi, 1993; Tabacchi *et al.*, 1996). The high species richness within floodplains is considered to be a consequence of the spatial heterogeneity resulting from the geomorphic processes operating within the valley floor (Tabacchi *et al.*, 1996). In particular the elevation of the landforms above mean water level is a primary control on diversity as this determines the frequency and duration of flooding (Décamps *et al.*, 1988). Species richness on floodplains has also been reported to be influenced by the velocity of the river, flood magnitude and frequency, and the mean discharge (Nilsson *et al.*, 1989; Roberts and Ludwig, 1991; Stromberg and Patten, 1990). Salo *et al.* (1990) stated that the fluvial dynamics of the river system are fundamental in creating and maintaining high biodiversity. In addition, the interaction between rivers and their floodplain are of great ecological

significance with regard to diversity (Heiler *et al.*, 1995). A glossary of the terminology applied herein is given in Appendix 1.

Much of the heterogeneity within floodplain environments has been lost as a result of cultural land use practices (e.g. Bravard *et al.*, 1986; Kondolf and Larson, 1995, Petts and Amoros, 1996b) causing riparian zones to become increasingly fragmented habitats. Rivers have been exploited more so than almost any other natural ecosystem (Boon, 1992), altering the natural functions and diversity of river systems. The construction of flood embankments in order to utilise the floodplain has prevented channel mobility and resulted in a loss of multiple channels, point bars, mid-channel bars and mid-channel islands within fluvial environments (Bravard and Petts, 1996). The connectivity of the river and its floodplain is consequently lost, eliminating the ecotone between the aquatic and terrestrial environments, which results in a loss of diversity (Petts and Amoros, 1996b; Ward, 1998). It is therefore necessary to undertake research into floodplain habitats and to manage these ecosystems in a sustainable way.

The recognition of the ecological value of floodplain landscapes has raised awareness that river systems need to be rehabilitated in order to re-establish the connectivity of the channel to its floodplain (Nilsson and Brittain, 1996). A 'Wild Rivers' initiative has since been established in Scotland to address the changes that need to be made to the management practices of floodplains (Gilvear *et al.*, 1995a). It is fundamental to examine and understand the functioning of the fragments of semi-natural floodplain landscapes that remain

in order to plan successful restoration projects (Nilsson *et al.*, 1991). Nilsson (1996) further reports that research into successful remediation of river systems needs to incorporate studies into the structure, function and the assemblage of the riparian plant communities. The main focus of this research is orientated towards examining the spatial and temporal patterns of diversity of the major landscape components, namely a) geomorphic landform, b) pedological properties and c) vegetation types, as these are the key factors determining landscape diversity patterns within riverine ecosystems (Ward, 1998). In addition, to fully quantify heterogeneity within the landscape, Aspinal (1996) states that diversity should be quantified for all components of the landscape.

1.2. Rationale: aims and objectives

The research aims of this thesis are two-fold. Firstly to investigate the spatial and temporal patterns of valley floor landscape diversity of a wandering gravel-bed river; a river type typical of Scottish rivers within semi-natural environments (see Figure 1.1). This will be achieved by quantifying the diversity of the flora and the number of vegetation types, soil/substrate heterogeneity, and the range of landforms within the study areas. This approach to diversity analysis therefore accounts for the intrinsic properties of a landscape, which are not obvious at the surface level, but are equally important for landscape ecological value. The research will also incorporate the role of river channel change in inducing habitat diversity within the

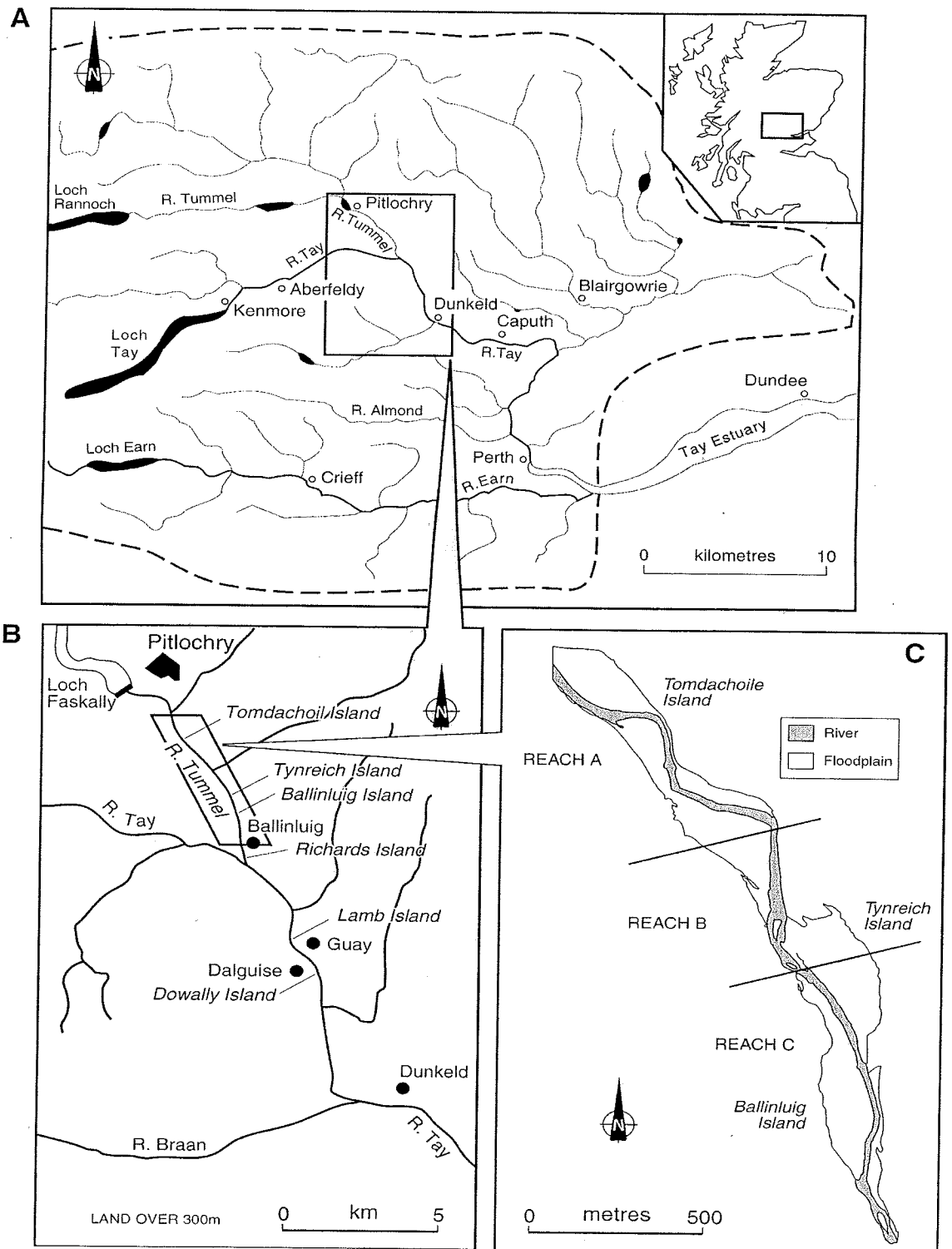
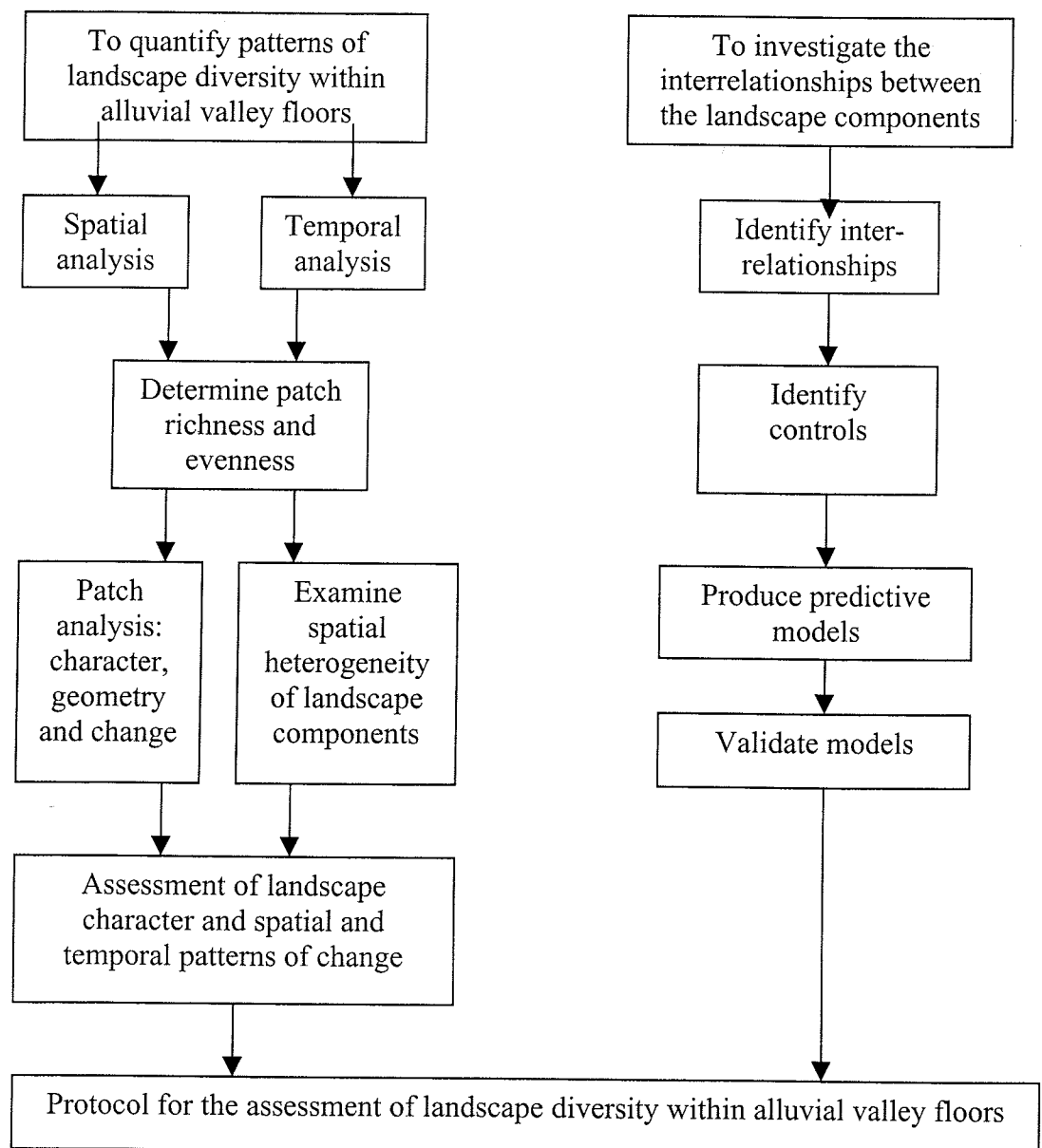


Figure 1.1: Location map of the River Tummel showing a) catchment area and b) the study reach. (See Plates 1.1 and 1.2 for aerial photographs of these reaches).

floodplain zones. With the aid of historical records, the temporal change in diversity of the habitat patches will be quantified. The second research aim of the thesis is to develop a methodology for quantifying alluvial valley floor landscape diversity in space and time (see Figure 1.2).

Figure 1.2: Flow diagram detailing the aims of the thesis and how they are achieved by addressing the various components of the objectives to arrive at the overall aim to propose a protocol for floodplain landscape diversity assessment.



1.2.1. Hypotheses.

Within the context of the two aims of this thesis the research will also test a number of scientific hypotheses. These are:

1. a) Geomorphic landform heterogeneity is a major control on the botanical and pedological diversity within semi-natural zones within alluvial valley floors.
b) Plant community type, vegetation composition and species diversity respond to an environmental gradient of elevation, substrate particle size and soil depth within alluvial valley floors.
2. The scale and pattern of botanical and pedological variation mirrors the scale and pattern of geomorphic landforms within alluvial valley floors.
3. Partial stabilisation of the floodplain land units as a result of river regulation increases landscape and botanical diversity within floodplain environments.

1.3. Study area: River Tummel, Scotland

The River Tummel, near Pitlochry, Perthshire (Figure 1.1a) is a large and active wandering gravel-bed river. The river has a wide floodplain resulting from a long history of channel change, which is well documented over the past 250 years (Gilvear and Winterbottom, 1992; 1998; Winterbottom, 1995). The patterns of channel change and vegetation development are illustrated in Plates 1.1 and 1.2 showing aerial photographs of the study areas since 1946. The

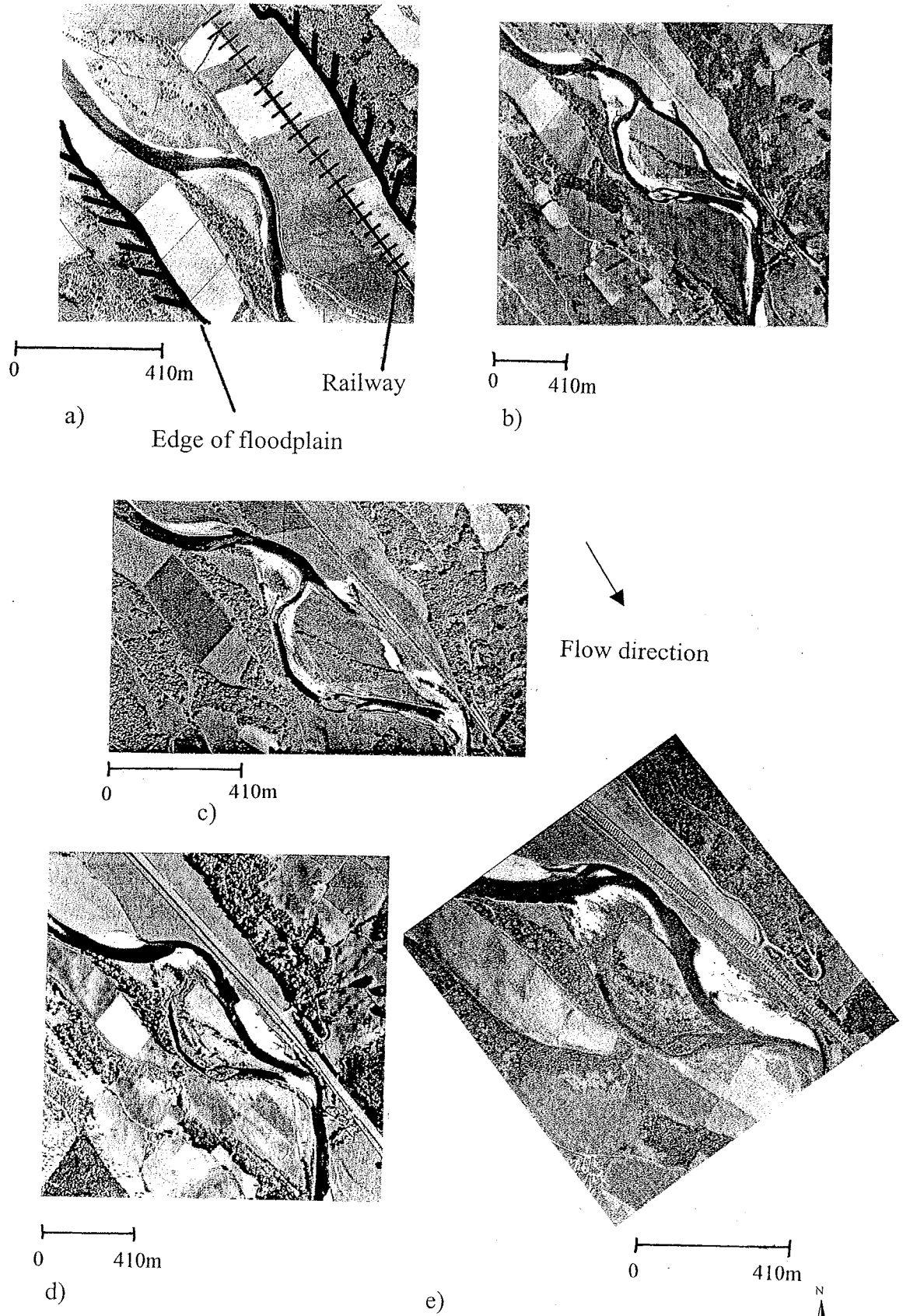


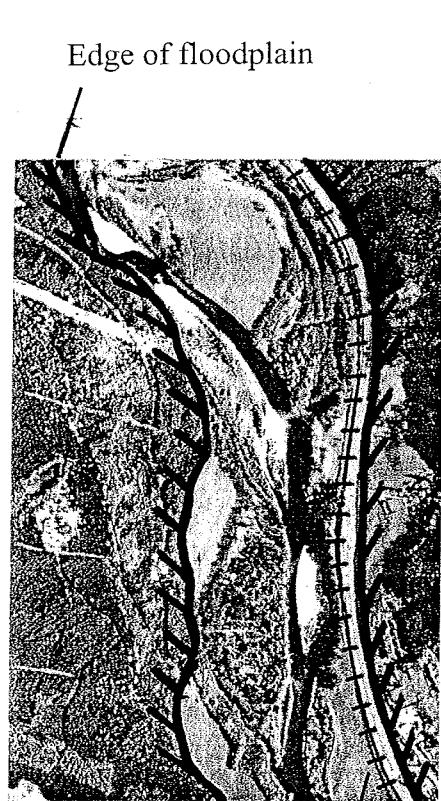
Plate 1.1: Aerial photographs of the Tomdachoille reach of the River Tummel in a) 1946, b) 1968, c) 1971, d) 1988 and e) 1994.



a) 0 380m



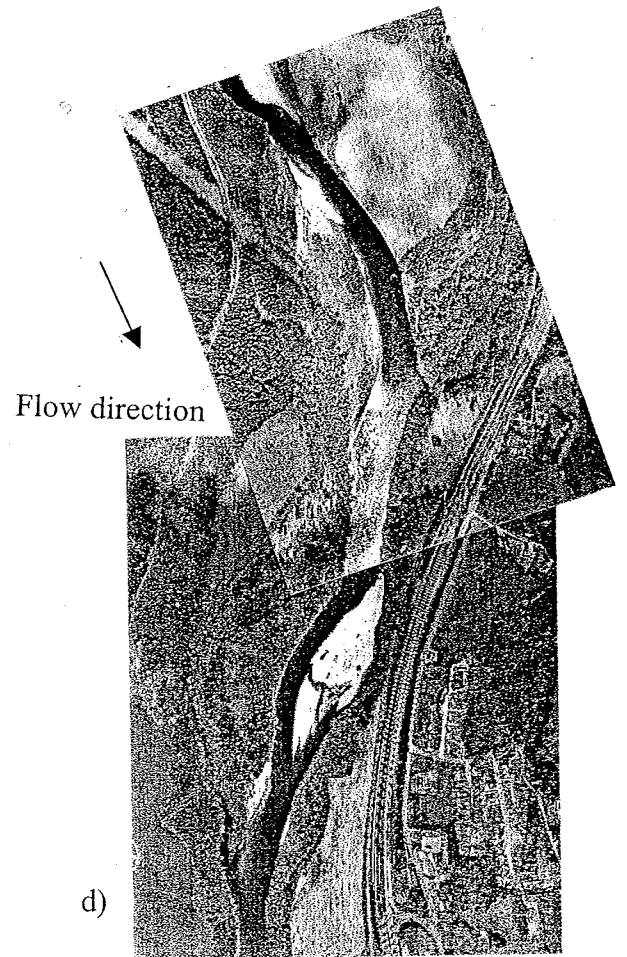
b) 0 380m



c)

Railway

0 380m



d)

Flow direction

0 380m



Plate 1.2: Aerial photographs of the Ballinluig reach of the River Tummel in a) 1946, b) 1968, c) 1988 and d) 1994.

Tummel catchment is mountainous in nature with its origin at Loch Rannoch in the western highlands. This valley receives a precipitation input ranging from more than 1 700 mm in the headwaters, to less than 800 mm in the eastern reaches of the catchment (Gilvear and Winterbottom, 1998; Bryant and Gilvear, 1999). Within the upper reaches of the catchment the low temperatures and high rainfall result in low evapo-transpiration rates, this coupled with thin soils and impermeable geology result in very high runoff. Consequently the River Tummel responds rapidly to high rainfall and snowmelt. The wettest month within this catchment is December (134 mm), with snow cover on the mountains contributing to high flow in early spring, and the driest month is April (80 mm) (Gilvear and Winterbottom, 1998). The River Tummel has a mean annual discharge of $70 \text{ m}^3 \text{ s}^{-1}$ (Bryant and Gilvear, 1999) and is a major tributary to the River Tay.

The ecological importance of the floodplains of the Rivers Tay and Tummel was first recognised and reported by Coates (1906; 1915). He described high levels of biodiversity on the floodplain at the confluence of the two rivers, where the river was unconstrained at the beginning of 20th century. Coates (1906; 1915) described the successional sequences occurring within the riparian areas as pioneer communities dominated by *Sarothamnus scoparius*, to herbaceous vegetation through to broad-leaved wooded islands. Knowledge of the vegetation changes within the Tummel valley is restricted, and is most accurately documented through aerial photograph interpretation, of which the earliest photograph is from 1946. However, Atholl Estate maps from the 1820's show that 57% of the floodplain was arable land, and only 6.5% of the

floodplain to be natural woodland vegetation (Gilvear and Winterbottom, 1998). Coates identified five landform units during his studies, consisting of upper haughland¹, lower haughland, islands, gravel bars and backwaters, and a species richness of 153 plants (Gilvear and Winterbottom, 1998). Of these species, a total of 75 species were unique to one landform unit and only 2 species were present in all zones (Gilvear and Winterbottom, 1998), emphasising the importance of topographic heterogeneity within floodplain zones. Coates also highlighted the influence of the asymmetrical shape of the gravel islands, which promote channel incision on one side, and accretion of sediment and woody debris on the other.

Historical records indicate that the River Tummel has always been dynamic in nature. Lateral instability is evident from the analysis of old maps and accounts of the river, and even to this day it is a characteristic of this river (Gilvear and Winterbottom, 1992; 1998). Early maps show the river to be multi-channelled with numerous mid-channel islands during the 18th and 19th centuries (Gilvear and Winterbottom, 1992). However, due to the 'wild' nature of this river, efforts were made during the late 1700's and 1800's to tame the river by constructing embankments along the most active reaches. This had the effect of confining the channel to a single course, and promoting the stabilisation of the gravel islands. In addition, the removal of riparian woodland in order to utilise the floodplain caused channel widening (Coates, 1906; Gilvear and Winterbottom, 1992). The dominant processes operating to cause the lateral migration of the channel across the floodplain are bank

¹ Haughland is a Scottish term to describe low-lying areas, typically alluvial riverside meadows.

erosion and sediment deposition. Channel avulsion is also a feature of this river, whereby the river changes course whilst leaving the floodplain in between untouched. Records of constructing flood defence along the river date back to 1733 (Gilvear and Winterbottom, 1998). Atholl Estate maps from the 1820's show little evidence of bank protection along the River Tummel (Gilvear and Winterbottom, 1992). However, following a major flooding event in 1837, the Duke of Atholl authorised flood protection along the banks of the River Tummel. The estate accounts show that vast sums of money were invested into the construction of flood embanking along the River Tummel between 1838 and 1850 (Gilvear and Winterbottom, 1992; 1998). The flood protection scheme was very extensive, and most of the Tay and Tummel had been embanked by the end of the 19th century (Gilvear and Winterbottom, 1992). Embankment breaches were common due to high stream power and rates of sediment movement during floods. Repairs of the breaches were costly, consequently the landowner made the decision to allow the embankments to fall into disrepair along the most active reaches following extensive flooding in 1903 (Gilvear *et al.*, 1994). The river has since returned to a more natural planform, thus permitting channel instability and channel change over the past 95 years. The river currently occupies one main channel, but a number of secondary channels are activated at high flow, and backwaters are also present. Within recent years however, rip-rap bank protection has had to be installed to prevent bank erosion adjacent to the railway line. Like many Scottish rivers, the River Tummel has its flow regime regulated by a hydro-electric dam. The dam at Pitlochry was constructed between 1950-1955 (Gilvear and Winterbottom, 1992; 1998).

Floodplain habitat diversity along the River Tummel has thus been affected due to partial loss of the disturbance regime with the regulation of the river, and the flood protected riparian areas were converted to agricultural land use. Examination of the historical records show that there has been a reduction in the number of mid-channel islands from 21 during 1747-53 (Gilvear and Winterbottom, 1998) to just 7 islands in 1994. However, where the flood embankments have been allowed to fall into disrepair, channel instability and semi-natural floodplain habitats have re-established in recent years.

Recent flooding, such as the flood events of 1990 and 1993, caused extensive damage to agricultural land, major channel changes and extensive gravel deposition. The highest flood on record was in 1814, with the flood in January 1993 being the second highest with a peak flow of $1048 \text{ m}^3 \text{ s}^{-1}$ (Bryant and Gilvear, 1999). This flood event caused extensive bank erosion and gravel reworking across the floodplain zones, creating new niches for primary colonisation (Gilvear and Winterbottom, 1998; Bryant and Gilvear, 1999). At present, channel change and instability appear to be the result of high magnitude flood events with a greater than 10 year return period (Winterbottom, 1995); the flood event of 1993 has an estimated return period of 40 years (Bryant and Gilvear, 1999). These recent flood events has led to increased interest into the management and functioning of this river system and its floodplain (Gilvear and Winterbottom, 1998).

The historical channel dynamics have left a legacy of landforms across the floodplain, with palaeochannels, cut-off channels, isolated gravel bars, secondary/abandoned channels and backwaters, thus creating a complex mosaic of landforms. The conservation value of the floodplain was officially recognised in conjunction with the construction of the hydro-power scheme on the river in 1952. Subsequently Ballinluig Island and Richard's Island were designated as part of a series of Shingle Island SSSI's on the Rivers Tay and Tummel in 1955 by Scottish Natural Heritage (SNH). A botanical survey carried out for SNH (Kinnes, 1987) recorded 377 species of flora on Tomdachoille Island, including many of lichenological importance. The survey reported that nationally rare species, including *Allium oleratum*, *Iris versicolour* and *Equisetum pratense*, and locally rare species, *Filago minima*, *Neottia nidus-avis* and *Vicia sylvatica*, are present. Areas of Tomdachoille however were grazed up until 1970, resulting in a species poor meadow. Tomdachoille Island was allocated SSSI status under the Wildlife and Countryside Act (1981). Designated SSSI's along the River Tummel now occupy approximately 224 ha.

1.4. Wandering gravel-bed rivers

A gradational change occurs between rivers with a meandering channel to braided planforms known as wandering gravel-bed rivers. Such rivers are unconfined and display episodic and possibly erratic changes in planform, with the development of gravel bars, multiple- and abandoned-channels, and channel avulsion is common during periods of high flow and flooding.

Wandering gravel-bed rivers are dynamic systems, which create a complex mosaic of landforms and habitat types due to relatively frequent disturbance (Bryant and Gilvear, 1999; Hughes, 1997; Marston *et al.*, 1995). The River Tummel provides an excellent example with a multitude of abandoned channels and shifting gravel bars, and evidence of channel avulsion. In active wandering gravel bed rivers, changes in planform can occur over very short time scales and the entire width of the floodplain can be swept by channel migration within a few centuries (Gilvear and Bravard, 1996). Wandering gravel bed rivers are likely to have highest diversity of all river types within temperate environments and, indeed on the River Tummel, channel instability is a major control on landscape diversity and the nature conservation value of the floodplain (Gilvear *et al.*, 1995).

1.5. Thesis structure

This thesis is organised by firstly giving an overview of the literature on landscape diversity studies within fluvial environments in Chapter 2. The chapter covers a wide range of topics relating to studies concerning purely geomorphology, pedology and ecology as well as publications which have taken a more integrated approach to understanding the functioning of the components of the landscape within riverine habitats. Chapter 3 details the methodology employed for the baseline survey undertaken to quantify the spatial patterns of diversity within the study area and to determine the relationships between the landscape components. From this predictive models for determining landscape diversity are presented. Various analytical

techniques are explored and the results are presented and discussed. The results of this baseline survey were used to derive a sampling strategy for undertaking a validation study along other reaches of the river. Chapter 4 presents the results of the validation study for the prediction of landscape diversity and discusses the congruence between the spatial patterns of diversity of the landscape components. Chapters 3 and 4 merely tackled the spatial patterns of diversity observed during field studies and subsequent data analysis. Temporal analysis of landscape diversity was carried out using historical records. The methodology and results are presented in Chapter 5. Finally, Chapter 6 discusses the overall spatial and temporal patterns of diversity along the study reach. Lessons to be learnt are presented along with methodological problems when sampling dynamic systems. Further research ideas are presented along with a suggested protocol for assessing landscape diversity of alluvial valley floors on other river systems. The findings of the research are finally discussed in relation to integrated floodplain management.

Chapter 2: Literature Review

2.1. Landscape diversity

2.1.1. The landscape diversity concept

The concept of diversity is fundamental to aspects of ecology. In ecological studies, diversity is a measure of the richness and heterogeneity of species or other attributes within a given landscape (Aspinall, 1996). Researchers in a number of disciplines have acknowledged that ‘although diversity may appear to be a clear and intuitive concept on first inspection, further study shows that it is a complex concept which cannot be measured quickly and simply.... The more it is examined, the less clearly defined it appears to be, and viewing it from different angles can lead to different perceptions of what is involved’ (Ibáñez *et al.*, 1995, page 215). Olsen *et al.* (1993) defined landscape diversity as ‘a function of the number and types of patches, their distribution (juxtaposition), and their shape’. Landscape diversity within alluvial valley floors refers to the heterogeneity of all landscape features within and around the riparian zone, to which very few studies have been devoted (Tabacchi *et al.*, 1996). Landscape heterogeneity is the result of the actions and interactions of the formative processes operating on a landscape at a point in time, for example, erosion, deposition, flooding, weathering, and climatic characteristics (Forman and Godron, 1986). Due to the complexity of this concept, hypotheses and methodology are required that can be interlinked to allow relationships to be identified and evaluated between the components of

the landscape studied, whilst also accounting for the effects of human impact (Aspinall, 1996). In this study diversity is analysed by comparing and combining the number, type, shape and distribution of patches of landforms, soil and substrate types and plant communities using a variety of descriptive indices.

In order to assess landscape diversity, it is necessary to measure the diversity of individual landscape components, as they contribute significantly to overall landscape complexity and heterogeneity. Only through amalgamating the component diversities will an overall measure of landscape diversity be achieved (Aspinall, 1996; Noss, 1983; Roberstson and Augspurger, 1999; Wondzell *et al.*; 1996). Recent developments in applied biogeography and landscape ecology have further complicated the concept of diversity. It has become increasingly important to measure the diversity of the whole landscape and its spatial and temporal dynamics, rather than just focusing on maintaining diversity at the species level (Noss, 1983; Roberstson and Augspurger, 1999; Tabacchi *et al.*, 1996; Wondzell *et al.*; 1996). New developments in the landscape ecology approach are increasingly allowing diversity measures to be combined not only within genetic groupings, but also between different genetic groupings (e.g. French, 1994). Methods that have been developed for this analysis are outlined in section 2.6.2. A summary table of key references relating to controls on the diversity of alluvial valley floors is given in Table 2.1.

Table 2.1: a number of key references detailing the controls on diversity in floodplain environments. (Continued overleaf).

Subject	Key theme	Reference	
Landscape structure/ Heterogeneity	Diversity	Tabacchi <i>et al.</i> 1996	
		Naveh 1994; 1995	
		Noss 1990; 1993	
	Landscape ecology	Kupfer 1995	
		Turner and Gardner 1991a	
	Spatial and temporal variability	Cellot <i>et al.</i> 1994	
		Turner 1990	
	Colonisation and vegetation patterns	Gustafson and Gardner 1996	
		Prach <i>et al.</i> 1990	
	Riverine landscapes	Diversity patterns	Gilvear <i>et al.</i> 2000
Ward <i>et al.</i> 1999			
Bornette <i>et al.</i> 1998			
Ward 1998			
Gregory <i>et al.</i> 1991			
Chiarello <i>et al.</i> 1993			
Impacts of disturbance		Piégay and Bravard 1997	
		Barrat-Segretain and Amoros 1996	
		Bornette and Amoros 1996	
		Miller <i>et al.</i> 1995	
		Sparks <i>et al.</i> 1990	
Rehabilitation/restoration		Nilsson 1996	
		Nilsson and Brittain 1996	
		Large and Petts 1994	
		Larson 1994	
		Sear 1994	
Geomorphic/vegetation relationships		Bryant and Gilvear 1999	
		Robertson and Augspurger 1999	
		Hughes 1997	
		Wondzell <i>et al.</i> 1996	
		Lewin 1978	
		Lewin and Manton 1975	
Colonisation of gravel bars		Langlade and Décamps 1994	
		Prach 1994	
		Malanson and Butler 1991	
Coarse woody debris		Piégay <i>et al.</i> 1999	
		Thevenet <i>et al.</i> 1998	
		Piégay 1993	
Methods/classification		Amoros <i>et al.</i> 1987	
		Gurnell <i>et al.</i> 1994	
		Nanson and Croke 1992	
Management		Gilvear and Winterbottom 1998	
		Piégay and Landon 1997	
		Harper <i>et al.</i> 1995	
		Gilvear 1993	
		Jongman 1992	
Landscape models		Indices	Hulshoff 1995
			French 1994
			Olsen <i>et al.</i> 1993
		Fractal geometry	Nestler and Sutton 2000
			Olsen <i>et al.</i> 1993

Subject	Key theme	Reference
Landscape models	Fractal geometry	Turner and Gardner 1991a
		Burrough 1981
Hydrology	Flood-pulse concept	Heiler <i>et al.</i> 1995
		Bayley 1991
		Junk <i>et al.</i> 1989
	Water allocation/regulation	Petts 1996
		Ward and Stanford 1995
		Gilvear 1994
River continuum concept	Vannote <i>et al.</i> 1980	
Diversity	Measurement	Krebs 1989
		Routledge 1977
		Peet 1974
		Hurlbert 1971
Historical	Tools for rehabilitation	Dirkx 1997
		Kondolf and Larson 1995
		Décamps <i>et al.</i> 1988
Pedology	Diversity	Ibáñez 1996
		Wright 1996
		Ibáñez 1995
		Ibáñez <i>et al.</i> 1990
	Alluvial soil classification	Sheremet and Afanas'yeva 1991
Geostatistics	Spatial dependence	Meisel and Turner 1998
		Rossi <i>et al.</i> 1992
		Oliver and Webster 1991
		Webster and Oliver 1990
		Robertson 1987
	Applications	Cressie 1991

The basic concept for maintaining diversity is for the continual regeneration of habitats by preserving ecosystem integrity and its structure and functioning at a range of successional stages (Noss, 1983). Forman (1995) hypothesises that

optimum diversity is achieved when a landscape is composed of large patches, interspersed with small patches within the landscape matrix. The heterogeneity of diverse landscapes complicates sampling strategies as the structure and functioning of its component parts, and their interactions are more complex and over a much wider range of spatial and temporal scales. Fundamental scientific problems arise here as there is no quantitative method for the selection of suitable scales of analysis, and decisions are made based on

human preconceptions. Further problems arise as it is difficult to determine at what scale diversity should be measured and managed (Noss, 1983). Although biodiversity receives the greatest research interest, it should be recognised that in order to maintain biodiversity, the diversity of the whole landscape, including biotic and abiotic components needs to be protected. Naveh (1995) suggests the term 'ecodiversity' as opposed to 'biodiversity', as conservation needs to be extended to incorporate variability to the ecosystem level and the landscape level. This would also encourage a preferable shift in terminology from biodiversity to ecological landscape heterogeneity and diversity.

The diversity of both soils and landforms has, until recently, received little attention of researchers (Iverson, 1988; Ibáñez *et al.*, 1990; Ibáñez *et al.* 1995; Ibáñez, 1996; Wright, 1996). The use of several parameters for identifying the formative processes of landscape pattern is a central theme to landscape ecology. Iverson (1988) tested the impact landscape attributes have had upon landscape pattern in Illinois using soil and vegetation data. GIS was used to compare soil and landscape attributes with historical land use and vegetation, and the current land use and management. In recent years Ibáñez *et al.* have led the field in research into pedodiversity. Ibáñez *et al.* (1990) found that patterns of botanical diversity, geomorphic diversity, and pedodiversity have great similarities. This suggests that the controls on the structure and organisation of biotic and abiotic ecosystems have universal similarities. Ibáñez *et al.* (1995) further report that the characterisation and quantification of the diversity of landforms, geology, and soils as a non-renewable natural resource should be considered when estimating a landscapes ecological value.

This stresses the need for a testable hypotheses to be formulated to explain, quantify, and model this phenomena, which incorporates the spatial and temporal dynamics of the landscape (Ibáñez *et al.*, 1995).

2.1.2. Landscape ecology approach: theory and application

Landscape ecology is a discipline with a theoretical core based around the development and dynamics of spatial heterogeneity. It focuses on spatial and temporal patterns, and their effects upon ecological processes and interactions in heterogeneous landscapes (Johnson and Gage, 1997; Kupfer, 1995; Meisel and Turner, 1998; Risser *et al.*, 1984; Turner, 1989; Wiens, 1992). In contrast, ecology is fundamentally concerned with understanding the influential factors which have created the spatial patterns (Turner, 1989; Meisel and Turner, 1998). Key research and the theoretical development of landscape ecology has been led by Forman and Godron (1981; 1986), and field studies applying the landscape ecology approach to fluvial environments has recently been adopted (e.g. Allan *et al.*, 1997; Chiarello *et al.*; 1993; Dirkx, 1997; Hanson *et al.*, 1990; Tabacchi *et al.*, 1996).

Landscape ecology is an important concept because it acknowledges that the structural components of a landscape are interactive (Forman and Godron, 1981; Noss, 1983; Robertson and Augspurger, 1999). Landscape ecology forms a link that has long been required between many disciplines that are involved with studies into the spatial and temporal dynamics of the landscape. Landscape ecology theory has developed because all landscapes share a

common structure to their organisation as they are composed entirely of patches and corridors, and surrounded by a background matrix (Forman and Godron, 1986). However, when a landscape is divided into its component parts, ecological systems display internal variability in their structure and functioning at different spatial scales. Therefore, the relationships between spatial patterns and ecological processes are not restricted to a particular scale within fluvial environments, and any biotic or abiotic processes operating may vary in their impact or importance at different spatial scales (Risser *et al.*, 1984; Meisel and Turner, 1998). Andersson *et al.* (2000), Forman and Godron (1981), and Ward and Stanford (1983) and have shown the relevance of landscape ecology in providing a better understanding of the dynamics of large alluvial river valleys.

Quantitative methods of analysis are required in landscape ecology in order to relate landscape patterns to ecological processes (Turner, 1989, Turner and Gardner, 1991a and Meisel and Turner, 1998). Such analysis has to be achieved through the development of models that incorporate the spatial and temporal dynamics of the system. There has been an abundance of statistical models and indices developed in the field of landscape ecology for the analysis of diversity; these methods have been evaluated and discussed by Turner and Gardner (1991a) and references summarised in Table 2.1. The landscape metrics available for spatial and temporal analysis of landscape diversity includes measurements for the diversity and connectivity of landscape elements, and the fractal dimensions of the landscape components and patches.

2.1.3. Landscape patterns

The 'edge-effect' is a fundamental ecological concept as the species found at the edge of a patch, where it is converging with the perimeter of an adjacent patch, has a different composition to the patch interior. Perimeter areas form transition zones that are high in diversity and food resources due to the rapid rates of primary production (Noss 1983, Forman and Godron, 1981, 1986). In addition to the edge effect, patch shape and patch juxtaposition is also important in determining ecological conditions (Forman and Godron, 1986; Rex and Malanson, 1990). The fractal dimensions of patches can be assessed according to their shape by analysing their interior-to-edge ratio (Forman and Godron, 1986; Olsen, 1993; and Nestler and Sutton, 2000), whereby isodiametric patches will have a greater interior value than elongated patches, thus ecological processes within these patches will be vastly different. The general spatial patterns of riparian areas can be conceived in the terms of landscape ecology proposed by Forman and Godron (1981, 1986). Shape is important as it determines the relation between area and perimeter. This distinction is important because of the edge effect. Forman and Godron (1986) presented several means for defining shape parameters and identified gradients in processes that would be associated with changes in interior to edge ratios. From an ecological perspective, patches represent relatively discrete habitat units, of which they share similar environmental conditions. Problems arise when measuring the characteristics of a patch as assumptions based on human preconceptions are typically made, which are often gross simplifications of nature.

2.1.4. Hierarchically structured landscapes: the nested hierarchy approach

Landscapes need to be described very precisely in order to study the role of heterogeneity in ecological processes, and their spatial and temporal dynamics. The dynamics of landscape pattern is organised in a structured way so that the landscape components and patches exist at characteristic scales that are positively correlated spatially and temporally (Urban *et al.*, 1987). The landscape ecology approach allows analysis at a range of spatial scales by taking a nested hierarchy approach. The basis to the application of landscape ecology is that a nested hierarchy exists within a landscape, and that the components of the landscape at each scale do not alter internally, but are transferable between scales (Buzer, 1995).

The hierarchy theory is concerned with systems that have an organised complexity, and predicts that as landscape complexity increases, so it develops a more complex hierarchical structure (Allen and Starr, 1982; Lavorel *et al.*, 1993; O'Neill *et al.*, 1988). Thus a landscape, and its attributes, can be organised into discrete functional components which operate at different scales: landscape elements, landscape facets, landscape system, and the landscape unit (Allen and Starr, 1982; Petts and Amoros, 1996b). Similar and interacting components at one level of the hierarchy become the functional aggregates at the next higher level (Urban *et al.*, 1987). The hierarchy approach to landscape studies has been adopted by a number of researchers (Buzer, 1995; Lavorel *et al.*, 1993; Noss, 1990 and Rice *et al.*, 1995). Buzer (1995) used hierarchy theory to examine patterning on sand dunes using data

derived from Landsat imagery through to small-scale field surveys. Hierarchically structured maps have also been commonly used for such analysis (Lavorel *et al.*, 1993; Turner and Gardner, 1991b). An integrated approach to riverine studies is given in 'Fluvial Hydrosystems', edited by Petts and Amoros (1996a). This book focuses on the dynamics of large floodplain rivers, detailing a multi-scale approach to fluvial research.

2.1.5. Human impact on floodplains

The natural controls on floodplain development have progressively lost their dominance over the centuries due to increasing human impact. The human impact on river systems dates back thousands of years with disturbance and modifications of various intensities being documented in the historical record. The resulting cultural landscape has consequently altered the structure and functioning of the entire drainage basin. The relationship between time and spatial scales has also been given attention (Delcourt and Delcourt, 1982).

Although humans have been influencing fluvial dynamics since first occupation, the most significant period of change has been during the last 300 years dating from the industrial revolution and the phase of rapid urbanisation (Bravard and Petts, 1996; Décamps *et al.*, 1988). The degree of impact the modification of rivers has had is difficult to assess because they are superimposed on changes in river channels that are occurring naturally as a result of climate change and isostatic uplift (Ward, 1998). Rivers and floodplains have been drastically modified and controlled, resulting in the

hydrologic regime of most European rivers being greatly affected (Bravard and Petts, 1996; Décamps *et al.*, 1988; Kondolf and Larson, 1995). Historically, flood embankment construction in Scotland was unplanned and most major rivers were effected (Gilvear *et al.*, 1995). The principal hydrological effect has been to reduce the frequency of floodplain inundation. Engineering works on rivers, such as channelisation for navigation (Brookes, 1988; Hughes, 1997), the harnessing of water for power generation, and land reclamation, have typically altered the ecology and morphological diversity of fluvial systems by isolating the floodplain from its main channel (Bravard and Petts, 1996; Large and Petts, 1994; Larsen, 1994; Petts, 1984). Dam construction, for example, prohibits the transfer of sediment from upstream to downstream, thus altering the fluvial dynamics and depriving the lower reaches of sediment. Another effect of human activity on rivers is possibly an exaggeration of low water conditions in dry summers due to the lowering of the floodplain water table (Décamps *et al.*, 1988). The low water condition is an important factor when considering the future evolution of fluvial landscapes.

Throughout history, rivers have been modified to protect against erosion and flooding (Bravard and Petts, 1996). Flood protection has advanced from basic embankments to highly sophisticated civil engineering works. Historically, valleys with braided rivers were the first to be targeted for flood protection and channel modification projects; the upper valleys of the Rhône and Rhine rivers being classic examples (Bravard *et al.*, 1992; Jongman, 1992; Bravard and Petts, 1996). The alteration of the Rhône eventually caused an almost

complete isolation of the floodplain from its river. With the floodplain deprived of periodic flooding, ecological succession proceeded resulting in the loss of habitat patches of communities at different seral stages (Bravard *et al.*, 1992; Bravard and Petts, 1996; Jongman, 1992). On many European floodplains, embankments and channelisation have accelerated the disappearance of alluvial forests, which is well documented in industrial valleys such as the Rhine and Rhône rivers (Bravard *et al.*, 1986; Pautou and Décamps 1985). Nilsson *et al.* (1991) evaluated the effects of river regulation on two rivers in Sweden by comparing a natural river with a regulated river, which was similar in character before being managed. They found that species richness and the percentage cover of vegetation were both lower on the regulated river. However, according to Décamps *et al.* (1988), by reintroducing a flood regime it should be possible to rejuvenate the landscape to represent more natural conditions.

Urbanisation of catchments has had the impact of altering the hydrology of the drainage basin by reducing the permeability of the catchment, by modifying the drainage networks, and the storage and transfer of water through the system. The overall impact of urbanisation has been to increase the frequency and intensity of flooding (Bravard and Petts, 1996). These activities have caused the fragmentation of riparian communities, the invasion and colonisation of 'exotic' species, and, coupled with flood protection measures, the dynamics and diversity of most floodplain landscapes have been negatively affected (Décamps *et al.*, 1988). The utilisation of floodplains for agriculture and industry has also led to a great reduction in floodplain habitats,

which has consequently altered the ecological complexity of rivers and their floodplain (c.f. Heiler *et al.*, 1995).

2.2. Floodplains

2.2.1. Historical perspective

The extrapolation of data from the historical record is a valuable source of information for understanding landscape formative processes and landscape pattern. It has become a fundamental issue to understand how the environment develops in space and time in order to manage ecosystems in a sustainable way (Kondolf and Larson, 1995). Historical analysis can provide information on the evolution of the alluvial valley, an insight into the structure and functioning of the landscape, and of the temporal variability of the channel (Kondolf and Larson, 1995). Temporal variability is difficult to analyse in field studies, as they are typically short in duration, thus requiring historical analysis. The information derived can aid the analysis of pattern change through time, and could possibly provide clues to the causes of change, and aid the interpretation of valley processes.

Kondolf and Larson (1995) outlined the importance of historical studies in fluvial research. They noted that the most informative means of deriving temporal data is via topographic maps, dendrochronology, narrative accounts, and especially sequential aerial photography over a period of years. Narrative accounts and aerial photography can also provide information on previous

plant community composition and structure. Aerial photography is particularly useful for documenting changes in riparian forest cover following the construction of a dam and channel abandonment.

Within temperate regions, rivers have evolved over millions of years under a diverse array of influential processes including tectonic adjustments and climatic change (Petts and Bravard, 1996). In Scotland, the landscape was drastically altered and sculpted during the Pleistocene glaciations. The climatic adjustment during the early Holocene led to the planform of the middle reaches of temperate rivers to range from braided to meandering channels as a direct result to rapid vegetation succession, which reduced the flooding frequency and sediment load (Petts and Bravard, 1996).

The fluvial dynamics of a floodplain landscape are the major controls on the system, and are responsible for the landscape features and their heterogeneity under natural/semi-natural conditions. Historical and palaeo-hydrological research can provide information on land use change, alterations in geomorphic variables, the location of former channels, and previous areas of erosion and deposition (Kondolf and Larson, 1995; Petts, 1989).

In the age of environmental protection and awareness, Kondolf and Larson (1995) set out guidelines for riparian and aquatic habitat restoration. An understanding of channel evolution is essential for successful restoration plans and for maintaining landscape diversity, particularly as the current functioning of the system must be understood in order to evaluate the impacts of every

stage of a restoration project. The identification of former channels, backwaters and cut-off channels is also of prime importance to planners, as they may become active again during floods.

2.3. Geodiversity on floodplains

2.3.1. Geomorphic processes

Floodplain landscapes are dynamic systems, which are controlled by a wide range of geomorphic processes, which are, in turn, largely determined by the prevailing environmental conditions and cultural landuse within the drainage basin. Rivers display diversity in their longitudinal profile (Vannote *et al.*, 1980), influenced by the valley form from source to mouth, slope gradient, discharge, and sediment load, in their latitudinal dimension across the floodplain, and in the vertical direction due to aggrading beds, channel incision, water table fluctuations, and floodplain stratigraphy (Gilvear and Bravard, 1996).

At the scale of the entire river system or drainage basin network, geomorphology and the fluvial dynamics are the driving force of the river system. The geomorphic processes have a major influence upon the diversity of riparian landscapes (Lewin, 1978; Gilvear and Bravard, 1996; Gilvear and Winterbottom, 1998; Gilvear *et al.*, 2000; Robertson and Augspurger, 1999; Tabacchi *et al.*, 1996). Greater levels of diversity tend to be found in dynamic fluvial landscapes where there is a shifting mosaic of land forms and communities due to semi-natural flooding events (Gilvear and Winterbottom,

1998; Gilvear *et al.*, 2000; Tabacchi *et al.*, 1996; Ward, 1998). However further research is required on the complex linkages between the components of the landscape and their formative processes in order to understand the spatial scales and patterns of diversity in fluvial environments (Hughes, 1997; Ward, 1998; Ward *et al.*, 1999).

The energy of a river is a factor controlling the rates of erosion and deposition, which influences the floodplain morphology and stratigraphy (Amoros *et al.*, 1996; Bryant and Gilvear, 1999; Lewin, 1978; Tabacchi *et al.*, 1996). The processes of lateral and vertical erosion and deposition of alluvial material are externally controlled by climatic adjustments, tectonic movements, and the type and seral stage of the floodplain vegetation (Vasil'yev, 1990). Vegetation also influences these processes as it either increases or reduces bank stability by affecting the hydraulic action of the flow (Rowntree and Dollar, 1999). Debris dams can also cause channel instability. In low gradient high order streams, the obstruction of flow by in-channel woody debris during high discharge may lead to local avulsion and overbank sedimentation on restricted areas of the floodplain (Piégay and Gurnell, 1997; Piégay *et al.*, 1999; Rowntree and Dollar, 1999), or to the development of chutes and meander cut-offs (Rowntree and Dollar, 1999). Mid-channel bars often form immediately downstream of obstructions formed by woody debris, with associated channel widening. Piégay (1993) stated that the restocking of woody debris within rivers and floodplains has the effect of diversifying the environment. The energy of the fluvial system is the prime determinant of the floodplain landforms as it controls the sedimentation rates (Lewin, 1978; Nanson and

Croke, 1992). In environments with a low-energy budget, floods may be prolonged with standing stagnant water and suspended sediment, producing fairly homogenous landscapes (Kozlowski, 1984). In contrast, high-energy environments with rapid floods with flowing water produce a geomorphic heterogeneity (Gilvear and Bravard, 1996; Kozlowski, 1984; Tabacchi *et al.*, 1996). Erosion and deposition cycles also operate over differing spatial and temporal scales, and of varying intensities (Vasil'yev, 1990).

The latitudinal dimensions of rivers and floodplains display morphological diversity due to the diminishing connectivity with the main channel towards the perimeter of the floodplain. Floodplain sediments are highly sorted by the river and can provide information on channel migration and flooding events. However, the stratigraphy of some floodplains is highly complex, as in the case of braided channels and wandering gravel bed rivers, due to the constant shifting of channels and channel avulsion.

Steep environmental gradients exist within the internal structure of riparian floodplains as a result of geomorphic and pedological processes. The connectivity of the floodplain surface to the water table is also a strong environmental control on the systems dynamics (Malanson, 1993). A paradox exists between the channel dynamics and the topography of the riparian zone as the fluvial processes create the topographic features, which, in turn, exert a control on the fluvial dynamics (Malanson, 1993). Where there are standing flood waters, fine sediment is deposited. As a result, the depressions within which the sediments are deposited have a low infiltration capacity, which

reduces time to ponding either during a flooding event or intense rain, thus creating a predominantly waterlogged habitat (Malanson, 1993).

2.3.2. Floodplain classification

Three main categories of floodplain morphology exist which reflect the dynamics of sedimentation and channel migration according to Lewin (1978). Stable channels dominated by overbank sedimentation represent the most simple floodplain type. An increasingly complex floodplain evolves, as river channels become more active. Actively meandering channels can leave a legacy of former channels with ox-bow lakes, neck cut-offs and point bars. Wandering gravel bed rivers and braided reaches can leave a trail of abandoned channels across the floodplain due to channel change and avulsion. Active rivers can, therefore create complex floodplain morphology and stratigraphy (Bravard and Gilvear, 1996; Hughes, 1997; Gilvear and Bravard, 1996; Gilvear and Winterbottom, 1998; Lewin, 1978).

The geomorphic features created via the complex processes operating can be classified taxonomically within a structured, multi-level hierarchy of morphological floodplain units, with each level of the hierarchy having its own spatial and temporal dynamics (Amoros *et al.*, 1996; Gellert, 1978; Nanson and Croke, 1992). The application of a hierarchical approach to geomorphic classification allows the river valley and its floodplain to be analysed using a consistent methodology over a range of spatial and temporal scales. This structured methodology will also provide a more detailed insight

into the spatial and temporal dynamics of the system (Gurnell *et al.*, 1994). Floodplains may be divided into 'functional sectors' that are characterised by the fluvial and biological processes (Petts and Amoros, 1996b). Functional sets are defined by either synchronic or diachronic analysis, preferably both. Synchronic analysis involves comparative studies of the structure and function of the landscape units. Each ecosystem patch identified can be then assigned to a successional stage. However, the different potential pathways of succession must be acknowledged as patches of the same age may differ in their composition, structure and function. The role of time in succession is addressed by diachronic analysis. Diachronic analysis examines temporal change in the landscape, thus successional models can be derived (Amoros *et al.*, 1987; Petts and Amoros, 1996b).

Floodplains of different river systems can show a diverse range of land features resulting from the localised geomorphic processes; therefore, their classification is an important aspect of floodplain studies. Lewin (1978) classified floodplain geomorphology and Nanson and Croke (1992) provide a genetic classification of floodplains. The 'genetic floodplain' is the area which is dominated by a 'horizontally bedded alluvial landform adjacent to a channel, separated from the channel banks, and built of sediment transported by the present flow-regime' (Nanson and Croke, 1992). Floodplains are initially classified according to the energy status of the river and subdivisions are made by analysing variations in their morphological and sedimentary characteristics. Three floodplain classes are recognised based upon stream power and sediment characteristics. These floodplain classes are composed of

a range of orders and suborders defined primarily by geomorphic processes. The main parameters for the genetic classification of floodplains are channel pattern (Petts and Forster, 1985; Schumm, 1977), lateral stability, morphological landforms and sedimentary characteristics (Lewin, 1978).

A genetic classification of floodplains accounts for the geomorphic processes that have created the landscape, thus providing a more thorough definition (Nanson and Croke, 1992). Geomorphology can be mapped in terms of a land systems approach whereby a landscape is classified by topography, soils, and vegetation. Within land systems, land units can be defined which are small simple forms which are commonly found on a single rock type or superficial deposit, for example, an alluvial fan and a terrace. Each classified unit must also exhibit a regular relationship within and between the other land units of which it forms a part (Vasil'yev, 1990). It should follow that the soils display consistency throughout the land unit, or vary in a consistent manner across the land unit (Cooke and Doornkamp, 1974).

2.4. Pedodiversity on floodplains

2.4.1. Geomorphology and soils

'Soilsapes' within drainage basins are sculpted by the geomorphic processes operating within the valley. Soils and landforms are physically inseparable as they have shared parent material and processes of development (Ibáñez *et al.*, 1990; Wright, 1996). Ibáñez *et al.* (1990) were the first researchers to reveal

that the increasing complexity of soilscapes is related to the stage of evolution of the fluvial system. This is due to the interacting relationships between the structure and genesis of fluvial and pedological systems. It is evident from this that soil landscapes also have a hierarchical organisation within the drainage basin, which corresponds to the valley landforms and morphology. From their research, Ibáñez *et al.* (1990) hypothesise that by regulating rivers, thus creating a less dynamic fluvial system, pedodiversity within the affected catchment area is reduced. Ibáñez *et al.* (1990; 1995) have shown how indices developed for biodiversity analysis can be applied to pedodiversity studies. Their work has shown that indices and models of diversity can be used for the quantification and comparison of the complexity of soil patterns within different areas and environments. Proportional abundance models are most popular for diversity analyses, which can be used for soil surveys and soil information systems in order to quantify pedological negentropy, pedorichness, and for determining the heterogeneity of a soil association or a soil mapping unit (Ibáñez *et al.*, 1995). Pedodiversity can be assessed using hierarchical methodology by classifying the landscape into geomorphic units (Wright, 1996). The diversity of soils and landforms have a marked quantitative and qualitative effects on the landscape (Ibáñez *et al.*, 1995). Both the soils and land forms, for instance, determine to an extent the drainage patterns and storage of water, which, in turn, influence the vegetation pattern across the landscape.

2.4.2. Soil inundation and its effects

The annual flood in riparian landscapes has an important functional role in the cyclic development of the system (Malanson, 1993). Flooding is important for the connectivity of the system as it facilitates lateral exchanges of nutrients, organic matter and organisms (Malanson, 1993). Most floodplain soils show characteristics of waterlogging and flooding (Sheremet and Afanas'yeva, 1993). The connectivity of the main channel with the floodplain and backwaters has an important ecological role (Malanson, 1993; Schwarz *et al.*, 1996). The inundation of the floodplain with floodwaters influences the nitrogen and organic matter levels found in the sediments. Schwarz *et al.* (1996) noted that sites which were least connected to the main channel were likely to accumulate organics during soil development and lentic deposition. These sites also had higher levels of organic matter and total nitrogen. Walker (1989) also found that surface soil nitrogen variability along a sub-arctic vegetation chronosequence on a central Alaskan floodplain was related to the interactions between stochastic flooding and the impact of the vegetation. These studies revealed that variation does occur across floodplains as a result of the level of connectivity with the main channel. Catchment processes are therefore important in determining small- and large-scale patterns and processes, demonstrating that the system acts in a hierarchical fashion. Cellot *et al.* (1994) examined the temporal and spatial variability of habitat types in relation to eight physical/chemical variables, and found that soil type (in particular particle size and organic content) explains much of the spatial variability.

Landforms and soils are so closely related on floodplains as the topography directly determines the proximity of the land surface to the water table. Topographic undulations also impact upon pedogenesis by influencing the particle size of the material in which the soil evolves (Malanson, 1993). In the process of alluvial soil genesis, particle size is one of the most important parameters at the onset of soil ripening, and will be a major influential factor in the soil type that evolves (Pons and Zonneveld, 1965). Asselman and Middelkoop (1995) analysed sediment deposition in a single flood to document spatial variability in sediment deposition and related the results to floodplain topography and identified possible mechanisms of sediment transport. The soil moisture content of floodplains has a strong control upon ecosystem structure and functioning, therefore, topography and elevation are important in determining soil wetness. Where soils are waterlogged, anoxic conditions create toxicities to plants and the mineralisation of organics is much reduced (Kozlowski, 1984; Schwarz *et al.*, 1996). Anoxia is considered the most important effect of flooding. Gaseous diffusion to soil decreases causing flooded soils to rapidly become oxygen depleted due to uptake by micro-organisms and plant roots, even when standing water is oxygen saturated (Kozlowski, 1984). Moisture conditions should be important as riparian areas include sites that range from extremely dry to saturated conditions. On saturated sites, the limiting factor is anoxia, only species that can tolerate anoxic conditions can survive. This range of conditions provides an environmental gradient on which species can separate. Differences in soil moisture content, being primarily affected by topography on floodplains and

also by channel dynamics, leads to complex spatial patterning (Malanson, 1993)

2.4.3. Classification of alluvial soils

The classification of alluvial soils is complicated due to the spatial and temporal variation in soil and sediments across the floodplain. A hierarchical classification system is required which allows terrace soils to be classed as alluvial due to their origin, whilst also differentiating them from the basic soils on the floodplain and the various stages of development according to their geographical location within the drainage basin. Particle size is perhaps the most important physical attribute to be considered in alluvial soil classification. Pons and Zonneveld (1965) provide methods for alluvial soil classification, and Sheremet and Afanas' yeva, (1991) have developed a set of new principles for alluvial soil classification.

2.5. Botanical diversity on floodplains

2.5.1. Riparian landscapes

There have been numerous botanical studies into floodplains and riparian landscapes (Bornette and Amoros, 1996; Bornette *et al.*, 1998; Gilvear *et al.*, 2000; Hughes, 1997; Malanson, 1993; Prach, 1994; Tabacchi *et al.*, 1996; Ward *et al.*, 1999) particularly within Europe on the rivers Rhine and Rhône (Bravard *et al.*, 1986; Bravard *et al.*, 1992; Jongman, 1992; Pautou and

Décamps, 1985; Statzner *et al.*, 1994). Despite this extensive research, the spatial patterns of riparian plant community diversity along rivers are still poorly understood (Décamps and Tabacchi, 1993; Tabacchi *et al.*, 1996; Ward, 1998). Recently the influence of landscape features on the diversity of riparian plant communities has been studied (e.g. Nilsson *et al.*, 1989; 1991; Tabacchi *et al.* 1996; Ward, 1998; Ward *et al.*, 1999). Chiarello *et al.*(1993) proposed a model of the spatial organisation of vegetation in river floodplains based on the generation of non-homogenous, anisotropic random patterns defined on a square lattice given the knowledge of the ecological functioning of these ecosystems. Progress in this field of research into floodplain habitats may facilitate the adoption of ecologically sound river management (Statzner *et al.*, 1994; Harper *et al.*, 1995).

2.5.2. Successional sequences in floodplain environments

Floodplain environments display habitats in transitional stages between the spectrum from aquatic to terrestrial environments. These stages within the riparian ecotone have an important function in the landscape diversity, which is also influenced by the width of the floodplain. In general, diversity is greater on wider floodplains (Malanson, 1993; Tabacchi *et al.*, 1996). Ecosystems can be divided into seral stages by analysing community development. Successional stages of the same age may show variations in their structure and function due to the processes of development (Amoros *et al.*, 1987) and as a result of environmental heterogeneity such as variations in elevation and particle size (Nilsson *et al.*, 1991, Robertson and Augspurger,

1999; Wondzell *et al.*, 1996). The spatial patterns of diversity may also be due to the impacts of secondary succession, which commonly occurs in cultural landscapes, producing a directional succession rather than a cyclic process where the seral stages repeat themselves over certain time-scales. Malanson (1993) cited that vegetation structure could be assessed according to the three stages. The first stage involves the identification of species, then the relative abundance of species, and finally, its spatial scale. Using this methodology of vegetation analysis, an assessment can be made of the internal structure of riparian landscapes (Malanson, 1993).

Riparian and floodplain succession is highly dependent upon the riverine environment and cultural land use. When considering the landscape in its semi-natural state, succession sequences are affected by the hydro-geomorphic dynamics and the characteristics of the landscape, such as geology and soil type. Floodplain vegetation patterns have been studied in relation to disturbance regimes and their role in creating a complex mosaic of habitat types within the fluvial landscape (e.g. Barrat-Segretain and Amoros, 1996; Bornette and Amoros, 1996; Gilvear and Winterbottom, 1998; Piégay and Bravard, 1997; Sparks *et al.*, 1990). Amoros (1991) and Amoros and Wade (1996) described successions occurring in two contrasting riverine environments by studying community development in relic channels on both meandering and braided rivers. Succession is an important process on floodplains as it increases the stability of the substrate, and reduces the erodability of the soil as succession progresses (Rowntree and Dollar, 1999; Wondzell *et al.*, 1996). In addition, horizontal heterogeneity is increased by

higher species diversity, which also corresponds to vertical heterogeneity as the ecosystem becomes structurally more complex (Amoros and Wade, 1996). The maintenance of hydrosystem connectivity is of fundamental importance to maintain highly productive river systems. The productivity of backwaters is usually higher in the lentic and standing waters of the wetland habitats than in the lotic zones of the main channel (Amoros, 1991). Bornette *et al.* (1994) studied the pathways of ecological succession on six former braided channels of the upper River Rhône, which have all been isolated from the main channel for equal time scales. They concluded that it is the nature of the flood that is the driving force behind successional sequences in floodplains. The results of the study showed that similar patterns of succession occurred throughout. On new sediment at low elevations, pioneer and flood tolerant species colonise. As elevation increases, more terrestrial and shade tolerant species dominate the community. As community development progresses, there is high mortality of early colonisers, thus providing a new niche for colonisation. Flooding is thus essential to maintain the connectivity of the river to its floodplain and to rejuvenate floodplain habitats by the destruction and creation of habitats maintaining the floodplain ecosystems at a range of successional stages (Junk *et al.*, 1989)

Species richness of floodplain vegetation generally increases with increasing water flow (Nilsson *et al.*, 1989; 1991). Flooding renews nutrients, increases sediment diversity and creates patches for colonisation (Ward, 1998). Floodplain forests are among the most productive of all natural communities and are characterised by the infrequent and temporary presence of standing

water and a variable depth to water table (Hughes, 1997; Ward *et al*, 1999; Van Splunder, 1998). Community studies of floodplain forest trees generally find that species composition, basal area, diversity and other community attributes are critically affected by elevation (Baker, 1990; Kalliola and Puhakka, 1988; Nilsson *et al*, 1989, Robertson and Augspurger, 1999). Flood tolerance is highly variable among plants and is determined by the species physiological adaptations. The nature of a flooding event is also of significant consequence and affects plant response to inundation, even in flood tolerant species. Aspects to consider are water quality, the duration of flooding, the timing of the flood, and the velocity of flow (Kozlowski, 1984). The timing of the flood is important as flooding during the growing season adversely affects plant development, the production of energy, its reproduction and dispersal of seeds (Kozlowski, 1984). Soil anoxia rapidly builds up during inundation; this reduces the translocation of photosynthetic products from the leaves. In addition, root growth is impeded, which affects the drought tolerance of the plant (Kozlowski, 1984). Flood water is also more harmful if it is slow moving or still as it rapidly stagnates due to the absence of gaseous exchange with the atmosphere (Kozlowski, 1984).

2.5.3. Geomorphic, soil, and vegetation, relationships

Tabacchi *et al.* (1996) examined the influence of landscape elements and cultural land use on the diversity of riparian plant communities at a range of spatial scales. Their study showed that riparian systems have become increasingly fragmented with greater pressure on the landscape resource by

human activity; this has also adversely affected the connectivity of the floodplain ecotone. Human impact on floodplain landscapes has also enabled the invasion of non-riparian species, thus altering the fabric of the landscape (Andersson *et al.*, 2000; Tabacchi *et al.*, 1996). High diversity is usually found along rivers due to the geomorphic processes creating a mosaic of shifting landforms (Bornette *et al.*, 1998; Bryant and Gilvear, 1999; Robertson and Augspurger, 1999; Tabacchi *et al.*, 1996). These patterns created by the geomorphic processes are reflected in the riparian vegetation that develops. The resulting land forms influence the patterns of vegetation that develop due to a multitude of parameters, including slope gradient, elevation, soil type and properties, in particular particle size and moisture content (Baker, 1990; Nilsson *et al.*, 1989; Ward, 1998; Ward *et al.*, 1999). Prach (1994) found that the elevation of the floodplain above mean channel level to be a major control on floristic patterns, which also relates to soil moisture. Wondzell *et al.* (1996) report that a close relationship exists between habitat types, landforms and geomorphic processes as a direct result of the redistribution of organic matter, moisture availability and the redistribution of water between landforms. The connectivity of adjacent landforms is related to the flow of water and sediment between them, thus determining the sharpness of the ecotone between these morphological units (Wondzell *et al.*, 1996). The vegetation composition of each landform plays a fundamental role in erosional and depositional processes operating. The complexity of floodplain landscapes can, therefore, be described by geomorphic processes, plant responses to land features, and to soil moisture, soil anoxia, and flooding (Large *et al.*, 1996; Malanson, 1993; Robertson and Augspurger, 1999).

2.5.4. Botanical diversity

Riparian systems form an important ecotone which have been intensely exploited, particularly in northern Europe, which has affected botanical diversity. Where riparian areas flourish in temperate regions, they have been described as some of the most species rich and productive ecosystems (Malanson, 1993). These systems are also fragile and very sensitive to human impact (Nilsson *et al.*, 1989; Tabacchi *et al.*, 1996), therefore their protection is important for diversity conservation. There are three scales of diversity: alpha diversity (e.g. Shannon index), beta diversity, and gamma diversity (Whittaker, 1972; 1975). Alpha diversity is concerned with the number of species present within a single habitat or community, the within area diversity measure. Beta diversity is a reflection of the changes that occur in community composition along an environmental gradient, otherwise known as the between area diversity (Noss, 1983; Aspinall, 1996). Beta diversity is, therefore, greatest where a landscape is composed of patches at different successional stages (Noss, 1983). This will also increase the edge effect, which is ecologically important for species richness and ecosystem functioning. Gamma diversity assesses diversity at a large scale, thus the total diversity of a large geographical region. Maximising landscape (gamma) diversity can thus be achieved by increasing the within habitat (alpha) diversity and between habitat (beta) diversity.

High diversity is generally attributed to several factors, including habitat heterogeneity from fluvial action, the floodpulse which allows different

species to colonise different portions of the elevation gradient, and to physiological adaptations to inundation (c.f. Ward, 1998). High levels of species- and genetic-diversity in floodplain zones can only be maintained by restoration of at least minimum and maximum flows at approximately natural conditions (Stromberg and Pattern, 1992). Ecological richness stems from the mosaic of habitats within floodplain zones. Researchers have shown that active channel migration enhances diversity within the floodplain (e.g. Bravard *et al.*, 1992; Gilvear and Winterbottom, 1998; Gilvear *et al.*, 2000; Salo *et al.*, 1990). However, Marston (1995) found that high instability truncated succession, thus reducing diversity on the Snake River, a wandering gravel-bed river, in Grand Teton National Park, USA.

The importance of floodplain environments for diversity has been acknowledged by the French government with the passing of a law in 1992 stating that there is a need to 'preserve the integrity of ecological hydrodynamics' (Marston *et al.*, 1995). Ten landscape units were recognised on the Ain River floodplain in France and the relative extent of these ten units has undergone dramatic change between 1945-1991. Unvegetated pioneer communities have declined by 76% and abandoned channels have declined by 46%. These changes are a reflection of a reduction in the lateral migration of the channel and associated entrenchment. Stability within the channel has also lead to less frequent overbank flows. Consequently, the process of terrestrialsation has rapidly occurred within the floodplain. Nilsson *et al.* (1989) studied the influence of human impact on floodplain diversity. Species were designated as native or those typical of man-made habitats, especially

wasteland, cultivated land, and meadowland as ruderal species. The high abundance of such species on a site is a good indicator of human impact.

2.6. Landscape indices

2.6.1. Analysing landscape diversity

The concept behind the assessment of diversity is to understand the taxonomic and environmental relationships of species and habitats along gradients of change, both spatially and temporally (Aspinall, 1996). Assessments of diversity commonly only relate to biodiversity, but the landscape and its attributes are an important function in ecological diversity.

Diversity measurements can be divided into three classes: indices of richness, abundance distribution models, and the proportional abundance of objects (Magurran, 1988). Richness indices relate to the number of species or features of interest in a location; in pedology this could be the number of soil types within a sampling unit. The oldest and most fundamental concept of diversity is species number (Peet, 1974). Measures of species richness are in frequent use and are among the least ambiguous of diversity measures. Richness is an indicator of the relative wealth of species in a community. The difficulty stems from the inherent dependence of any richness measure on sample size; the larger the sample the greater the expected number of species. Abundance distribution models describe the distribution of species or a given attribute in a landscape, and their abundance. The proportional abundance of objects is the

most frequent means of estimating diversity, and gives the most complete mathematical description of the data (Ibáñez *et al.*, 1995). This index may be assessed in terms of richness and evenness. Richness is concerned with the number of objects present in a sampling unit, and evenness with the relative abundance of the objects. Thus, when comparing two landscapes of equal size and richness, the landscape which has a more equal distribution of the different patches will be the most diverse as each patch has relative equally probability. A landscape which possesses a more or less equal distribution of patches will also have a greater edge effect, which is important for maximising local diversity (Noss, 1983). However it is frequently argued that species richness alone is the most fundamental issue of diversity, and that the abundance of these species and the evenness of their distribution within an area are secondary (Kent and Coker, 1992). In terms of conservation and of biodiversity, then species richness is the most desirable measure of diversity, and has been the prime focus of many ecological diversity studies (Baker, 1990; Nilsson *et al.*, 1989). However, a highly species rich environment, such as floodplain habitats, could be highly fragile. In addition, a habitat with high species richness but only few individuals of each species present is also an unstable community and change and succession could eliminate many of the rare species present. Consequently many ecologists consider species evenness and abundance to be important in diversity analyses. This is because communities which have high species abundance and evenness, but which could have low species richness, for example heather moorland, are more stable and resilient to disturbance. The long debate over the relationships between species richness and stability has concluded that the two cannot be

compared as they are in essence measuring different phenomena (c.f. Kent and Coker, 1992). In the case of floodplain environments species richness could be argued as being the most important measure of diversity as the floodplain is inherently unstable in nature due to flooding disturbance.

2.6.2. Indices for measuring diversity

Landscape indices are descriptive statistics of landscapes. They are measures of size, shape, variation, diversity and the spatial arrangement of patches in two or three dimensions (Fry, 1996). The most commonly used diversity indices are the Shannon Index and the Brillouin Index, although the Shannon Index is preferred for its relative ease of calculation (Ibáñez *et al.*, 1995; Kent and Coker, 1992). Although the Shannon index is primarily used in ecological studies, Ibáñez *et al.*, (1990; 1995) have shown that it can be applied, amongst other phenomena, to assessing pedodiversity.

Due to increased focus on sustaining biodiversity, much ecological research has been directed into the development of new landscape indices that can be easily applied to land management practices (e.g. Aspinall, 1996; French, 1994; Fry, 1996; Hulshoff, 1995; Ibáñez *et al.*, 1995; Ibáñez *et al.*, 1996; Iverson, 1988; Noss, 1983; O'Neill *et al.*, 1988; Olsen, 1993; Tabacchi *et al.*, 1996). O'Neill *et al.* (1988) developed three indices of pattern for assessing landscape diversity with the objective of developing a set of indices that can be correlated to ecological processes. The first index is designed to measure the dominance of one or a few land uses in the landscape. The second index is

a measure of contagion, which describes the connectivity and aggregation of landscape patches. The third index measures the fractal geometry of the landscape describing patch complexity, which correlated with the extent of human modification of the landscape. This index is calculated by regressing the polygon area against the perimeter for each patch within a classified GIS image. However, the regression technique is not suitable for use in small landscapes (Olsen, 1993).

Olsen (1993) also used fractals to develop landscape indices, as fractals are a useful aid for describing spatial patterns and the geometric complexity of landscape features. This paper evaluated landscape diversity, accounting for patch shape, patch juxtaposition, and patch evenness, at a range of spatial scales using a modified fractal dimension within a classified image in a grid-based GIS. This modified fractal dimension methodology allows the analysis of perimeter-area relationships, and accounts for patch geometry and perimeter complexity, which are ecologically important for maintaining diversity and the edge effect. This method modifies the fractal dimension measured by accounting for the geometry of the patches, and their juxtaposition with other patches to give a better description of landscape diversity. This method has the added advantage that in moving away from the traditional regression technique for calculating fractal dimensions, so smaller landscapes can be analysed (Olsen *et al.*, 1993).

Many indices for assessing diversity confuse the concepts of evenness and richness. French (1994) produced an index that combines these two concepts

to give a measure of variety and abundance by developing a Hierarchical Richness Index (HRI). The HRI is a versatile index which can be applied to any data set which can be divided into mutually exclusive groups at any hierarchical level (French, 1994). In addition, different HRIs can be compared provided the sampling and grouping criteria are identical. These groups can be formed by using any suitable criteria for the data set.

Hulshoff (1995) used indices developed in the USA to evaluate temporal change in diversity in a Dutch landscape. This was achieved by comparing a change index with pattern indices. The pattern indices measured the distribution and abundance of each land use type, the number of patches, mean patch size, and two shape indices. The change index examined how the landscape had altered over a 140-year period using the values from the pattern indices for different time periods. The pattern and change indices are a useful tool for examining landscape evolution, provided that reasonably accurate historical data is available, and for assessing human impact. However, these indices do not detail information in the change in geographical position of the landscape patches, or patch interior and patch perimeter complexity.

The only index discovered to date which incorporates cultural impacts is the method developed by Tabacchi *et al.* (1996). Landscape diversity was measured in this instance using a one-way ANOVA on each parameter thought to influence diversity. The parameters included in the study were divided into intensity classes and included human influence, the main land use, river zonation, and the level of urbanisation.

This section has briefly outlined the various methods for assessing landscape diversity and reviewed a range of indices that have the potential for its evaluation. An index, or group of indices, has yet to be developed to fully, simply, and comprehensively measure landscape diversity, which allows diversity analyses to be conducted for each landscape attribute, and their combination to evaluate overall diversity at a range of spatial and temporal scales.

2.7. Spatial analysis

2.7.1. Geostatistics: semivariance and kriging

There has been a multitude of techniques developed for assessing spatial patterns in landscapes, summarised by Turner and Gardner (1991a). However, many of the methods do not account for spatial autocorrelation (Augustin *et al.*, 1996). Techniques that do incorporate autocorrelation include the Moran Coefficient, Geary Ratio and Cliff-Ord statistic (Qi and Wu, 1996). The use of geostatistics is therefore becoming increasingly popular in ecological spatial analysis. By calculating the semivariance of a given property via the semivariogram, the range of spatial dependence can be determined, thus eliminating the problem of autocorrelation in ecological data. Recent ecological research that has tested the application of geostatistics in landscape studies includes Meisel and Turner (1988), Roberstson (1987) and Rossi *et al.* (1992). Meisel and Turner (1988) recommend semivariance analysis as a tool

for quantifying some spatial characteristics of ecological data. This analysis may also be employed to derive information on the spatial scales of variation of a given landscape property.

Landscape pattern is important in ecological studies to assess diversity. Geostatistics is a means of assessing spatial patterns and has been applied in landscape ecology, but it has not been employed in floodplain environments despite the recognition that they are among the most diverse habitats in temperate zones and are of interest in current ecological studies. There is high spatial variability inherent in semi-natural floodplain areas, but few studies have quantified this spatial heterogeneity. Moreover there still remains no accepted methodological approach to assessing landscape diversity in floodplain environments.

**Chapter 3: The Development of a methodology for interrogating
floodplain landscape diversity: Tomdachoille Island SSSI case study.**

3.1. Introduction

A medium-sized dynamic wandering gravel-bed river system with zones of semi-natural vegetation was selected as the study area as it is known to have developed important riverine habitats. A pilot study was conducted on Tomdachoille Island SSSI on the River Tummel, Perthshire to develop a methodological approach and to answer the aims and objectives of this thesis over a defined area. The first aim of this chapter is therefore to investigate the relationships between landscape components and to examine the spatial patterns of diversity within the floodplain. The second aim is to develop a model of the controls on diversity within the floodplain, to be tested and validated on other reaches of the river.

3.2. Methodology

3.2.1. Criteria for the selection of study areas

A floodplain area exhibiting a mosaic of riparian habitats, with a long chronology of channel adjustment, is required in order to assess the role of river channel change on patterns of diversity. The study area was selected objectively by constructing a table of river and floodplain characteristics relating primarily to geomorphic controls (Appendix 2). From this table,

wandering gravel-bed rivers were selected for analysis as they display medium stability between meandering and braided channels. River channels showing a moderate degree of instability also tend to have the highest diversity (Petts and Amoros, 1996b). They are generally more dynamic locally than meandering rivers, which have highly managed floodplains in the UK, and are more stable than truly braided channels that frequently change course over the floodplain. Braided channels are also rare in the UK context, as these rivers were historically the first rivers to be managed due to their inherent instability (Bravard and Petts, 1996).

The initiative behind selecting wandering gravel-bed rivers is that the fluvial dynamics will create a diverse range of landforms and provide disturbance through regular flooding. These landforms will be of varying stability across the floodplain, from highly unstable to very stable. This will result in a mosaic of vegetation types across the floodplain at different stages of succession. Such rivers are sinuous and multi-channelled with a mosaic of erosion and deposition land features, producing a patchwork of landforms, soil and substrate variation, and, consequently, a variety of habitats. Numerous wandering-gravel bed rivers were studied from maps, aerial photographs and field visits throughout Scotland and northern England. For each river and its floodplain considered for research, a criteria checklist was completed. The SSSI areas of the River Tummel floodplain were selected as the study areas, meeting all the criteria; and permission to carry out research on the floodplains was easily granted.

Tomdachoille Island SSSI was initially selected for the primary study area due to its geomorphic complexity and botanical diversity. A representative 3.5 ha area of the site, (Plate 3.1), predominantly undisturbed by human activity over at least 100 years was selected as the study area.

3.2.2. Historical analysis and aerial photograph interpretation

Historical records were acquired, including maps from 1867, 1900 and 1990, aerial photographs from 8th May 1946, 7th August 1968, 6th July 1971, 15th May 1988 and 16th May 1994. Botanical reports (Coates, 1906; 1915), surveys and records held by Scottish Natural Heritage (SNH) were also collected and collated. Changes in channel course, landforms, vegetation patterns, land use change, channel modifications and other engineering works were examined. Maps of topography, vegetation and channel change were derived from aerial photograph interpretation of the study area. Possible soil boundaries can also be superimposed upon the base map. The base map thus derived was used to aid the location of the sampling grid in order to incorporate maximum variability of the landscape features.

3.2.3. Field sampling strategy

3.2.3a. Sampling strategy

Field sampling was conducted on a stratified, systematic, unaligned strategy.

This method was selected as an unbiased approach to sampling when the

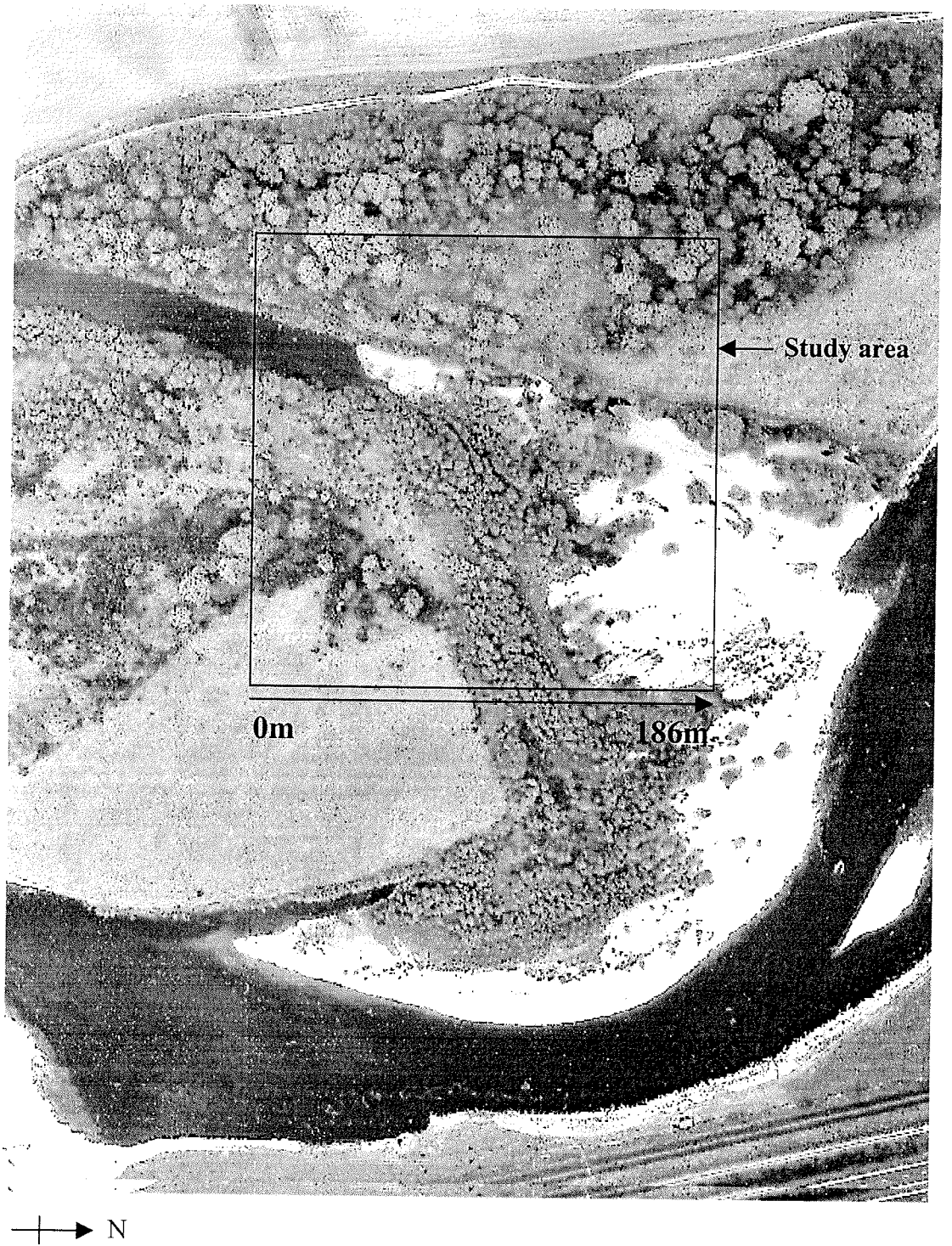


Plate 3.1: Tomdachoille Island SSSI study area incorporating a diverse mosaic of semi-natural habitat types.

underlying trends are unknown. This method provides more accurate estimates of variance and mean values than other sampling techniques (Smart and Grainger, 1974). This mode of sampling also provides the advantages of randomisation and even spatial coverage of the study area. A sampling grid was overlain on an enlarged air photo of the study area, illustrated in Plate 3.1. The grid consists of 144 cells measuring 15.5m^2 . The relatively fine grid was chosen in order to obtain an extensive data set and to derive sufficient information on the fine scale of variation in vegetation patterns, soil properties and elevation.

Sampling points were located in the cells with the y-axis co-ordinates varying randomly along the rows of cells and the x-axis co-ordinates varying randomly along the columns. Thus, a random co-ordinate for the x-axis was selected for the top left grid cell. This co-ordinate remains static for the entire top row of the grid. A random y-axis co-ordinate is then selected anew for each grid cell in the top row to locate the sample point. Likewise the y-axis values selected for each grid cell remain static for each column and the x-axis co-ordinates are re-selected for each new row of the grid. These random co-ordinates were translated into meters to locate the sampling points in the field.

3.2.3b. Vegetation survey

Vegetation patterns were initially mapped and classified from aerial photograph interpretation using the UK National Vegetation Classification (NVC) Phase 1 Habitat Survey (Nature Conservancy Council, 1990). The

mapping units were subsequently verified by field inspection and boundaries adjusted where appropriate.

The vegetation was surveyed and recorded using the NVC nested quadrat approach (Rodwell, 1995b) during June and July 1997. The information was recorded on the standard NVC sample card (Rodwell, 1991a). Quadrats were re-surveyed during February and March 1998 in order to include early flowering species missed during the summer survey. All species within the quadrat was recorded and its abundance estimated on the Domin scale (Rodwell, 1995b). However, due to the fine sampling grid and the small extent of woodland stands, total tree cover was recorded, with the grid square being the unit of measure. Floristic data was amalgamated where more than one quadrat size was required to record a sample.

3.2.3c. Soil sampling

Soil profiles were examined at each sample point with soil development, and samples collected for subsequent laboratory analysis. Soil profiles were examined in the field using a Dutch auger and described according to Soil Survey of Scotland. Soil profiles were recorded to the depth of the underlying alluvial gravel deposits. Fixed depth samples were taken at 15-30cm and 60-75cm to represent the topsoil and subsoil respectively due to the lack of horizon development. In areas with no soil development, substrate size was recorded with the use of a pebble plate. Pebbles were allocated to one of 14

size classes, and the abundance of each size class was expressed as a percentage cover.

3.2.3d. Topographic survey

The floodplain was initially mapped and classified on the basis of geomorphic characteristics. Quantitative topographic data of relative height was recorded at each sample point during November 1997 and January 1998 using an Electronic Distance Measure (EDM). Summer base-flow was estimated by recording the level of the water along the riverbank with the EDM between June and August.

3.2.4. Field data handling and processing

The data were analysed using a variety of statistical packages to identify patterns and relationships between environmental variables on Tomdachoille Island SSSI. From this preliminary analysis a model of the controls on floodplain diversity within the study area will be formulated and tested along different reaches of the river.

3.2.4a. Vegetation data

Quadrat data of species records and environmental variables was entered into a DOS editor file as a standard NVC data-file using the formal FORTRAN format (I8,2X,10(I4,I3)) right justified spacing. The resulting data file was

prepared for the multivariate analyses TWINSpan (two-way indicator species analysis) (Hill, 1979) and CANOCO (canonical correspondence analysis) (Ter Braak, 1987) using the SELECT routine in VESpan III (Malloch, 1997a). TWINSpan classifies multivariate data by divisive cluster analysis. This procedure makes a dichotomy of the main axis of ordination and splits the data into two groups, which are subsequently split again to the specified level of divisions. A maximum of 5 divisions was requested for this analysis and default settings were accepted. Following the initial run of TWINSpan, it was evident that four of the samples (K3, L3, M2 and M3) were exceptionally different from the other samples. These samples were segregated from the remaining 140 quadrats at the first level of divisions. This resulted in the bulk of the data being divided on the negative branch of the dendrogram. These four samples were accepted as forming an end group and a discrete vegetation type for entering into the TABLE routine. The TWINSpan routine was re-run with these four samples omitted from the analysis to produce a balanced dendrogram.

The end groups of samples derived from the TWINSpan analysis were input into the TABLE routine. Sample order was entered into the TABLE routine in the order derived from the final table end groups produced by TWINSpan. Constancy tables for the species and summary statistics for the environmental variables were calculated. All other default settings were accepted.

Data were prepared within TABLE for community classification using MATCH (Malloch, 1997b). This routine uses the Czekanowski co-efficient of

similarity to compare the sample data with the NVC frequency tables for the standard British Plant Community types. The co-efficients for the ten closest matching sub-communities were examined for community classification. MATCH is only an aid to classification and should be used in consultation with the British Plant Community publications. In addition, a low co-efficient is not necessarily a poor fit due to the highly variable nature of vegetation (Malloch, 1997b). Some of the vegetation types encountered on Tomdachoille Island have not been classified within the British Plant Community system to date. These communities are classified and described using the indicator species and species with high constancy and frequency.

Relationships between species, samples and environmental variables were analysed using CANOCO for WINDOWS version 4.0. CANOCO quantitatively relates species composition of communities to the environment. Species data was log-transformed in order to approximate a normal distribution. Rare species were downweighted to reduce bias in the analysis. The analysis was carried out using inter-species distances. Environmental variables were tested for their influence on explaining species patterns and variation using manual forward selection with the Monte Carlo permutation test. Permutations were carried out under the full model. The Monte Carlo test tests the significance of each variable in its effect on the species distribution. It also examines whether one variable has an effect on the species distribution after taking into account the effect of another variable. This method plots species distributions at the centre of their niche in the ordination diagram, and the samples with these species present are located around that point. The

output displays the pattern of variation of species distribution within a community in relation to environmental variables (Ter Braak, 1987), making it more efficient than multiple regression analysis. Canonical correspondence analysis therefore provides a simple technique for analysing the impacts of environmental variables upon the distribution of species and pattern within communities. The resulting ordination diagram displays the distribution of species along axes of variation. The position of the environmental variables indicates the major direction of change and the strength of the relationship between the variables and the species. Caution should be taken when examining the ordination diagram as species that bear no relation to the variables included in the analysis are plotted in the centre of the diagram. Interpretation of this area of the diagram should thus be carried out with reference to the species-by-site data table in order to distinguish those species that are truly located there from those which are not (Ter Braak, 1987).

Due to the stratified sampling procedure for vegetation analysis, the differences in sample area of the quadrats was compensated for as species richness typically increases with sample area. Species richness was transformed to accommodate this source of variation. Species richness values approximated a normal distribution therefore the transformed species richness index (TSR) was applied to the data:

$$\text{Species richness} = \text{number of species} / \log_{10} \text{ of the area sampled}$$

(Whittaker, 1972; Whittaker, 1975).

Where more than one quadrat size had been used for one sample, the mean of the TSR index for each quadrat size was taken to calculate the final TSR index

3.2.4b. Soil and substrate data

Soil samples collected in the field were analysed for moisture content (SMC) using the methodology given in Rowell (1994). The remaining soil was air dried for further analyses. The air-dry soil was gently ground to break up the aggregates prior to sieving. Particle size was assessed using the mechanical sieve analysis technique (Rowell, 1994). All other analyses were carried out on the fine earth fraction (<2mm). Soil pH was determined in both water and 0.125M CaCl₂ (Rowell, 1994). Organic matter content (OMC) was measured by loss-on-ignition (Bascomb, 1982).

Particle size data was summarised using indices to describe the nature and distribution of the size classes. Indices calculated using the phi scale are minimum (MINDOM), maximum (MAXDOM), median (MEDOM), mode (MODOM) and mean (MEAN) size class (Wright *et al.*, 1984). The MEAN was calculated by weighting the phi classes by the percent composition of the sediment based on 5 phi classes using the following equation:

$$M\phi = (\phi_{10} + \phi_{30} + \phi_{50} + \phi_{70} + \phi_{90})/5$$

(c.f. Wright *et al.*, 1984)

Particle size heterogeneity was measured by counting the number size classes present in each sample (Nilsson *et al.*, 1991). The range of particle size classes was calculated as a further measure of heterogeneity by subtracting the smallest size class from the largest size class present in each sample. The measure of heterogeneity when compared with the other statistics can also be used to infer the moisture holding capacity of the substrate. Where samples with a high percentage of fines and a small range within the finer end of the scale can be said to have relatively high retention ability, and coarse substrates with a large range having lower moisture retention capacity. Diversity indices of soil and substrate data were calculated in accordance with Ibáñez *et al.* (1990; 1995) and Ibáñez, (1996).

Soil and substrate data were classified into groups using cluster analysis. Observations were clustered by variables using between groups linkage-squared Euclidean distance model in MINITAB version 12 cluster analysis. The variables used in the analysis are soil depth, SMC, OMC and particle size indices. Soil groups were assigned a reference number according to the order of the end groups in the analysis results.

3.2.4c. Elevation data

Topographic data of relative height recorded with an EDM was downloaded and processed in LISCAD Plus version 4.0. Elevation data was exported into Excel for statistical analysis. The elevation of sample points was expressed as height above or below summer base-flow by subtracting the mean water-level

values from the elevation readings for each sample point. Absolute values of elevation were used as correction for channel slope was not essential due to the relatively small spatial area covered by the study area and also due to the fact that the drop in water surface elevation through the study area was low. Landforms were classified by field mapping and cluster analysis of elevation data. The landform classes were allocated a reference number from low to high according to height above the channel and described according to their geomorphic structure.

3.2.5. Statistical analysis: examination of heterogeneity and relationships

3.2.5a. Diversity indices

Species richness is the most commonly applied index of diversity (Magurran, 1988). This simply involves summing up the number of different species encountered within a sample. Species richness is a robust index of diversity as it accounts for rare plants, which is relevant for conservation issues. The Shannon index (H') is most commonly applied for evaluating both species richness and abundance, but it also accounts for rare species. Basic assumptions to be met when applying this index are that sampling was undertaken randomly and from an 'infinitely large' population and that all species present within the community are included in the analysis (Kent and Coker, 1992). The Shannon index is calculated by the equation:

$$\text{Diversity } H' = - \sum_{i=1}^s p_i * \ln p_i$$

where:

s = the number of species

p_i = the proportion of the individuals or the abundance of the i th species
expressed as a proportion of total cover

\ln = log base _{n}

For this analysis p_i was estimated as the abundance of the i th species expressed as a proportion of the total cover. Any base of log may be used in calculating the index (Kent and Coker, 1992), with \log_e commonly being employed for the Shannon index (Greig-Smith, 1983). For this analysis the natural log was used as it gave values between 1.5 and 3.5, typical of Shannon index results (Margalef, 1975). For diversity studies it is frequently important to estimate evenness, which is calculated from the equation:

$$\text{Equitability (evenness) } J = \frac{H'}{H' \text{ max}} = \frac{-\sum_{i=1}^s p_i * \ln p_i}{\ln s}$$

where:

s = the number of species

p_i = the proportion of the individuals or the abundance of the i th species
expressed as a proportion of total cover

\ln = log base _{n}

The higher the returned value of J, the higher the diversity of the sample as the species are more evenly distributed within the sample area. In calculating both of these indices, the Shannon index provides a means of quantifying both species richness and evenness of species abundance (Kent and Coker, 1992). Diversity scores derived for a number of quadrats from the same population using the Shannon index tend to show a normal frequency distribution, thus allowing parametric test to be performed to analyse relationships between diversity and environmental variables (c.f. Ibáñez *et al.*, 1995).

Habitat diversity within the study area was calculated along and across transects. This describes the pattern of habitat diversity both parallel and perpendicular to the main channel, enabling conclusions to be drawn on how diversity varies spatially in relation to the river. Habitat diversity along transects was calculated using a modified version of the Shannon Index:

$$\text{Habitat diversity } H_v = - \sum_{i=1}^n \frac{l_i}{l} \log_e \frac{l_i}{l}$$

where:

l_i = length of a transect occupied by a vegetation unit i

l = total length of a transect

n = the number of habitat types identified along a transect.

(Prach *et al.*, 1990)

Diversity indices were calculated with the data grouped according to plant community, soil/substrate group and landform class respectively. Bio-, pedo- and geo-diversity were also calculated perpendicular and parallel to the main

channel to measure variability across the floodplain in relation to the river. An average value was calculated for transect diversity scores to assess landscape diversity based upon these three components.

3.2.5b. Exploratory data analysis (EDA)

Exploratory data analysis was carried out on the whole data set and within the end groups produced by TWINSPAN and cluster analysis of soil and elevation data as a prerequisite to further statistical analyses. These involved plotting histograms to view the distribution of the data, normality tests, scatterplots and calculating descriptive indices of the data (mean, minimum, maximum and standard deviation). In the occurrence of the data not having a normal frequency distribution, transformations were made to approximate a normal distribution. Positively skewed data was transformed using natural log, square root or reciprocal transformation, and negatively skewed data was corrected using the exponential, square or cube transformation. Where a given property displayed a normal frequency distribution, the mean and the variance (the standard deviation) was used as a measure of heterogeneity (Wright, 1996).

3.2.5c. Hypothesis testing

All data was entered into MINITAB version 12 and organised into landform classes for analysis. The strength of linear relationships between variables was tested using Pearson's correlation coefficient. This test assumes a normal frequency distribution, however Moore and Cobby (1998) report that the test

can be performed with confidence on data that does not have a normal frequency distribution provided the data does not show asymmetry or discrete groupings. The resulting correlation coefficient was tested for significance with $n-2$ degrees of freedom.

Causal relationships were examined using least-squares regression analysis. Hypotheses were formulated to test causal relationships between variables. In cases where more than one independent variable held a significant relationship with the dependent variable, best subsets regression analysis was performed prior to multiple regression.

The landform groups were tested to assess whether the means of the variables within one group were significantly different to the means in the other groups by one-way analysis of variance (ANOVA). Test results were validated with Bonferroni post-hoc test.

3.2.5d. Geostatistics (semivariance and kriging)

Geostatistics was employed to explore the scale and pattern of landscape diversity. Geostatistical analysis was performed using GS+ for WINDOWS version 3.1. The analysis assumes that data approximates a normal frequency distribution. Log normal or square root transformations were applied where appropriate with weighted- and standard- back-transformations respectively. Eastings and northings co-ordinate data was derived from EDM data. GS+ defines semivariance as:

$$\gamma(h) = (1/2N(h)) \sum (Z_i - Z_{i+h})^2$$

where:

$\gamma(h)$ = semivariance for interval distance class h

Z_i = measured sample value at point i

Z_{i+h} = measured sample value at point i+h

$N(h)$ = total number of sample couples for lag interval h.

GS+ calculates $\gamma(h)$ for every combination of points within the data and allocates each pair to an interval class. The sample point is compared with itself at lag zero at the outset of semivariance analysis. As the lag distance increases, the points that are compared to each other are increasingly different. This causes semivariance to increase with an increase in the lag distance. A critical distance is eventually reached whereby the samples become spatially independent and the squared differences of the paired points is equal to the average variance of the data causing the curve to level off (Meisel and Turner, 1998). GS+ automatically calculates the active lag and uniform interval for the data range. The semivariogram is constructed by plotting h with semivariance for each class. Semivariance typically increases with lag distance up to *sill variance* which is where the curve levels off. The *sill variance* is an estimate of the *a priori* variance of the random variable (Webster and Oliver, 1990). The point at which *sill variance* is obtained defines the range, indicating the scale of spatial dependence on the x-axis of the semivariogram. At lag zero, semivariance typically intercepts the y-axis at a positive value. This is called the *nugget effect* (Webster and Oliver, 1990). *Nugget variance* estimates the

variability in the parameter value that occurs around the sample point. A *nugget variance* of close to zero indicates minimal localised variation of the property measured. Semivariance was scaled to sample variance in order to compare semivariograms constructed for each variable analysed.

Isotropic and anisotropic (direction dependent) semivariograms were calculated. Anisotropic semivariograms were computed for 0°, 45°, 90° and 135°. These orientations are particularly suited to data sampled on a regular grid (Rossi *et al.*, 1992). GS+ gives the option of five models to fit to the measures of semivariance. These models are spherical, exponential, linear, linear to sill, and gaussian. GS+ selects the best-fit model using three statistics: proportion of spatial structure ($C/(C_0+C)$), R^2 (regression coefficient) and RSS (reduced sum of squares). The RSS provides a precise measure of how well the model fits the semivariance data. The lowest RSS indicates the best-fit model. Linear models are not suited to two-dimensional data (Webster, *pers.comm*).

The hypothesis tested is that the scale of botanical and pedological variation in the landscape mirrors the pattern of topography, in that the geomorphic evolution of the floodplain is the primary controlling factor on the landscape habitat mosaic. A second hypothesis is that biodiversity is also influenced by pedological variation within the study area. Semivariograms were constructed to measure the scale of spatial dependence for vegetation diversity indices and pedological variables which hold significant correlations with elevation within the whole data set. Semivariograms were compared to assess congruence

between the degrees of spatial dependence within the study area. Similarity in the range of spatial dependence between variables can be loosely used to infer linkages and interactions.

Kriging analysis was subsequently performed using information on spatial dependence derived from semivariance analysis using GS+. Kriging is a sophisticated method of local averaging and spatial interpolation as it estimates unknown values with known variance (Webster and Oliver, 1990). By mapping the variance of the kriging estimates it can be determined whether sufficient sampling has been undertaken. Where the variance results are high, the map will show the areas where more samples need to be collected to improve the analysis and interpolation.

Block kriging was performed as average values of a given property over the interpolated area are more meaningful than exact predictions for a single point in space calculated using punctual kriging (Burgess and Webster, 1980b). Kriging estimates were tested for accuracy by jack-knife cross-validation. This provides a regression coefficient of goodness of fit for the least squares model. The kriging results were plotted using the Map routine in GS+. Maps of the variance (standard deviation) of the kriging estimates were also plotted.

3.3. Results

3.3.1. Historical data interpretation

Historical changes in the planform of the river are described in chapter 1, section 1.3 and are discussed further in relation to landscape pattern change in Chapter 5. The aerial photographs presented in Plate 1.1 show how the channel has changed course and planform over the past 50 years in the vicinity of Tomdachoille Island. Examination of the plates reveals that the channel became more complex post 1946. Unfortunately there is little knowledge of how the river and floodplain landforms changed between 1903, following embankment abandonment, and 1946 due to there being no aerial photography or map data for this period. This, along with the subsequent channel change, has had the effect of enhancing habitat richness diversity within this zone.

3.3.2. Vegetation classification and description

The NVC Phase 1 Habitat Survey map is presented in Figure 3.1. The end group communities derived from TWINSPAN analysis correspond to the habitat boundaries on the NVC Phase 1 habitat survey map. This validates the accuracy of mapping vegetation purely by aerial photograph interpretation. This gives confidence in mapping the vegetation from earlier aerial photographs for which quantitative floristic data cannot be attained for analyses on patch size, shape and change, which is covered in Chapter 5.

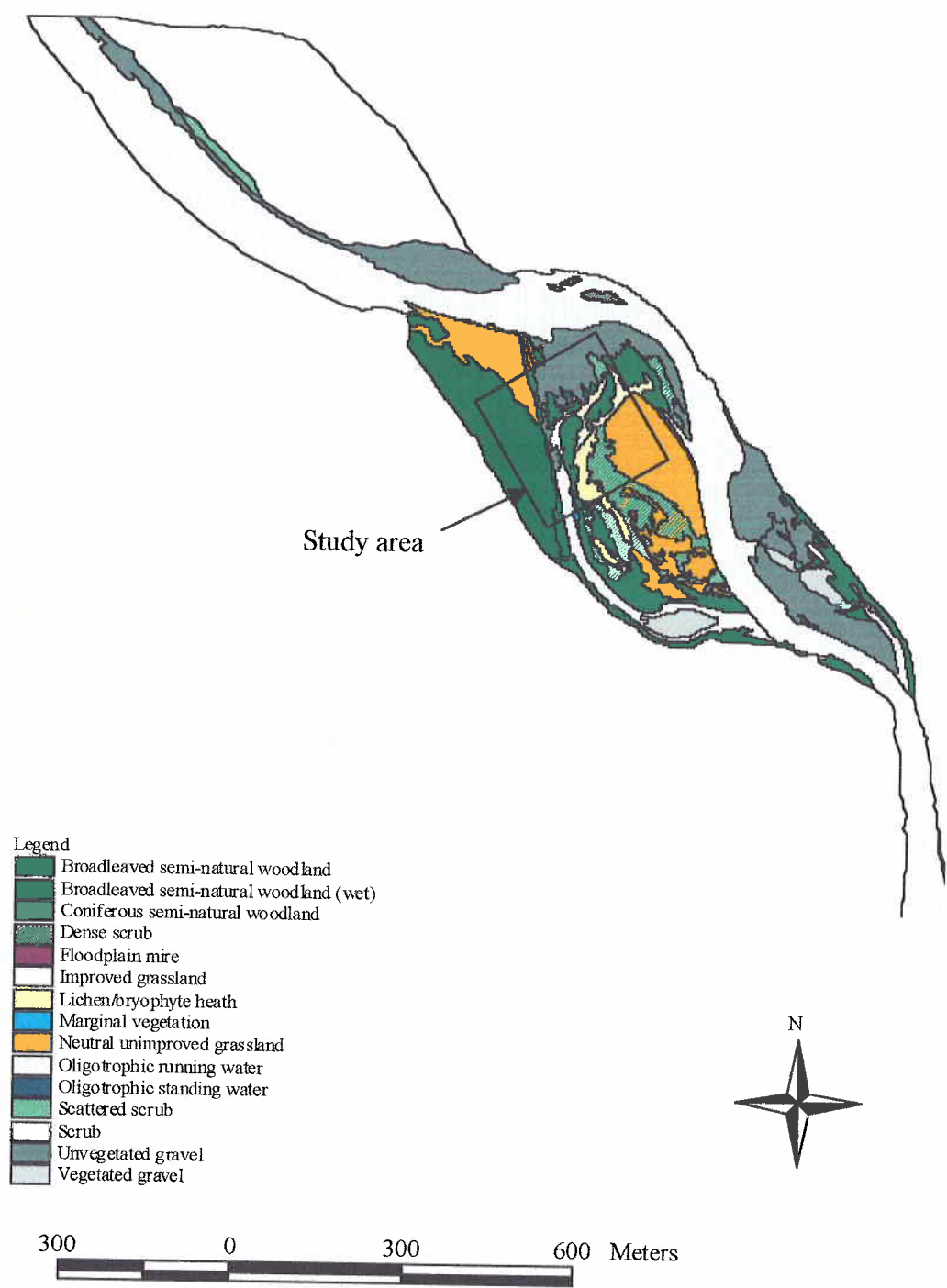


Figure 3.1: NVC Phase 1 Habitat Survey map of Tomdachoille Island SSSI study area.

3.3.2a. TWINSpan interpretation

On the initial run of TWINSpan, samples K3, L3, M2 and M3 were split from the other 140 samples at the first level of divisions. The eigenvalue measuring the strength of this division is 0.498. The positive indicator species characterising this community is *Glyceria fluitans*, which is an aquatic species typical of swamp vegetation. The following paragraphs describe the divisions made on the sample data with these four samples omitted from the TWINSpan analysis.

The first split in the TWINSpan sample divisions has a relatively high eigenvalue of 0.434. The diagram of divisions is presented in Figure 3.2. From the dendrogram and examination of the sample divisions on the TWINSpan final table it is evident that the samples have been initially split dividing the drier and more elevated areas of the floodplain from the low-lying and wetter areas. The negative indicator species for the drier zones are *Stellaria graminea*, *Anthoxanthum odoratum*, *Festuca rubra* and *Rhytidiadelphus squarrosus*; the positive indicator species is *Impatiens glandulifera*, which is a typical invasive species of streamside and riverbank habitats.

The following paragraphs discuss the divisions made on the negative side of the dendrogram only. At the second level of divisions, the next split was made with an eigenvalue of 0.357 separating early succession stages on the abandoned gravel bar from the meadows and woodlands. The negative

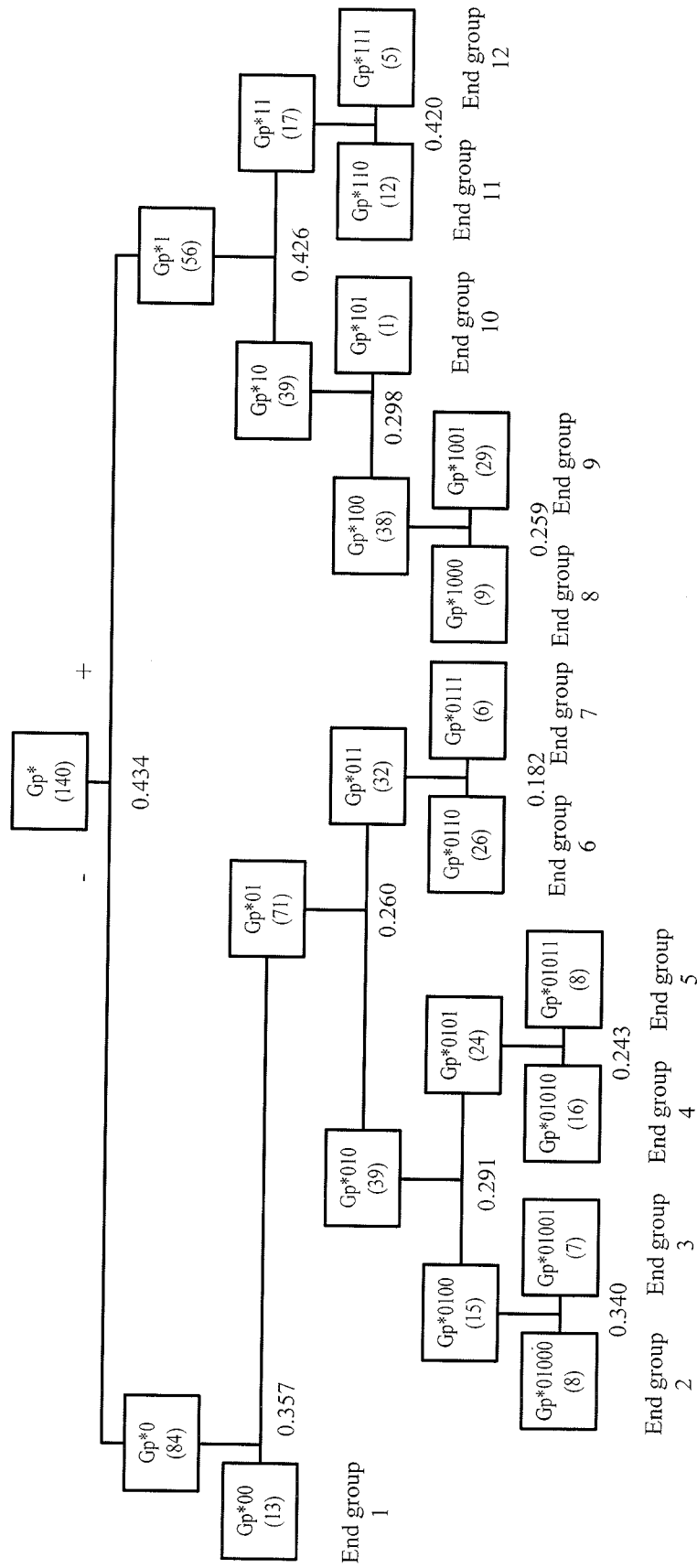


Figure 3.2: Dendrogram showing the sample divisions by species from TWINSpan analysis. Eigenvalues indicate the strength of split at each level, the figures in brackets indicate the number of samples in each group. The negative branches are split to the left and the positive branches are to the right.

indicator species for this split is *Thymus drucei*. Level two of the divisions was accepted as the final end group (end group 1) for the samples on the negative side of the split. On the positive side of level 2 divisions, the meadow areas and scrub were separated from the woodland. The eigenvalue of the split is 0.260 and the positive indicator species are *Acer pseudoplatanus*, *Betula* seedling, *Betula pendula*, *Oxalis acetosella* and *Geum rivale*.

The negative group at level 3 of the divisions was split with an eigenvalue of 0.291 separating the scrub vegetation from the meadows. The negative indicator species associated with the scrub are *Rubus fruticosus* agg., *Sarothamnus scoparius* and *Alnus glutinosa*. The positive indicator species for the meadows is *Galium verum*. The samples characterised by scrub species were separated down to the final level 5 of the divisions with an eigenvalue of 0.340. The positive indicator species is *Chrysanthemum leucanthemum*. The negative end group (end group 2) from this split is made up of samples taken on the former river embankment, which is now colonised by a dense layer of *S. scoparius*. The scrub community making up the positive end group of this division lies adjacent to the riparian woodland areas and has a relatively rich field layer.

The meadow communities are separated on the positive branch of the fourth level of divisions with an eigenvalue of 0.243. The negative indicator species for this split are *Arrhenatherum elatius*, *Cirsium vulgare*, *Hypericum perforatum* and *Centaurea nigra*. These species are characteristic of the Arrhenatherata meadow, which these samples are taken from. The indicator

species for the positive end group (end group 5) are *Trifolium repens* and *Succisa pratensis*. These samples are taken from the herb rich meadow adjacent to the *Betula* woodland.

The positive group at level 3 was further split at level 4 to separate out those samples dominated by *Betula* species, with the negative indicator species being *Betula* seedlings, and the quadrats which were dominated by alder. The eigenvalue of the split is low at just 0.182, however the floristic composition and structure of these two habitats justifies the division. Level 4 divisions were accepted as the end groups for these woodland communities (end groups 6 and 7).

The following paragraphs describe the divisions made on the positive tail of the sample dendrogram. The division at level 2 has an eigenvalue of 0.426 with negative indicator species *A. glutinosa* and *Galium aparine*. This split separates out the samples that were recorded from riparian woodland areas and the point bar. Level 3 of the divisions separated the riparian communities from the aquatic vegetation running along the stream emerging from the riparian woodland flowing to the backwater. The eigenvalue of this split is 0.298 and the positive indicator characterising the separation is *Agrostis stolonifera*. The negative group at level 3 was further split with an eigenvalue of 0.259 dividing the riparian woodland community with gravel substrate from the riparian woodland with sandy substrate. The basis of the split was due to variation in the field layer vegetation resulting from substrate texture. The negative indicator species typical of the riparian community with gravel substrate are *A.*

pseudoplatanus sapling and *Salix viminalis*. The positive indicator species for the woodland with sandy substrate are *Stachys sylvatica*, *Ranunculus acris*, *G. aparine* and *Filipendula ulmaria*. For both of these groups (end groups 8 and 9), the level 4 divisions were accepted as the end groups. The positive group at the level 3 division forms the end group as it only contains one sample (end group 10).

The positive group at level 2 of the divisions was split with a relatively high eigenvalue of 0.420. The negative indicator species is *Digitalis purpurea* and the positive indicator species is *B. pendula* saplings. This split separates out the areas of the point bar that are sparsely vegetated from those areas that are colonised by scrub species. The divisions made at level 3 for this group were accepted as the end groups (end group 11 and 12).

3.3.2b. Community classification

A total of 13 vegetation types were identified by the TWINSpan analysis. The constancy tables produced in the TABLE routine for each of these habitats are given in Appendix 3. These tables show the floristic composition of the communities along with a summary table of the environmental variables. The best fitting British Plant Communities for each end group are presented in Table 3.1 along with the MATCH co-efficient. Descriptions of the floristic characteristics of these habitats are given in the British Plant Community publications (Rodwell, 1991a; 1991b 1992, 1995a). The MATCH

Table 3.1: The 'best fitting' British Plant Community allocated to the vegetation types on Tomdachoille Island SSSI.

End group	British Plant Community	British Plant Community name	MATCH coefficient
1	SHhr	<i>Thymus drucei-Pilosella officinarum-Racomitrium canescens</i> gravel community	N/A
2	W23a	<i>Ulex europaeus-Rubus fruticosus</i> scrub, <i>Anthoxanthum odoratum</i> sub-community	32.9
3	W23	<i>Ulex europaeus-Rubus fruticosus</i> scrub	31.1
4	MG1e	<i>Arrhenatherum elatius</i> grassland, <i>Centaurea nigra</i> sub-community	51.2
5	U4b	<i>Festuca ovina-Agrostis capillaris-Galium saxatile</i> grassland, <i>Holcus lanatus-Trifolium repens</i> sub-community	50.8
6	W11d	<i>Quercus petraea-Betula pubescens-Oxalis acetosella</i> woodland, <i>Stellaria holostea-Hypericum pulchrum</i> sub-community	42.7
7	W7c	<i>Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum</i> woodland, <i>Deschampsia cespitosa</i> sub-community	36.7
8	W6	<i>Alnus glutinosa-Urtica dioica</i> woodland	37.2
9	W7a	<i>Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum</i> woodland, <i>Urtica dioica</i> sub-community	37.4
10	M23	<i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture	20.3
11	SHscb	<i>Digitalis purpurea-Rubus fruticosus-Acer pseudoplatanus</i> (g) gravel community	N/A
12	SHpc	<i>Betula pendula</i> (g)- <i>Senecio viscosus-Lepidium heterophyllum</i> gravel community	N/A
13	S22a	<i>Glyceria fluitans</i> water-margin vegetation, <i>Glyceria fluitans</i> sub-community	70.9

routine failed to allocate a suitable vegetation type to the gravel habitats, as these communities have not been sampled in the British Plant Community system. Habitat names for these communities have been given according to the dominant and most abundant species characteristic of the community. Vegetation maps are presented in chapter 5.

3.3.3. Floristic relationships with environmental variables

The results of the forward selection of environmental variables in the CANOCO routine are given in Table 3.2. The table shows the cumulative variance of each variable in explaining the pattern of species distribution, and the order in which the significant variables ($p < 0.05$) were included into the model. A summary of the CANOCO output is given in Table 3.3. The total inertia is a measure of the total variance in the species data (4.594). The eigenvalues are a measure of the importance of an ordination axis. The species-environment correlations are a measure of the strength of the relationship between the species and environment for a given axis, with axes 1 and 2 having high values (0.935 and 0.870 respectively). The cumulative percent variance of the species-environment relation shows that 57.9% of the variation in the species distribution is explained by the environmental variables in the first two axes. The resulting ordination diagram produced when plotting the species scores with the biplot scores of environmental variables is given in Figure 3.3. The analysis shows that 10 environmental variables are significantly correlated to the pattern of the species distribution. The direction and length of the arrows on the ordination diagram denote the

Table 3.2: Forward selection of significant environmental variables ($p < 0.05$) in CANOCO. Total variance describes the cumulative variance each property explains when added to the model. The variables are presented in the order they were included into the model.

Variable	Total variance	p-value
Soil depth	0.26	0.005
Tree cover	0.49	0.005
Open water	0.62	0.005
Elevation	0.67	0.010
Unvegetated gravel	0.80	0.005
Unvegetated soil	0.88	0.005
Particle size range	0.94	0.010
Heterogeneity	0.98	0.020
MEDOM	1.02	0.040
Tall herb cover	1.07	0.025

Table 3.3: Summary statistics of the CANOCO results for the first 4 ordination axes.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.373	0.246	0.125	0.098	4.594
Species-environment correlations	0.935	0.870	0.659	0.702	
Cumulative percent variance:					
Of species data	8.1	13.5	16.2	18.3	
Of species-environment relation	34.9	57.9	69.6	78.8	
Sum of all unconstrained eigenvalues					4.594
Sum of all canonical eigenvalues					1.068

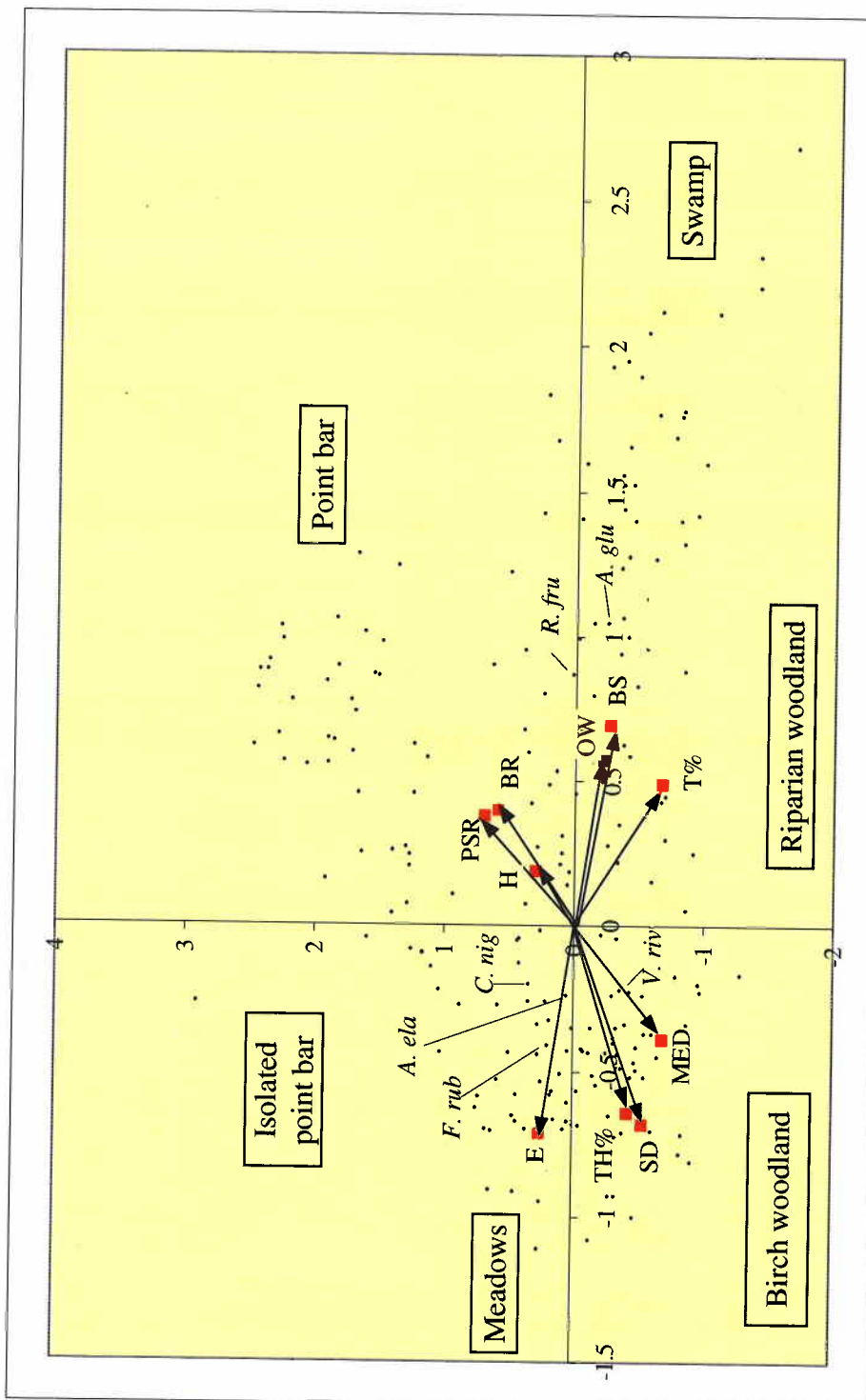


Figure 3.3: Ordination diagram of species and environmental variables on Tomdachoille Island SSSI. Environmental variables are denoted by arrows and red squares; the species carrying a high weight for its species score are marked on the diagram. Legend:

- E: elevation (m)
- BS: unvegetated soil
- H: heterogeneity (particle size index)
- A. glu: *Alnus glutinosa*
- V. riv: *Viola riviniana*
- TH%: tall herb cover
- OW: open water
- MED: MEDOM (particle size index)
- R. fru: *Rubus fruticosus*
- A. ela: *Arrhenatherum elatius*
- SD: soil depth (cm)
- BR: unvegetated gravel
- MED: MEDOM (particle size index)
- C. nig: *Centaurea nigra*
- T%: tree cover
- PSR: particle size range
- F. rub: *Festuca rubra*

direction of greatest influence the variables have upon species distribution. On the left-hand side of the ordination, the species and habitats are occurring in areas of relatively high elevation with substantial soil profile development in terms of soil depth, finer substrate and a high percent ground cover of tall herbaceous species. On the right-hand side of the ordination, the plant communities are in lower lying zones with poor soil profile development and little vegetation cover. The variables that are correlated with the species distribution on this side of the axes are dense tree cover, open water, a high proportion of bare ground cover and coarse substrate texture. The species being most influential in the ordination diagram have been labelled. These are the species that carry a high weight for their species score, as calculated in CANOCO. Species carrying a weight greater than 65 have been labelled on the diagram. These species scores are given in Appendix 4. The species labelled on the ordination diagram show that *A. glutinosa* and *R. fruticosus* are highly correlated with areas of high bare soil cover, the presence of open water and zones of low elevation. *C. nigra*, *A. elatius* and *F. rubra* are very highly correlated with elevation as these species points occur in very close proximity to the elevation arrow on the diagram. Thus the abundance of these species increases with elevation across the study area. These species decrease in abundance under wetter conditions and where the ground is poorly colonised. The presence of *V. riviniana* is highly correlated with particle size indices. This species is highly abundant where the soil is well mixed, denoted by the MEDOM statistic, and its abundance decreases as the material becomes coarser in nature with gravel and pebbles being dominant, as indicated by high

heterogeneity, high particle size range and a high percent of unvegetated gravel cover.

The CANOCO routine examines sample heterogeneity as a measure of species diversity using the N_2 statistic (reciprocal of Simpson's diversity index). A summary of these results is given in Table 3.4 showing those samples with very low diversity and species poor (Table 3.4a) and those samples with high diversity, species rich, in Table 3.4b. The samples presented in Table 3.4a are from areas of poorly colonised gravel or zones of inundation by ponds, streams or the backwater. The samples in Table 3.4b are from W11d woodland, riparian woodland W7a and W7c, SHhr and W23 scrub community. Table 3.5 shows summaries of the species tolerance analysis in CANOCO. Table 3.5a shows species having a low tolerance ($N_2 < 3$), meaning they are more site-specific species only existing under certain habitat conditions. Table 3.5b shows species with a high tolerance ($N_2 > 60$), meaning that these species are tolerant of environmental variation and occur in many samples across the study area.

3.3.4. Soil classification and description

Cluster analysis identified six major soil/substrate groups based on soil profile and substrate characteristics within the study area. The variance of the soil properties within group 6 was high and therefore reanalysed in order to produce more homogenous groups with lower internal variance. The final divisions of the data led to eight groups being defined. Tables of the soil

groups showing summary statistics and the samples belonging to each group are presented in Appendix 5.

Table 3.4: Sample heterogeneity expressed by N_2 . Showing (a) samples with low N_2 (species poor) and (b) samples with high N_2 (species rich).

(a)

Sample	N_2
B7	6.15
B8	7.59
C6	2.85
C9	6.24
C12	8.11
D5	1.73
D6	7.03
D10	8.01
D11	4.87
E5	1.98
F4	3.26
F5	7.30
K3	1.00
L3	1.00
M2	1.00
M3	1.00

(b)

Sample	N_2
B1	30.54
C2	30.30
C3	34.10
D1	32.44
D2	33.08
D3	36.63
E2	33.26
E3	36.26
F1	30.03
F2	31.56
G1	38.27
G2	32.26
G10	32.08
H1	32.73
H2	33.14
H3	31.10
I1	30.93
I2	30.42
I3	34.07
I7	30.41
I8	31.47
I10	30.08
J2	31.48
K1	30.45

Table 3.5: Summary of the CANOCO output of species with (a) low tolerance ($N_2 < 3$) and (b) high tolerance ($N_2 > 60$).

a)

Code	Species name	N_2
144	<i>Alliaria petiolata</i>	1.90
174	<i>Anthyllis vulneria</i>	2.89
252	<i>Bromus arvensis</i>	2.92
319	<i>Carex echinata</i>	1.99
350	<i>Carex romota</i>	1.99
359	<i>Carex sylvatica</i>	2.97
407	<i>Chrysosplenium alternifolium</i>	1.90
450	<i>Crepis vesicaria</i>	1.90
535	<i>Equisetum palustre</i>	1.90
570	<i>Fagus sylvatica</i>	2.00
640	<i>Glyceria maxima</i>	2.00
661	<i>Heracleum sphondylium</i>	2.00
698	<i>Hypericum humifusum</i>	1.97
699	<i>Hypericum maculatum</i>	1.80
702	<i>Hypericum pulchrum</i>	1.90
715	<i>Iris pseudacorus</i>	1.89
729	<i>Juncus conglomeratus</i>	2.96
855	<i>Mentha aquatica</i>	1.97
891	<i>Myosotis sylvatica</i>	1.97
1043	<i>Potentilla anserina</i>	2.53
1059	<i>Prunella vulgaris</i>	2.00
1065	<i>Prunus spinosa</i>	2.00
1089	<i>Ranunculus flammula</i>	2.85
1188	<i>Sambucus racemosa</i>	2.00
1259	<i>Silene vulgaris</i>	1.93
1320	<i>Teesdalia nudicaulis</i>	2.96
1349	<i>Trifolium pratense</i>	1.97
1593	<i>Climacium dendroides</i>	2.85
1795	<i>Plagiomnium rostratum</i>	2.00
1888	<i>Polystichum aculeatum</i>	2.00
1934	<i>Rhodobryum roseum</i>	1.97
2023	<i>Tortula ruralis ssp ruraliformis</i>	2.00
2471	<i>Parmelia saxatilis</i>	1.97
2614	<i>Fraxinus excelsior (s)</i>	2.00
2622	<i>Prunus avium (g)</i>	2.00
2639	<i>Ulex europaeus (g)</i>	2.00
2950	<i>Rosa caninia (s)</i>	2.00
3042	<i>Sarothamnus scoparius (g)</i>	1.90

b)

Code	Species name	N_2
171	<i>Anthoxanthum odoratum</i>	62.53
197	<i>Arrhenatherum elatius</i>	80.45
371	<i>Centaurea nigra</i>	68.66
576	<i>Festuca rubra</i>	72.25
1296	<i>Stellaria graminea</i>	60.89
1396	<i>Veronica chamaedrys</i>	67.51
1429	<i>Viola riviniana</i>	78.04
1940	<i>Rhytidiadelphus squarrosus</i>	61.02

Group 1 is composed of unvegetated gravel substrate, characterised by coarse pebbles and small boulders. The coarse texture of this substrate group is indicated by the phi values in the MODOM particle size index, which range from -4 to -8. Coarse substrate classes are present in all samples where pebble counts were made. Heterogeneity of the particle size classes is high with a mean value of 12 classes and a standard deviation of 4. The mean range is high at 239.76mm. A high percentage of unvegetated gravel is present virtually throughout this group (mean value 86%).

Group 2 gravel substrate is also composed of coarse substrate but the range and heterogeneity of the particle size classes is lower than group 1. Mean particle size heterogeneity is 8 classes and the mean range is 99.32. Finer substrate is absent from these samples. The amount of unvegetated gravel is more variable within this group.

Group 3 is composed of gravel and occurs on the more sorted areas of the point bar and within the isolated gravel habitat. Substrate texture is finer than in the other two groups, but is still dominated by large pebbles. Mean particle size heterogeneity is 10 classes and mean range is 149.13mm. There is a high proportion of unvegetated gravel.

Group 4 is composed of the samples with the most developed soil profiles within the study area. The soil is dominated by fine sand particle size throughout. The particle size range varies from silt to fine gravel. Heterogeneity of the particle size classes is fairly high, ranging between 6-8

classes. Soil profiles are relatively deep with a mean value of 110 cm. Soils are well drained with a mean SMC of 12%. The percent bare soil cover is low with a mean of 3%.

Group 5 varies from group 4 in that the soil texture is slightly coarser with the maximum particle size class being coarse gravel. Silt sized particles are absent from some of the profiles within this soil type. Fine sand is the dominant particle size class. Particle size heterogeneity and range is greater in this soil group. Soil profiles are shallower with a mean value of 63 cm. The soil is well drained with a mean moisture content of 13%.

Group 6 is characterised by shallow immature soils developing on the isolated gravel habitat. Mean soil depth is 23cm. Very coarse sand and very fine gravel dominate these profiles. Silt is present in all samples. Mean range and heterogeneity of the particle size is 12.6mm and 9 classes respectively.

Group 7 varies from group 6 by being composed of finer substrate. This soil is also immature and only very shallow, with a mean soil depth of 22 cm. SMC is higher in these soils with a mean value of 28%, possibly due to the greater moisture retention capacity of the finer matrix. The mean MODOM particle size class for this group is medium sand. Particle size range and heterogeneity within this group is lower than in group 6 with mean values of 8.64mm and 9 classes respectively. This soil type is commonly found underneath scrub vegetation.

Group 8 is composed of immature soil profiles with a mean depth of 14 cm. These profiles are typical to the riparian woodlands and have a high proportion of bare soil and higher moisture content than the other soil types. Mean soil moisture is at 40%. The mean MODOM particle size class is very coarse sand, MAXDOM is fine to medium gravel, and the MINDOM is very fine sand. The range of particle size classes is intermediate between groups 6 and 7, and the heterogeneity is fairly low with a mean of 6 classes.

3.3.5. Landform classification and description

Six landform classes were identified within the study area. The landforms present are backwater, abandoned channel, point bar, abandoned point bar, floodplain and embankment. Floodplain is defined as the land either side of the bank top and point bars are defined as bank features. The samples associated with each landform type are given in Appendix 6.

3.3.6. Diversity analysis

3.3.6a. Data grouped by plant community

3.3.6ai. Richness

The results in Figures 3.4 - 3.6 show the spatial variation of species richness within the floodplain. Figure 3.4 shows that the woodland communities are the most species rich habitats within the study area, in particular W11d and W7a.

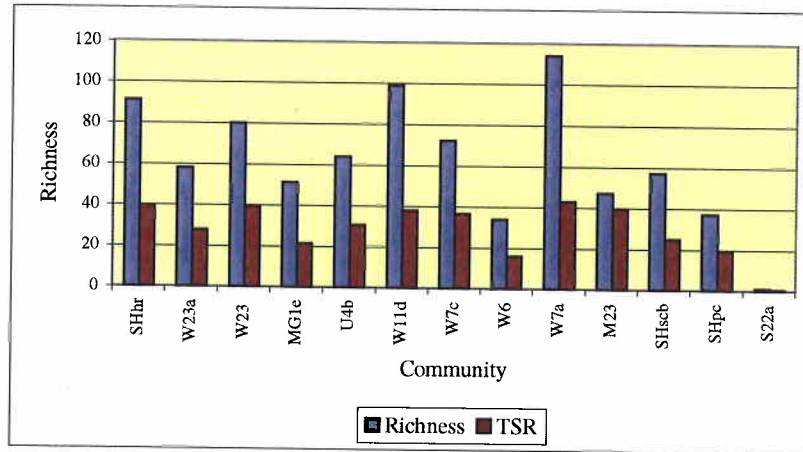


Figure 3.4: Total species richness and TSR within the plant communities on Tomdachoille Island SSSI.

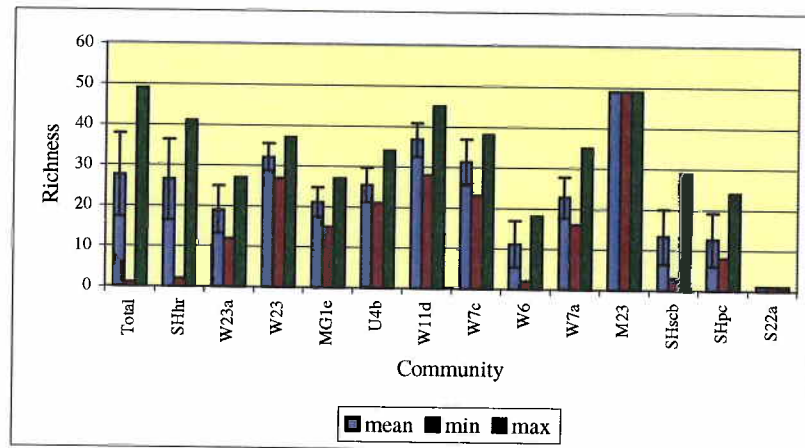


Figure 3.5: Summary statistics for plant species richness on Tomdachoille Island SSSI calculated per quadrat.

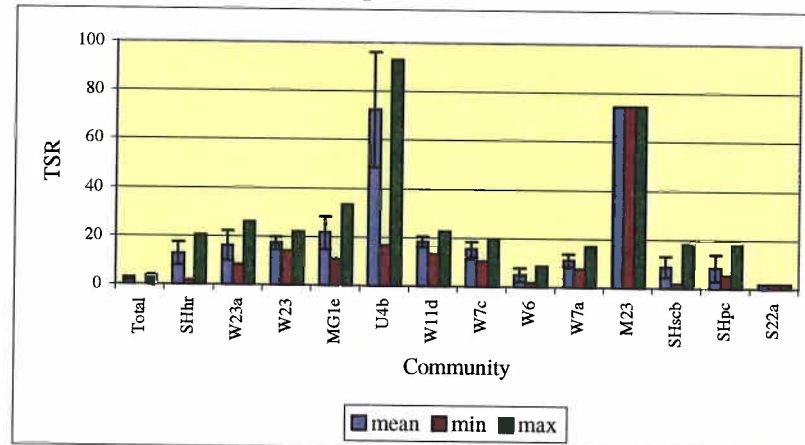


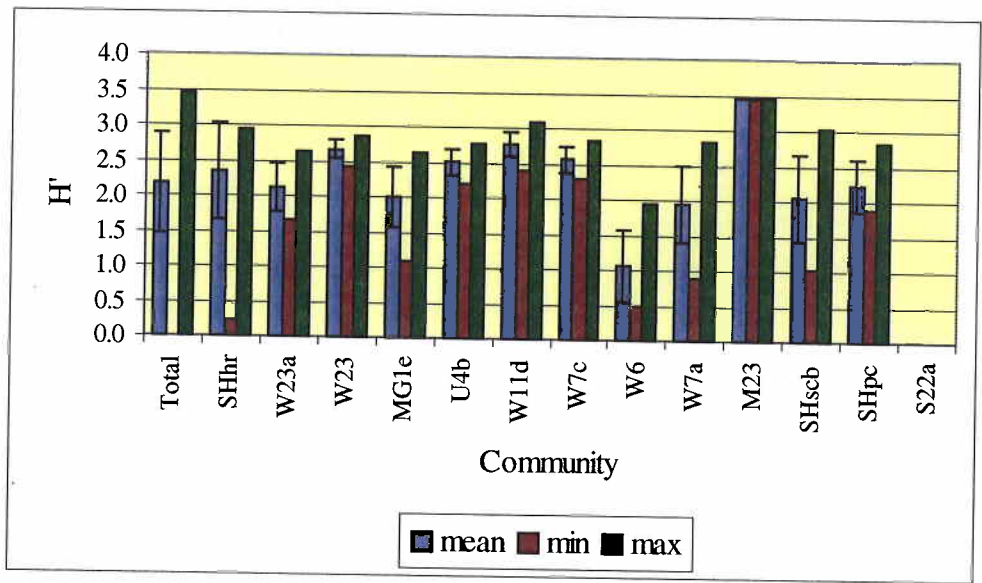
Figure 3.6: Summary statistics for TSR within each plant community on Tomdachoille Island SSSI calculated per quadrat.

These communities have 99 and 114 species present respectively. Intermediate levels of species richness occur within the grassland and scrub communities. The gravel habitats show that although total species richness is typically low in the zones most prone to inundation, these areas show a rapid increase in species richness with isolation from disturbance. This is clearly indicated in the SHhr community which has 91 species. This rapid colonisation has occurred since the 1970's due to channel abandonment. Species richness is lowest in the S22a swamp community. Although this community contributes little to the species richness, it is important in creating diversity of landscape patches. It is also an important aquatic community. Little variation is present in the pattern between total species richness and TSR within the communities and the two indices show similar patterns in distribution. The only notable difference is in the M23 habitat, which scores relatively low in real terms, but ranks high in diversity when the community area is accounted for. Figure 3.5 shows the M23 fen habitat to be the most species rich within the study area. It is also the smallest habitat in terms of its spatial scale. The W11d woodland ranks second with a mean of 37 species and a relatively low standard deviation. The communities SHhr, W23 and W7c also have relatively high species richness in comparison to the other vegetation types. Relatively high variation in species richness tends to occur within the communities with a high ground cover of unvegetated gravel. These communities also have the lowest species richness, with the exception of SHhr. However, this community has the highest variation in species richness among the habitat types present within the study area.

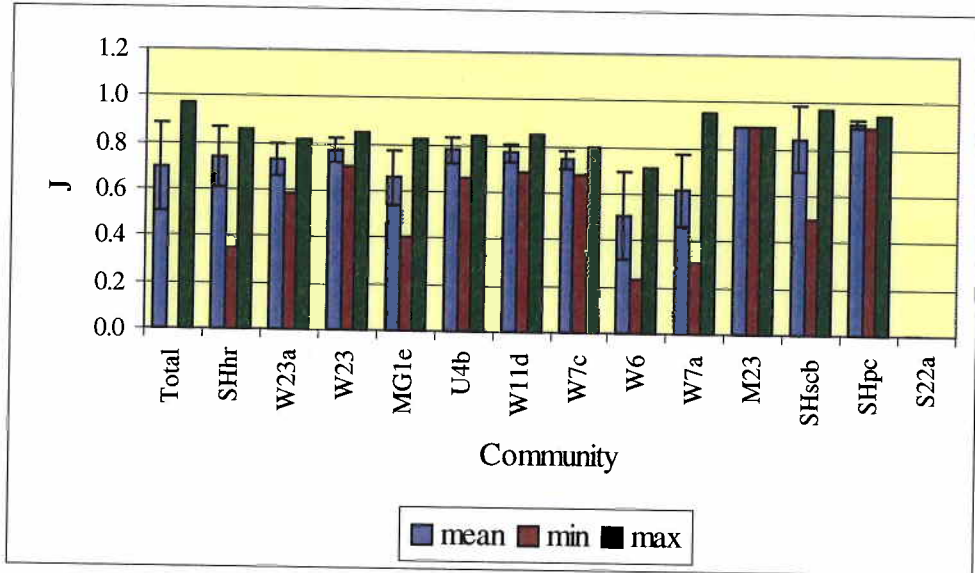
The results of species richness within the communities is markedly different when richness is corrected for sample area, as shown in Figure 3.6. The M23 plant community remains the most diverse in terms of richness. However the U4b community is now shown to have high species richness in comparison to the other vegetation types sampled. The pattern of species richness is highly variable within this habitat though, indicated by the high standard deviation. Variation in species richness diversity when accounting for area is negligible among the other plant communities. Riparian woodlands W6 and W7a, gravel habitats SHscb and SHpc and S22a have the lowest diversity.

3.3.6a.iii. Shannon index H' and J

The Shannon index results for the floristic data are presented in Figure 3.7a. The graph shows summaries of the diversity values for all plant communities and the whole study area. Maximum diversity is found within the M23 community. However, this community is small in scale and composed of only one sample point, and is a unique vegetation type to the study area. The woodland and scrub communities W23, W11d and W7c and the U4b meadow all have relatively high diversity and low internal variability indicated by the minimum, maximum and standard deviation values. Moderate levels of diversity are found within W23a and SHpc, with relatively low variance. The SHhr, MG1e, W7a and SHscb habitats all have a Shannon index diversity of approximately 2.0. All of these communities have a relatively high level of variance in their overall diversity. S22a and W6 score lowest on the Shannon index.



a)



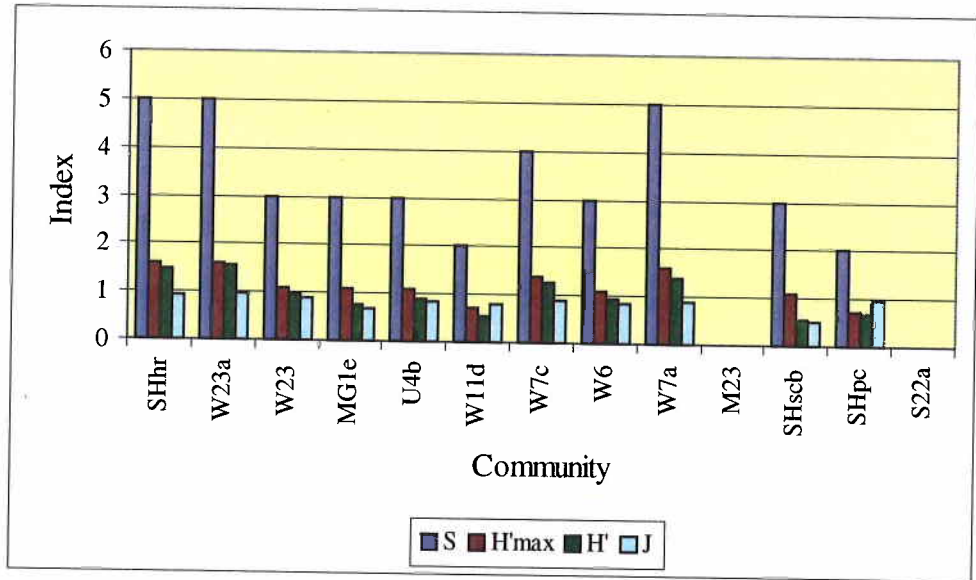
b)

Figure 3.7: Summary statistics showing species diversity in terms of richness H' (a) and evenness J (b) measured by the Shannon index on Tomdachoille Island SSSI.

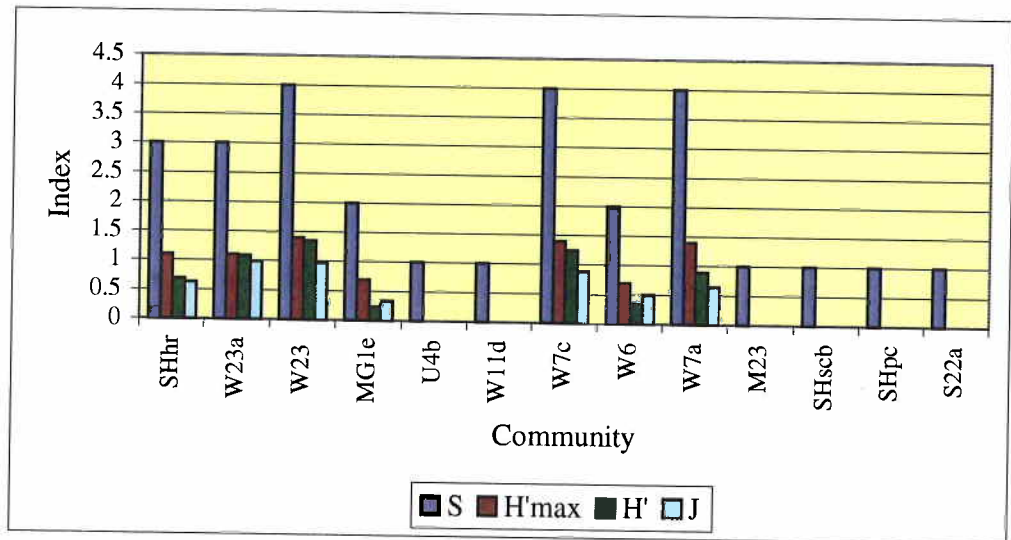
The diversity of the habitat types is expressed in terms of evenness in Figure 3.7b. Communities SHpc and M23 are the most diverse in terms of evenness. These habitats have a high means and low variance. SHscb also scores high in the equitability index. Other habitats scoring high on this index are W11d, U4b, W23, W23a and SHhr, the latter however having high variance. Communities scoring low, with high variance, in this index are W6, W7a and MG1e. In comparing Figure 3.7a and 3.7b it is clear that the evenness index closely mirrors the Shannon index results within the plant communities.

3.3.6aiii. Pedodiversity within the plant communities

Figure 3.8a shows the results of pedodiversity within the plant communities. The communities with the greatest soil heterogeneity are SHhr, W23a and W7a, indicated by the high richness score. The community with the most homogenous pedodiversity is W11d. The majority of habitats have a pedo-richness value of three soil/substrate groups. There is little variation between the maximum negentropy and the Shannon index throughout, with the exception of the SHscb community, which equates with the evenness of the distribution. The Shannon index scores highest within SHhr, W23a and riparian woodlands W7c and W7a. The lowest pedodiversity occurs in the older more stable habitats of MG1e and W11d, and the point bar area SHpc where the substrate will typically be well sorted by the river.



a)



b)

Figure 3.8: Pedodiversity variation (a) and geodiversity variation (b) within the plant communities on Tomdachoille Island SSSI. S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

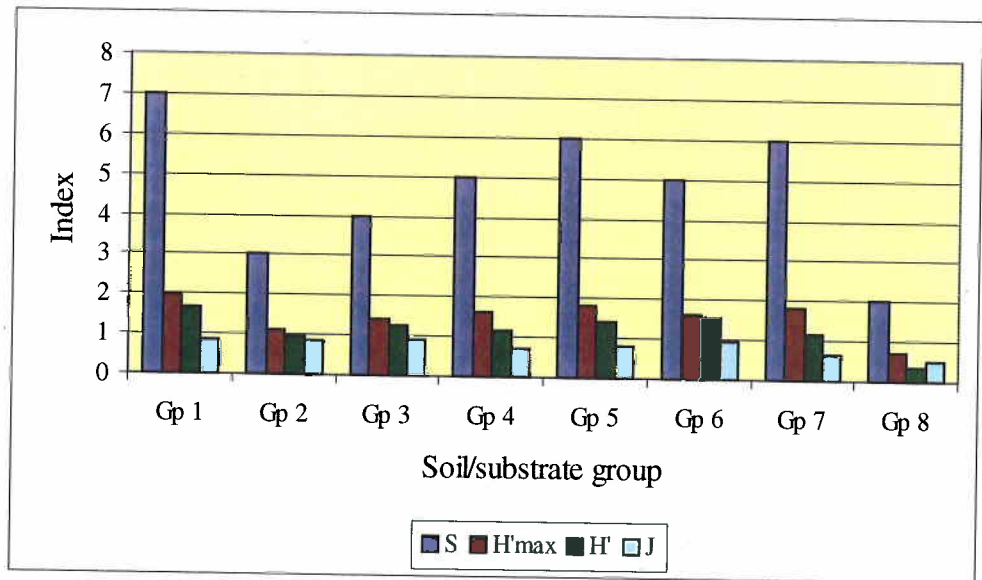
3.3.6aiv. Geodiversity within the plant communities

Figure 3.8b shows the results of geodiversity within the plant communities. Geodiversity is variable throughout the floodplain, ranging from plant communities occurring on only one landform to habitats spanning over four landform classes. A total of six vegetation groups are unique to a single landform category. The plant communities with a relatively high landform richness score mainly occur in the more dynamic areas of the floodplain that are prone to disturbance by inundation, thus modifying the geomorphic structure of the study area. Where landform richness is one, the other indices score zero. The communities with the highest geodiversity in terms of H'_{max} , H' and J are W23a, W23 and W7c. The diversity scores are notably high for W23a and W23 and there is little variation between H' and H'_{max} . The habitats also have an even distribution on the landforms indicated by the equitability score of close to 1.00. The communities with two landform types score low on H'_{max} , H' and J .

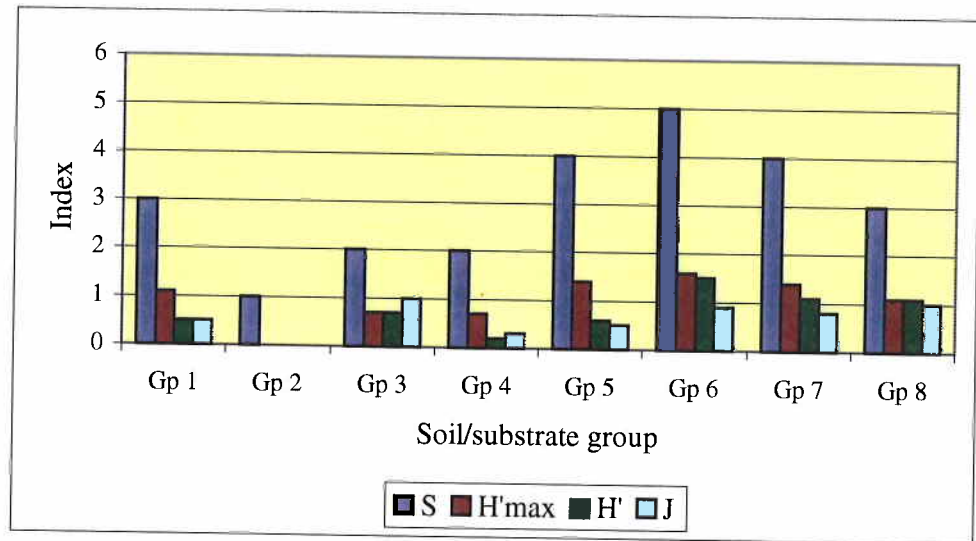
3.3.6b. Data grouped by soil/substrate group

3.3.6bi. Biodiversity within the soil/substrate groups

Pedo-richness within the floodplain is eight, composed of 3 groups characterised by gravel substrate, and 5 groups of sandy immature alluvial soils. The plant community diversity within each of the soil groups is summarised in Figure 3.9a. The figure shows biodiversity within the soil



a)



b)

Figure 3.9: Biodiversity variation (a) and geodiversity variation (b) within the soil/substrate groups on Tomdachoille Island SSSI. S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

groups is highly variable within the study area. Soil/substrate groups 1, 5 and 7 have the highest community richness. These groups also have the highest diversity in terms of H'_{max} , H' and J indices. Soil groups 2 and 8 have the lowest plant community diversity in terms of all four measures of heterogeneity, with group 8 also having a very low evenness score, indicating an uneven distribution of vegetation types on this soil type. Groups 3 and 6 have the highest equitability.

3.3.6bii. Geodiversity within the soil groups

Figure 3.9b shows the results of geodiversity analysis within the soil groups. Soil group 6 has the highest geodiversity of all the soil/substrate groups. This soil group is present on five landforms within the study area. This soil group shows little variation between the maximum negentropy and the Shannon index and has a high evenness index of 0.9 indicating that the landforms are evenly distributed within this soil type. Soil groups 5 and 7 have a relatively high landform richness of four. However, the H' and J indices in group 5 are both low. Overall, high geodiversity tends to occur where soil profiles have developed, and low geodiversity occurs within the gravel substrate areas undergoing the initial stages of pedogenesis. The lowest geodiversity occurs within the soil/substrate groups 1, 3 and 4, with group 4 scoring lowest on the evenness index.

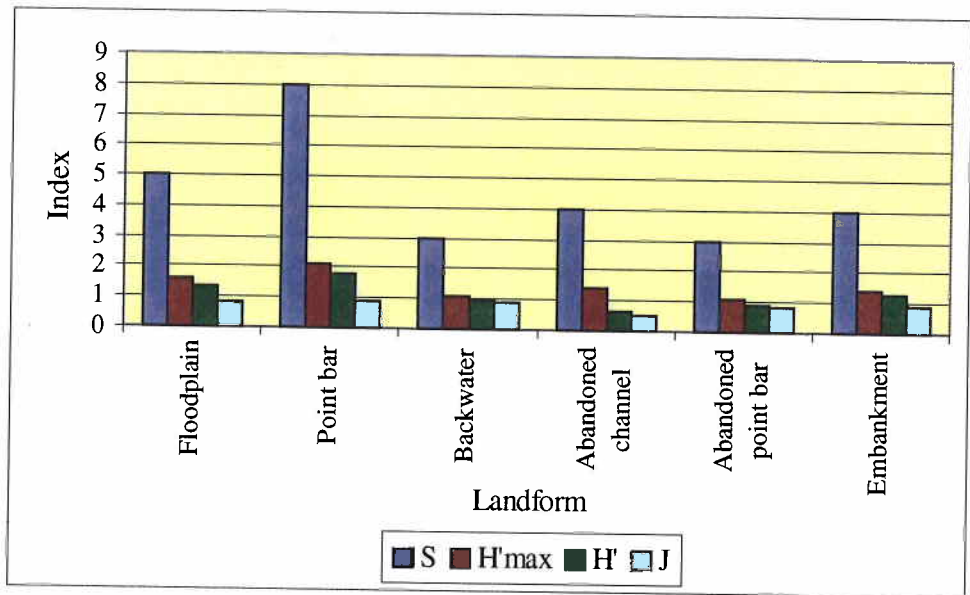
3.3.6c. Data grouped by landform

3.3.6ci. Biodiversity within the landform classes

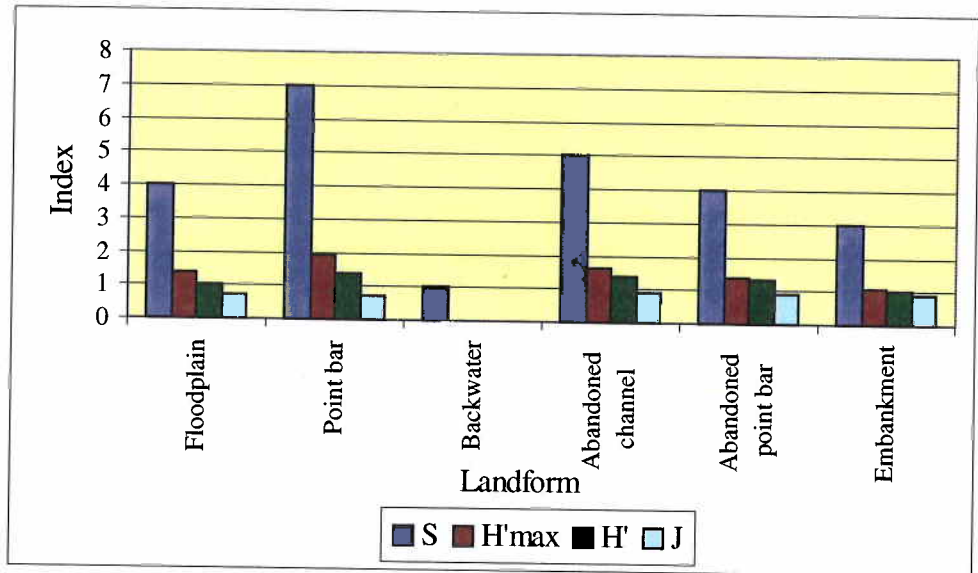
Figure 3.10 shows biodiversity within the landform categories. The highest habitat diversity in terms of richness occurs within the point bar. This landform also scores highest with the other diversity measures showing that this landform supports several plant communities and that their distribution is fairly even throughout. The floodplain areas have the next highest diversity, with five plant communities occurring on this landform with an evenness score of 0.8 showing a reasonably even coverage of the vegetation types. The abandoned channel and the embankment have intermediate habitat richness score within the study area. The embankment scores modestly on the other diversity measures, but the abandoned channel shows poor habitat diversity. The backwater and abandoned point bar score lowest on habitat richness, but both have high evenness scores.

3.3.6cii. Pedodiversity within the landform classes

Figure 3.10b shows the results of pedodiversity analysis within the landform categories within the study area. The point bar landform scores highest on all diversity measures, with very high 'species' richness. The soil/substrate groups have a reasonably even distribution, indicated by the evenness score of 0.7. The abandoned channel also has high diversity on all counts, and has a



a)



b)

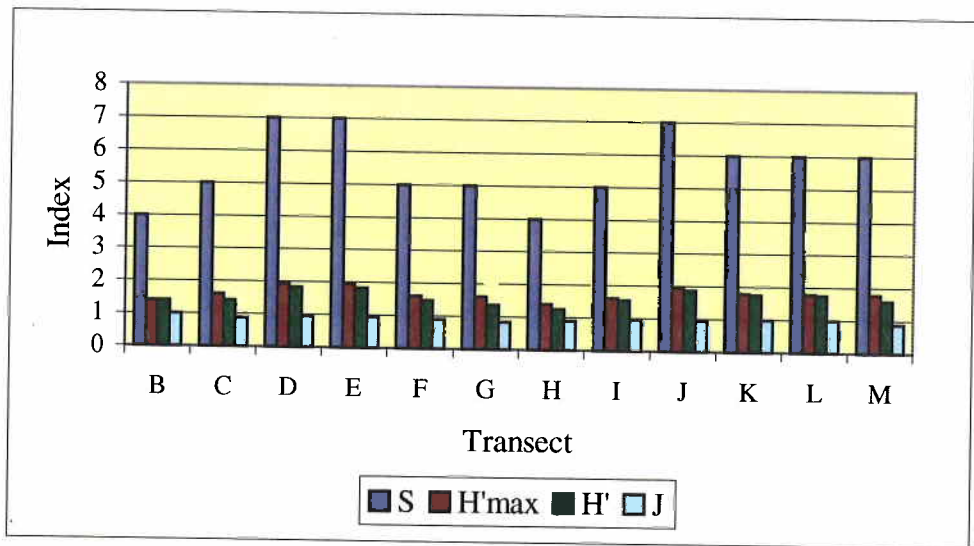
Figure 3.10: Biodiversity variation (a) and pedodiversity variation (b) within the landform classes on Tomdachoille Island SSSI. S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

high evenness distribution of 0.9. The floodplain, abandoned point bar and embankment landforms have intermediate pedodiversity and the backwater scores low on all measures.

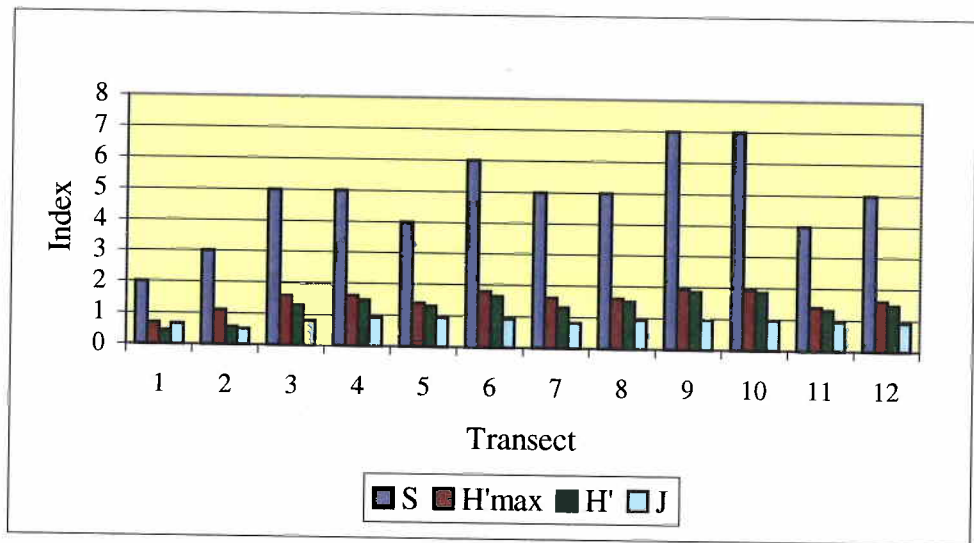
3.3.6d. Diversity variation perpendicular and parallel to the main channel

3.3.6di. Habitat diversity

Figure 3.11a shows how habitat diversity varies on the floodplain perpendicular and parallel to the main channel. The graphs show that habitat diversity is generally higher in the perpendicular dimension to the river channel. This describes the hydrologic gradient that occurs across the floodplain between the aquatic and terrestrial zones. Habitat richness varies between four and seven land cover types in this direction to the channel. Habitat diversity is lowest along the transect running through the secondary channel that was formerly occupied by the channel (transect H), and is now colonised by riparian woodland. The size of the habitat patches along transects are approximately even, expressed by the high evenness index throughout. Figure 3.11b shows habitat diversity in the parallel direction to be highly variable across this reach of the floodplain. Diversity is lowest at the furthest transects from the channel (the lower range of transect numbers). Habitat diversity shows the general trend of increasing in the longitudinal dimension the closer to the main channel, with a decline in diversity at the nearest transect. Evenness scores are more variable and generally lower in the longitudinal direction.



a)



b)

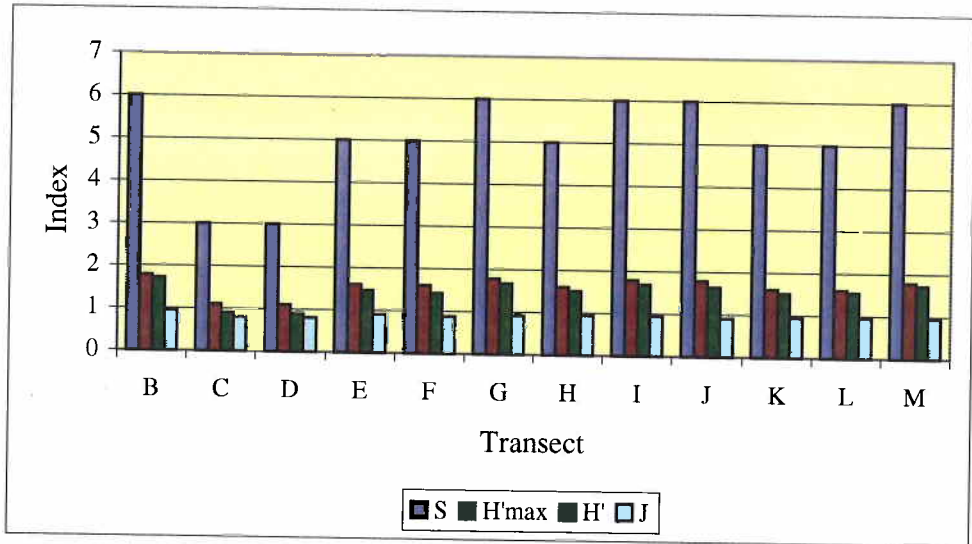
Figure 3.11: Habitat diversity variation across the study area perpendicular (a) and parallel (b) to the main channel. S = richness; H'_{max} = maximum negentropy; H' = Shannon index; J = evenness index.

3.3.6dii. Pedodiversity

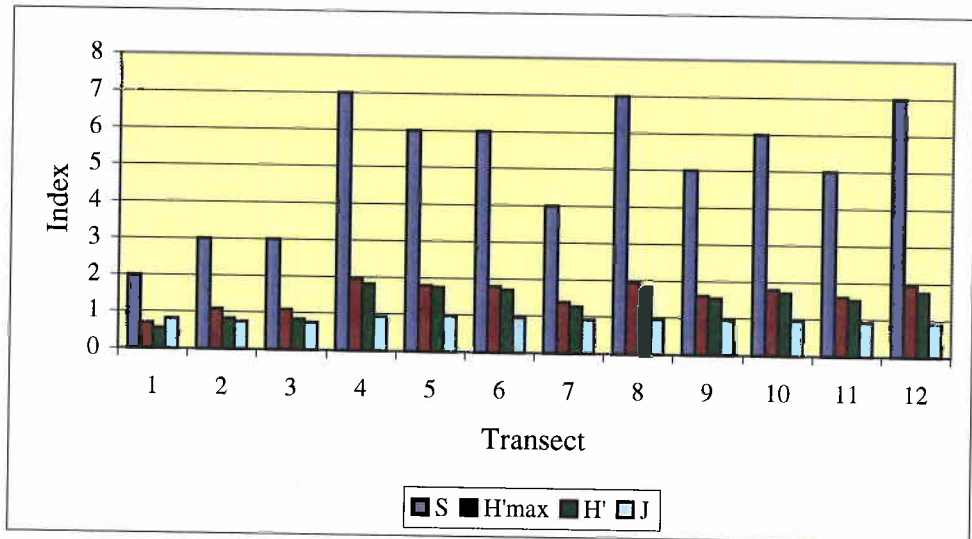
Figure 3.12 shows the pedodiversity results perpendicular and parallel to the main channel. The results show that overall there is little variation in pedodiversity along the different axes. The main differences occur within the latitudinal transects C and D and the longitudinal transects 1, 2 and 3. Transects C and D are dominated by gravel in the zone of active deposition and substrate sorting. Transects 1, 2 and 3 are furthest from the main channel and occupy the relatively old and stable floodplain area dominated by deep sandy soils (group 4). Pedodiversity is highest in both orientations along transects running through the abandoned channel zone (H, I, 5-12).

3.3.6diii. Geodiversity

Figure 3.13 shows the geodiversity results perpendicular and parallel to the main channel. Geodiversity is highest along transect J for all indices. Geodiversity perpendicular to the river peaks in the zone of the former channel along transects H through to M. Overall geodiversity is greater in the parallel orientation to the main channel. Geodiversity is relatively high throughout, with the exception being along transects 1 and 2, which run through the floodplain area.

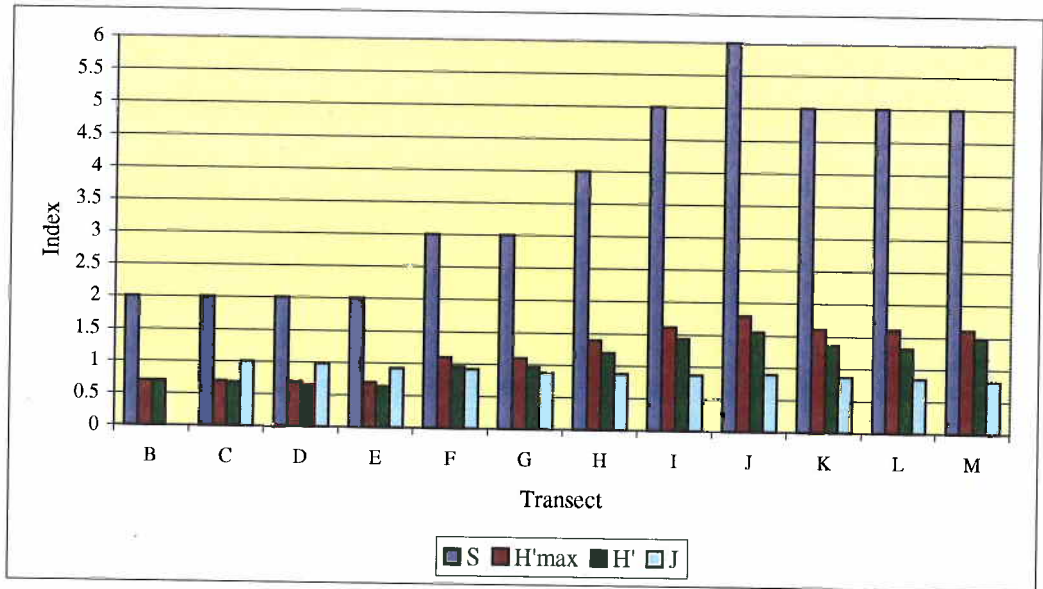


a)

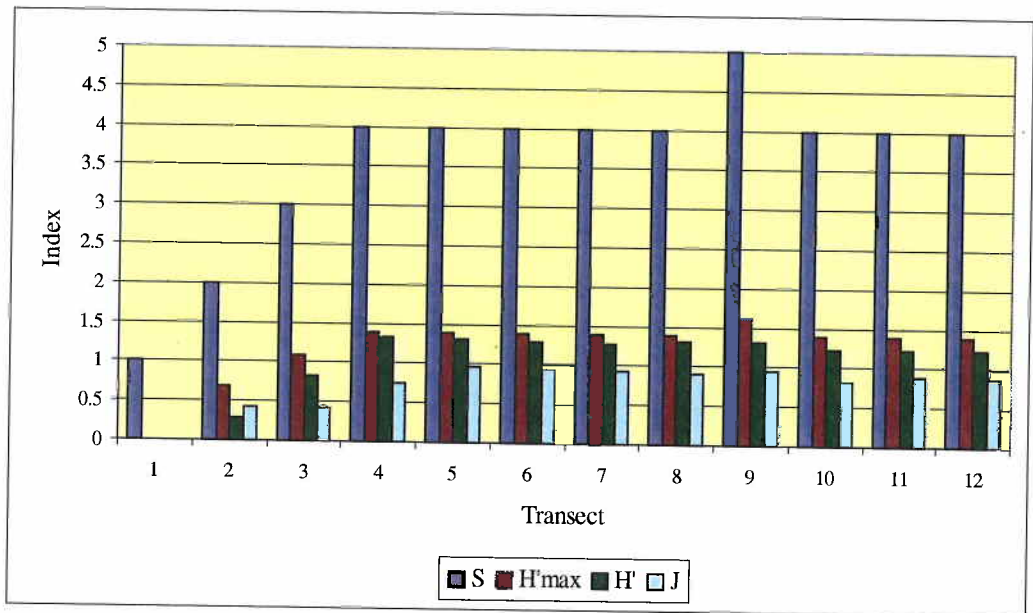


b)

Figure 3.12: Pedodiversity variation across the study area perpendicular (a) and parallel (b) to the main channel. S = richness; H'_{max} = maximum negentropy; H' = Shannon index; J = evenness index.



a)



b)

Figure 3.13: Geodiversity variation across the study area perpendicular (a) and parallel (b) to the main channel. S = species richness; H'max = maximum negentropy; H' = Shannon index; J = equitability index.

3.3.6e. Landscape diversity

3.3.6ei. Species unique to landform classes

The distribution of species among the landforms was examined in order to assess the importance of the mosaic of geomorphic features in influencing species diversity. The results of the analysis are presented in Table 3.6. The results in Table 3.6a show that very few species are present in all landform classes present in the study area. The general trend shows that the number of species unique to a given number of landform classes increases with a decrease in the number of landforms. This supports the need for geomorphic heterogeneity within river-floodplain zones in order to maintain species richness and provide suitable habitats for species with low tolerance to conditions for which they are not physiologically adapted to. Due to the high number of species being found in only one landform type, further analysis was carried out to assess which landforms the species are unique to. This was performed for those species occurring only in one landform class and only in two landform classes. The results are presented in Table 3.6b.

The results in Table 3.6b show that the majority of species unique to one landform class are present in the floodplain zones. This is possibly a result of the inherent geomorphic diversity within floodplain areas as they are composed of relic features such as palaeochannels and former point bars. The abandoned channel also has a relatively high count of species unique to only this landform type. All six landform classes present within the study area have

unique species with the semi-natural geomorphic units scoring higher than the former

Table 3.6: Count of species unique to the landform classes. Showing (a) the number of species encountered in all landform classes through to the number of species unique to one landform class; (b) the number of species unique to only one or two landform classes; and (c) the count of the number of rare species nationally, locally and the total number of species occurring within each landform class within Tomdachoille Island SSSI study area.

a)

89 species found only in one landform
70 species found only in two landforms
26 species found only in three landforms
32 species found only in four landforms
19 species found only in five landforms
7 species found in all six landforms

b)

Landform	One landform	Two landforms
Backwater	14	10
Abandoned channel	23	38
Point bar	10	19
Abandoned point bar	7	20
Floodplain	32	37
Embankment	3	6

c)

Landform	Nationally rare	Locally rare	Locally very rare	Total number of species
Backwater	2	4	1	53
Abandoned channel	1	3	1	143
Point bar	1	4	1	79
Abandoned point bar	1	3	1	93
Floodplain	0	1	1	149
Embankment	0	1	0	61

embankment landform for both species unique to either one or two landform classes. The floodplain and abandoned channel also score high for having species unique to two landform classes. The low number of species unique to

two landform classes of within the backwater show that this landform provides a habitat for fairly site specific species tolerant of frequent inundation. The species unique to each landform class along with their frequency estimates are given in Appendix 8. These results are summaries in Table 3.6c giving a count of the number of rare species within the landform classes. The results show that rare species both nationally and locally occur within all landform types, especially within the landforms prone to frequent disturbance or those that have been disturbed in the recent past. For example *Aquilegia vulgaris* and *Mentha piperita* within the backwater, and *Petasites albus* within the abandoned channel. These species are typical of fens, marshes and wet woodlands. The very rare species *Euphrasia nemorosa* is found on the gravel habitats of the River Tummel and is locally abundant in places. This species is also present within the floodplain zones and forms dense patches in place, however it was present outside of the study area.

3.3.6eii. Landscape diversity evaluation

The result for the overall assessment for landscape diversity is presented in Table 3.7. The landscape diversity score is based on the Shannon index for richness. The results show that the landforms are the least diverse element of the landscape. This infers that they are the templates for development to occur and that they are the basic unit of the landscape matrix. The table shows that there is a relative balance between biodiversity and pedodiversity, and that both of these landscape components are more diverse in the perpendicular orientation to the main channel.

Table 3.7: Mean diversity (H') values calculated along transects within the study area showing variation in diversity between the landscape components and an average score for overall landscape diversity.

	Biodiversity	Pedodiversity	Geodiversity
Perpendicular to channel	1.6	1.5	1.2
Parallel to channel	1.3	1.4	1.2
Average	1.45	1.45	1.2
Landscape diversity score	1.36		

3.3.7. Results of exploratory data analysis

Exploratory data analysis showed that the landforms are the basic unit of the landscape. Therefore data was grouped by landform for subsequent analysis. The mean and the standard deviation for diversity indices and key geomorphic and pedological variables were calculated within each landform as a measure of heterogeneity within the landscape. This was also done to evaluate the strength of the grouping of data to check within group variance. The results are presented in Table 3.8. Overall the standard deviation of the variables within each landform is low, indicating sound grouping of the data. The low variance indicates relative homogeneity of the variables within the landforms, which is important in ecological terms for ecosystem survival. The landforms display the greatest variance in pedological properties, namely soil depth, SMC and particle size range. These landforms therefore provide a wide variety of micro-habitats creating niches for a diverse array of species to colonise as a result of localised undulations in topography within the land units. The variance in soil/substrate properties tends to decline with greater

Table 3.8: Mean and standard deviation of diversity indices and key geomorphic and pedological variables within each landform on Tomdachoille Island SSSI.

	Backwater		Abandoned channel		Point bar		Abandoned point bar		Floodplain		Embankment	
	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
S	14	18.50	27	6.42	22	7.42	31	6.58	33	9.28	23	10.10
H'max	1.43	1.80	3.19	0.29	2.60	0.69	3.26	0.22	3.35	0.30	2.93	0.43
H'	1.08	1.43	1.93	0.62	1.90	0.75	2.42	0.31	2.48	0.44	2.17	0.38
J	0.32	0.40	0.59	0.10	0.73	0.21	0.74	0.10	0.73	0.09	0.75	0.03
Elevation	-0.02	0.69	1.71	1.36	2.11	0.76	2.41	1.08	2.96	0.40	3.16	0.95
Soil depth	7.14	12.54	19.85	13.22	5.57	10.20	18.05	13.32	87.35	30.43	60.00	37.64
SMC	81.12	25.06	30.92	18.89	33.69	9.07	13.94	12.43	12.41	4.23	8.16	4.71
MINDOM (phi)	5	0.00	4	2.52	0	3.30	3	3.37	5	0.00	5	0.00
MAXDOM (phi)	-2	0.00	-3	1.96	-6	2.15	-5	2.34	-2	1.10	-3	0.96
MODOM (phi)	1	2.12	1	3.18	-4	3.77	-3	4.34	2	1.14	1	3.37
MEDOM (phi)	1	1.41	1	1.76	-1	1.68	-1	2.67	2	1.00	1	1.92
Range	3.94	0.00	26.57	64.07	161.24	105.59	68.07	94.69	5.32	4.32	10.94	6.00
Heterogeneity	8	0.00	9	3.10	11	2.87	10	1.79	8	1.07	9	0.96

levels of soil profile development. The floodplain areas are the most diverse floristically with the highest mean values for S and H'. The abandoned point bar also scores high on the floristic indices of diversity showing that river channel change causing bank features to become isolated from the main channel create diverse habitats within floodplain environments. This habitat is also colonised by locally and nationally rare species. The general pattern of low variance indicates high diversity due to an even distribution of variables within the landforms.

The degree of variance of properties in the whole data set was analysed. The results are given in Table 3.9. The floristic diversity results show that there is relatively high diversity within the study area. The species have a fairly even distribution, indicated by the mean score for J. Variance within the diversity indices is low suggesting high diversity and an even distribution of the variables. The variance within the particle size indices is on the whole greater than the variance within the landform classes. This indicates heterogeneity of substrate size across the study area. The standard deviation for soil depth is also greater showing considerable variation in soil profile development within the study area.

The results in Table 3.10 show the mean and variance of diversity indices calculated for the landscape components perpendicular and parallel to the main channel. The results show that diversity is greater perpendicular to the main channel, indicated by the higher mean values and lower variance. The

Table 3.9: Mean and standard deviation of diversity indices and key geomorphic and pedological variables within the whole data set on Tomdachoille Island SSSI.

	Mean	Stdev
S	27	10.26
H'max	3.00	0.75
H'	2.16	0.71
J	0.70	0.19
Elevation	2.35	1.06
Soil depth	41.73	42.91
SMC	18.73	15.77
MINDOM (phi)	3	3.04
MAXDOM (phi)	-4	2.57
MODOM (phi)	0	4.06
MEDOM (phi)	1	2.17
Range	61.55	96.31
Heterogeneity	9	2.53

Table 3.10: Variance in diversity indices measured by the mean and the standard deviation (a) perpendicular and (b) parallel to the main channel on Tomdachoille Island SSSI.

a)

	S		H'max		H'		J	
	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
Biodiversity	6	1.08	1.7	0.2	1.59	0.21	0.93	0.05
Pedodiversity	5	1.08	1.60	0.25	1.47	0.29	0.91	0.05
Geodiversity	4	1.03	1.31	0.29	1.17	0.31	0.89	0.08

b)

	S		H'max		H'		J	
	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
Biodiversity	5	1.47	1.52	0.35	1.34	0.44	0.86	0.14
Pedodiversity	5	1.73	1.56	0.41	1.43	0.45	0.90	0.08
Geodiversity	4	1.6	1.28	0.54	1.17	0.56	0.81	0.30

trend within the landscape components is for biodiversity to be the greatest perpendicular to the channel and geodiversity the lowest. Geodiversity also scores lowest in the parallel orientation to the channel. In this orientation, pedodiversity has a marginally higher mean value for the diversity scores than biodiversity.

3.3.8. Relationships between variables- correlation and regression

3.3.8a. Correlation

Diversity indices calculated perpendicular and parallel to the channel were correlated. The results reveal that the evenness of pedodiversity distribution perpendicular to the channel is negatively correlated to the evenness of geodiversity ($p = -0.625^*$) and maximum pedodiversity is positively correlated with H' for geodiversity ($p = 0.579^*$). The analysis shows the diversity indices are highly correlated in the parallel orientation to the channel, Table 3.11. Strong positive correlations exist between all indices with the exception of biodiversity- and pedodiversity-richness score (S). The indices for biodiversity and pedodiversity are most strongly correlated with the geodiversity scores.

Table 3.11: Correlations between diversity indices parallel to the channel on Tomdachoille Island SSSI.

$n = 10$ (two-tailed test); critical value = 0.5760; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

		Geodiversity				Pedodiversity			
		S	H'_{max}	H'	J	S	H'_{max}	H'	J
Biodiversity	S	0.810**	0.785**	0.737**	0.628*	-	0.629*	0.607*	0.693*
	H'_{max}	0.882***	0.892***	0.842**	0.744**	0.630*	0.724**	0.685*	0.693*
	H'	0.918***	0.891***	0.884***	0.782**	0.720**	0.792**	0.783**	0.794**
	J	0.872***	0.825**	0.891***	0.795**	0.776**	0.814**	0.841**	0.791**
Pedodiversity	S	0.748**	0.754**	0.812**	0.811**				
	H'_{max}	0.840**	0.855***	0.890***	0.899***				
	H'	0.830**	0.820**	0.888***	0.891***				
	J	0.787**	0.726**	0.789**	0.804**				

The results of the correlation analysis between environmental variables and indices within the whole data set and within the geomorphic landform classes

are presented in Tables 3.12 – 3.18. Table 3.12 shows the significant correlations for the whole data set. Table 3.12a shows the relationships between plant species diversity indices, vegetation coverage and geomorphic variables. The table shows that the floristic variables are highly significantly correlated with landform type and elevation within the study area. With the exception of tree cover, the other floristic variables increase with an increase in elevation and landform stability. Tree cover is negatively correlated with the geomorphic variables. Plant community type is also significantly correlated with landform type and elevation. Table 3.12a shows that the coverage of herbaceous species is most significantly positively correlated with the species diversity indices.

Table 3.12b shows the significant correlations between geomorphic and floristic variables with soil/substrate properties. The table shows that landform class is significantly correlated with most of the soil/substrate characteristics. In addition, plant community type, species diversity indices and herbaceous- and bryophyte-cover are significantly correlated with the soil/substrate properties. Soil depth appears to be the most important variable in terms of relationships with the other environmental variables due to the high correlation coefficients when compared to the other results. Table 3.12b also shows that plant community type is correlated with soil/substrate particle size indices. Plant community type holds a negative relationship with the indices, with the exception of the range and heterogeneity measures. These relationships show that the mature and more stable communities occur where the substrate mix is finer, and the younger pioneer and inundation communities occur in zones

Table 3.12: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the whole data set for Tomdachoille Island SSSI. $n = 142$ (two-tail test); critical value = 0.1593; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

(a)												
	Landform	Elevation (m)	Plant community	H'	H'max	J	S	TSR	Shrub cover	Tall herb cover	Herb cover	Moss cover
Community	-0.555***	-0.452***	-0.349**									
H'	0.448***	0.352***	-0.424***	0.837***								
H'max	0.454***	0.312***	-0.424***	0.828***	0.544***							
J	0.366***	0.398***	-0.203*	0.839***	0.850***	0.535***						
S	0.411***	0.300***	-0.344***	0.850***	0.850***	0.535***	0.221**					
TSR	0.356***	-0.256**	-0.256**	0.351***	0.328***	0.225**	0.221**					
Tree cover	-0.287***	-0.327***	0.265**	-0.180*	-0.241**							-0.267**
Shrub cover	0.201*	-0.302***										
Tall herb cover	0.605***	0.408***	-0.470***	0.397***	0.454***	0.173*	0.492***					
Herb cover	0.674***	0.414***	-0.564***	0.524***	0.559***	0.258**	0.562***					0.269**
Moss cover	0.509***	0.263**	-0.455***	0.358***	0.341***	0.212*	0.313***					0.390***

(b)													
	Landform	Elevation (m)	Plant community	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover
Soil depth	0.716***	0.389***	-0.302***	0.401***	0.447***	0.180*	0.487***	0.372***			0.695***	0.671***	0.390***
pH	-0.281**	-	-	-0.313**	-0.213*	-0.318**	-0.253*		0.483***	-0.269**	-0.316**	-0.534***	-0.202*
SMC	-0.674***	-0.632***	0.543***	-0.313**	-0.213*	-0.318**	-0.253*				-0.219*		-0.288**
OMC	-0.291**	-0.206*	-	-	-	-	-						
Unvegetated gravel	-0.303***	-	0.404***	-0.189*	-0.332	0.166*	-0.327***	-0.299***					
Sand drupe	-0.423***	-0.411***	0.236**	-	-	-0.222**	-						
Leaf litter	-0.250**	-0.356***	-	-	-	-	-						
MEAN	0.301***	-0.172*	-0.172*	0.378***	-0.192*	0.299***	0.299***	0.252**			0.494***	0.358***	0.195*
MINDOM	0.385***	-0.344***	0.257**	0.571***	-	0.380***	0.319***	0.215*			0.553***	0.578***	0.294**
MAXDOM	0.388***	-0.246**	0.248**	0.568***	-	0.401***	0.377***	0.300***			0.564***	0.564***	0.299***
MODOM	0.399***	-0.243***	0.182*	0.508***	-0.190*	0.342***	0.341***	0.237**			0.568***	0.493***	0.280**
MEDOM	0.381***	-0.377***	-0.265**	-0.633***	0.192*	0.281**	0.295**	0.255**			0.527***	0.411***	0.226**
Range	-0.377***	-0.293**	-0.257**	-0.481***	-0.332***	0.192*	-0.411***	-0.339***	-0.232**		-0.565***	-0.614***	-0.303***
Heterogeneity	-0.291**	-0.306***	-	-	-	-0.370***	-	-0.296***			-0.410**	-0.478**	-0.240**
Soil/substrate class													
Large cobbles	-0.245**	-	-	-0.211*	0.200*	-0.207*	-0.270**	0.247**			-0.476***	-0.416***	-0.195*
Coarse gravel	-0.273**	-	0.308***	-0.171*	-0.284**	-	-0.312***	-0.240**			-0.463***	-0.492***	-0.257**
Medium gravel	-	-	-	-	-	-	-	-			-0.282**	-0.195*	-
Coarse sand	-0.392***	-0.306**	-	-	-	-0.203*	-	-			-0.346***	-0.352***	-0.209*
Medium sand	0.271**	0.272**	-0.193*	-	-	0.281**	0.231**	0.297***			0.191*	0.203*	0.290***
Fine sand	0.435***	0.268**	-	0.237**	-	0.281**	0.231**	0.282**			0.483***	0.385***	0.282**
Silt	0.348***	0.199*	-0.291***	0.186*	-	0.215*	0.195*	0.28**			0.429***	0.358***	0.28**
Coarse sand	0.233**	-	-	-	-	-	-	-			0.179*	0.258**	-
Medium sand	0.603***	0.311***	-0.218**	0.303***	0.294***	0.341***	0.337***	0.342***			0.542***	0.539***	0.342***
Fine sand	0.622***	0.353***	-0.235**	0.303***	0.325***	0.420**	0.420**	0.296***			0.632***	0.537***	0.296***
Silt	0.552***	0.333***	-0.236**	0.215*	0.267**	0.331***	-	0.604**			0.471***	0.471***	0.23**

with a coarser substrate matrix. The positive correlation between plant community and unvegetated gravel indicates that gravel habitats are important within floodplain landscapes for producing vegetation heterogeneity. The substrate particle size indices are correlated with the floristic diversity indices and herbaceous and bryophyte cover. The findings are therefore consistent with the hypothesis that plant community type is related to geomorphic and pedological heterogeneity within the floodplain. These relationships also support the hypothesis of Ward and Stanford (1983) which states that species diversity is related to environmental heterogeneity along rivers.

Table 3.13 shows the significant correlations within the backwater. Table 3.13a shows that the diversity indices and vegetation cover are strongly correlated with plant community type. This indicates that marked variation in species diversity and vegetation structure occurs within this landform class. In terms of vegetation cover, bryophytes and shrub species appear to be the most important species groups in producing species rich and diverse plant communities.

Table 3.13b shows that again plant community type is significantly correlated with soil depth. The substrate particle size indices are highly correlated with the floristic diversity indices and vegetation coverage. Tree and herbaceous cover are also positively correlated with soil depth, whereas bryophytes tend towards the shallower soil/substrate deposits. The results of the correlation analysis within the abandoned channel are presented in Table 3.14. Within this

Table 3.13: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the backwater on Tomdachoille Island SSSI.
 $n = 5$ (two-tail test); critical value = 0.7545; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, - = not significant.

(a)											
	Plant community	Elevation (m)	H'	H'max	J	S	TSR	Shrub cover	Tall herb cover	Herb cover	Moss cover
H'	-0.872*	-	-	-	-	-	-	-	-	-	-
H'max	-0.947**	-	0.982***	-	-	-	-	-	-	-	-
J	-0.935**	-	0.989***	0.998***	-	-	-	-	-	-	-
S	-0.785*	-	0.987***	0.942**	0.952**	-	-	-	-	-	-
TSR	-0.782*	-	0.986***	0.941**	0.950**	1.000***	-	-	-	-	-
Tree cover	-0.928**	-	0.772*	0.758*	-	-	-	-	-	-	-
Shrub cover	-	-	0.951**	0.885**	0.989***	0.989***	-	-	-	-	-
Tall herb cover	-0.869*	-	-	-	-	-	-	-	-	-	-
Herb cover	-0.877**	-	-	-	-	-	-	-	-	-	-
Moss cover	-	-1.000***	1.000***	1.000***	1.000***	1.000***	1.000***	-	-	-	-

(b)												
	Plant community	Elevation (m)	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover
Soil group	-	-	-	-	-	-	-	-	-	-	-	-
MEAN	-1.000***	-1.000***	1.000***	1.000***	1.000***	1.000***	1.000***	1.000***	-	-1.000***	-1.000***	1.000***
MINDOM	-	-1.000***	-	-	-	-	-	-	-	-	-	-
MAXDOM	-	-	-	-	-	-	-	-	-	-	-	-
MODOM	-	-	1.000***	1.000***	1.000***	1.000***	1.000***	1.000***	-	-1.000***	-1.000***	1.000***
MEDOM	-	-1.000***	1.000***	1.000***	1.000***	1.000***	1.000***	1.000***	-	-1.000***	-1.000***	1.000***
Range	-	-	-	-	-	-	-	-	-	-	-	-
Heterogeneity	-	-	-	-	-	-	-	-	-	-	-	-
Soil depth	-0.812*	-	-	-	-	-	-	0.905**	-	0.939**	0.895**	-1.000***
pH	-	-	-	-	-	-	-	-	-	-	-	-
SMC	-	1.000***	-1.000***	-1.000***	-1.000***	-1.000***	-1.000***	-1.000***	-	1.000***	1.000***	-1.000***
OMC	-	1.000***	-1.000***	-1.000***	-1.000***	-1.000***	-1.000***	-1.000***	-	1.000***	1.000***	-1.000***
Medium gravel	-	-	-	-	-	-	-	-	-	-	-	-
Fine gravel	-	-	-	-	-	-	-	-	-	-	-	-
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	-
Medium sand	-	-	-	-	-	-	-	-	-	-	-	-
Fine sand	-	-	-	-	-	-	-	-	-	-	-	-
Silt	-	-	-	-	-	-	-	-	-	-	-	-
Fine gravel	-	-	-	-	-	-	-	-	-	-	-	-
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	-
Medium sand	-	-	-	-	-	-	-	-	-	-	-	-
Fine sand	-	-	-	-	-	-	-	-	-	-	-	-
Silt	-	-	-	-	-	-	-	-	-	-	-	-

Table 3.14: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the abandoned channel on Tomdachoille Island SSSI.

$n = 15$ (two-tail test); critical value = 0.4821; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, - = not significant.

(a)

	Plant Community	Elevation (m)	H'	H'max	J	S	TSR
H'	-0.682**	-					
H'max	-0.699**	-	0.935***				
J	-0.601*	-	0.986***	0.872***			
S	-0.764***	-	0.855***	0.960***	0.767***		
TSR	-0.772***	-	0.886***	0.973***	0.804***	0.991***	
Tree cover	0.681**	-	-0.561*	-0.616**	-0.496*	-0.696**	-0.689**
Shrub cover	-	-	-	-	-	-	-
Tall herb cover	-0.660**	-	0.553*	0.605*	0.497*	0.630**	0.597*
Herb cover	-	-	0.662**	0.628**	0.666**	0.600*	0.612**
Moss cover	-0.601*	-	-	-	-	-	-

(b)

	Plant Community	Elevation (m)	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover	Soil group
Soil group	-	-	-	-	-	-	-	-	-	-	-	-	-
MEAN	-	-	-	-	-	-	-	-	-	-	-	-0.723**	0.530*
MINDOM	-	-	-	-	-	-	-	0.496*	-	-	-	-	0.737**
MAXDOM	-	-	-	-	-	-	-	-	-	-	-	-0.638*	0.713**
MODOM	-	-	-	-	-	-	-	-	-	-	-	-0.763**	0.700**
MEDOM	-	-	-	-	-	-	-	-	-	-	-	-0.719**	0.663**
Range	-	-0.493*	0.544*	0.547*	0.535*	-	-	-	-	-	-	0.631*	-0.518*
Heterogeneity	-	-	-	-	-	-	-	-	-	-	-	-	-
Soil depth	-	-	-	-	-	-	-	-	-	-	-	-	-
pH	-	-	-	-	-	-	-	-	-	-	-	-	-
SMC	0.613*	-	-	-	-	-0.583*	-0.546*	-	-	-	-	-	0.665**
OMC	-	-	-	-	-	-	-	-	-	-	-	-	-
Coarse gravel	-	-	-	-	-	-	-	-	-	-	-	-	-
Medium gravel	-	-	-	-	-	-	-	-	-	-	-	0.693*	-
Fine gravel	-	-	-	-	-	-	-	-	-	0.925**	-	-	-
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	0.658*	-
Medium sand	-	-	-	-	-	-	-	-	-	-	-	-	-
Fine sand	-	0.687**	-	-	-	-	-	-	-	-	-	-	-
Silt	-	-	-	-	-	-	-	-	-	-	-	-	-
Fine gravel	-	-	-	-	-	-	-	-	-	0.543*	-	-	-
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	-	-
Medium sand	-	-	-	-	-	-	-	-	-	-	-	-	-
Fine sand	-	-	-	-	-	-	-	-	-	-	-	-	-
Silt	-	-	-	-	-	-	-	-	-	-	-	-	-

landform species diversity indices hold strong negative correlations with plant community type, again showing that this landform supports a variety of vegetation types with differing diversity. Vegetation structure also varies within the plant communities indicated by the significant correlation between vegetation type, tree-, tall herb- and moss-cover. Tree and herbaceous cover are also strongly correlated with the diversity indices where diversity tends to decline with an increase in tree density.

Very few significant correlations were found between geomorphic and floristic variables with soil/substrate properties, shown in Table 3.14b. Elevation is negatively correlated with substrate particle size range index and positively related to the fine sand fraction as might be expected from models of floodplain sedimentology. The diversity indices H' , H'_{max} and J are all correlated with the particle size range index. Plant community type and species richness indices are correlated with the SMC, where species richness declines as SMC increases. The particle size indices are strongly correlated with moss cover where bryophyte cover increases with an increase in the finer substrate size classes. Herb cover holds a strong positive correlation with the presence of medium gravel, with taller herbaceous species being correlated with the presence of silt deposits.

Significant correlations within the point bar landform are presented in Table 3.15. Elevation is shown to hold a strong negative correlation with tree cover in Table 3.15a. Elevation is positively correlated with the equitability index J . This suggests that diversity in terms of evenness is greater within the more

Table 3.15: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the point bar landform on Tomdachoille Island SSSI. $n = 40$ (two-tail test); critical value = 0.3044; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

a)

	Elevation (m)	Plant community	H'	H'max	J	S	TSR
Plant community	-	-	-	-	-	-	-
H'	-	-	-	-	-	-	-
H'max	-	-	-	-	-	-	-
J	0.433***	0.320*	0.746***	-	-	-	-
S	-	-	0.832***	0.830***	0.416*	-	-
TSR	-	-	0.756***	0.831***	0.911***	-	-
Tree cover	-0.659***	-	-0.585***	-	-0.775***	-0.340*	-
Shrub cover	-	-	0.352*	-	-	-	0.341*
Tall herb cover	-	-0.642***	0.380*	0.452***	-	0.606***	0.586***
Herb cover	-	-0.376*	0.439***	0.460***	-	0.532***	0.481***
Moss cover	-	-0.349*	0.356*	0.359*	-	0.429***	0.575***

b)

	Elevation (m)	Plant community	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover	Soil group cover
Soil group	-0.584***	-	-	0.539***	-	0.469**	0.535***	-	-	0.421**	0.313*	0.369*	-
Soil depth	-0.399**	-0.324*	-	0.443***	-	0.380*	0.440**	-	-	0.406**	-	0.318*	0.805***
pH	-	-	-	-	-	-	-	-	-	-	-	-	-
SMC	-	-	-	-	-	-	-	0.825**	-	-	-	-	-
OMC	-	-	-	-	-	-	-	-	-	-	-	-	0.664*
Leaf litter	-0.606***	-	-	0.357*	-	-	-	-	0.335*	-	-	-	-
MEAN	-0.408*	-0.565***	-	-	-	-	-	-	-	-	-	-	0.649***
MINDOM	-0.490**	-0.427**	-	0.527**	-	0.469**	0.494**	0.343*	-	0.453**	-	0.383*	0.432**
MAXDOM	-0.579***	-0.407*	-	0.551***	-	0.418**	0.470**	0.413**	-	0.442*	0.328*	0.397*	0.720***
MODOM	-0.513**	-0.432**	-	0.495**	-	0.360*	0.407*	0.334*	-	0.401*	0.331*	0.359*	0.905***
MEDOM	-0.550***	-0.321*	-	0.433**	-	0.350*	0.350*	0.402*	-	0.346*	0.334*	0.738***	0.836***
Range	0.582***	0.452**	-	-0.605***	-	-0.457**	-0.518**	-0.388*	-	-0.530**	-0.455**	-0.360*	0.738***
Heterogeneity	-	-	-	-	-	-	-	-	-0.394*	-0.325*	-0.424**	-	-0.696***
Boulders	0.498**	-	-	-	-	-	-	-	-	-	-	-	-0.503**
Large cobbles	0.496**	0.403**	-	-	0.432**	-	-0.306*	-0.474**	-	-0.390*	-	-	-0.623***
Small cobbles	0.322*	0.446**	-	-	0.351*	-	-0.311*	-0.403**	-	-0.359*	-	-	-0.418**
Coarse gravel	-	0.556***	-	-	-0.331*	-	-0.371*	-	-	-0.415**	-0.362*	-0.339*	-0.633***
Medium gravel	-	-	-	-	-	-	-	-	-	-	-0.372*	-	-0.408**
Fine gravel	-	-	-	-	-	0.320*	-	-	0.324*	-	-	0.501**	0.412**
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	0.321*	-
Medium sand	-	-	-	-	-	-	-	-	-	-	-	-	-
Fine sand	-	-	-	-	-	-	-	-	-	-	-	-	-
Silt	-0.399**	-	-	-	-	-	-	0.365*	-	0.388*	-	-	0.460**
													0.587***

elevated areas of this landform, which also have less tree cover. This is supported by the strong negative correlation between tree cover and J. The coverage of the herbaceous and bryophyte species and the evenness of distribution (J) are significantly correlated with plant community type. The amount of herbaceous and bryophyte cover are also positively related to the diversity indices.

Table 3.15b shows that elevation and plant community type are significantly correlated with many of the soil/substrate characteristics. The substrate particle size indices, soil depth and soil/substrate group have significant correlations with the vegetation and elevation variables. Variations in elevation within this landform are related to soil/substrate class heterogeneity. The biodiversity indices also show relationships with the soil/substrate type.

Significant correlations within the abandoned point bar landform are presented in Table 3.16. Significant correlations are found between evenness (J), tree cover, elevation and plant community type (Table 3.16a). Tree cover increases with a decrease in elevation. An increase in tree cover is correlated with a decline in the equitability index. Elevation is positively correlated with the diversity indices H' and J and with shrub cover. Shrub cover holds a positive relationship with the evenness index however species richness (S) tends to decrease with an increase in shrub species.

Few significant correlations were found between vegetation characteristics, elevation and soil/substrate properties, shown in Table 3.16b. The

Table 3.16: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the abandoned point bar on Tomdachoille Island SSSI.
 $n = 17$ (two-tail test), critical value = 0.4555; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, - = not significant.

(a)										
	Elevation (m)	Plant community	H'	H'max	J	S	TSR			
Plant community	-0.537*									
H'	0.509*									
H'max	-	0.608**								
J	0.614**	-0.550*	0.825***							
S	-	0.569*	0.898***	-						
TSR	-	0.586**	0.964***	-	0.863***					
Tree cover	-0.535*	0.569***	-	-0.578*	-	0.508*				
Shrub cover	0.483*	-	-	0.533*	-0.502*	-				
Tall herb cover	-	-	-	-	-	-				
Herb cover	-	-	-	-	-	-				
Moss cover	-	-	-	-	-	-				

(b)													
	Elevation (m)	Plant community	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover	Soil group
Soil group	-	0.588**	-	-	-	-	-	0.659**	-	-	-	-	-
MEAN	-	-	-	-	-	-	-	-	-	-	-	-	-
MINDOM	-	-	-	-	-	-	-	-	-	-	0.655**	-	0.840***
MAXDOM	-	0.561*	-	-	-	-	-	0.569*	-	-	-	-	0.708**
MODOM	-	0.519*	-	-	-	-	-	0.654**	-	-	-	-	0.623**
MEDOM	-	-	-	-	-	-	-	0.590*	-	-	-	-	0.483*
Range	-	-	-	-	-	-	-	-	-	-	-	-	-
Heterogeneity	-	-	-	-	-	-	-	-	-	-	-	-	-
Soil depth	-	-	-	-	-	-	-	-	0.482*	0.594**	0.576*	-	-
pH	-	-	-	-	-	-	-	-	-	-	-	-	-
SMC	-	-	-	-	-	-	-	-	-	-	-	-	-
OMC	-	-	-	-	-	0.544*	-	-	-	-	-	-	-
Boulder	-	-	-	-	-	-	-	-	-	-	-	-	-
Small cobble	-	-	-	-	-	-	-	-	-	-	0.961*	-	-
Medium gravel	-	-	-	-	-	-	-	-	-	-	-0.602**	-	-
Fine gravel	-	-	0.484*	-	0.495*	-	-	-	-	-	-	-	-
Coarse sand	-	-	-	-	0.600**	0.524*	-	-	-	-	-	-	-
Medium sand	-	-	0.521*	-	0.486*	0.470*	-	-	-	-	-	-	-
Fine sand	-	-	0.560*	-	0.484*	0.459*	-	-	-	-	-	-	-
Silt	-	-	-	-	-	-	-	-	-	-	-	-	-

soil/substrate class and particle size indices are correlated with plant community type. Tree cover is notably correlated with the particle size indices. Shrub and herbaceous cover are positively related to soil depth. Species richness tends to increase where there is greater OMC and finer substrate particle size classes. H'_{max} is positively correlated with the finer substrate.

Table 3.17 shows the significant correlations within the floodplain. Few significant correlations were found between elevation and the variables tested. This landform supports a variety of plant communities and the diversity indices of these communities show considerable variation indicated by the highly significant correlations between the diversity indices and vegetation type. Species diversity is shown to hold a positive relationship with tree cover.

Table 3.17b shows that soil/substrate class, soil depth and particle size indices are strongly correlated with vegetation type. These variables are also strongly correlated to the floristic diversity indices. The negative correlation between tree cover and the particle size index 'range' and 'heterogeneity' suggest that tree cover is greater on the more developed and more sorted soil profiles within this landform.

The results of the correlation analysis within the remnant of the former embankment are presented in Table 3.18. Overall very few significant correlations were found. Table 3.18a shows that shrub cover holds a strong negative correlation with the species diversity indices. Species richness tends

Table 3.17: Significant Pearson correlations ($p < 0.05$) between indices and environmental variables within the floodplain landform on Tomdachoille Island SSSI.

$n = 53$ (two-tail test); critical value = 0.2732; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

		Plant community	Elevation (m)	H'	H'max	J	S	TSR				
		H'	-	-	-	-	-	-				
		H'max	-	0.843***	-	-	-	-				
		J	-	0.917***	0.569***	-	-	-				
		S	-	0.795***	0.955***	0.514***	-	-				
		TSR	-	0.490*	-0.294*	-	-0.402**	-				
		Tree cover	-	0.533***	0.563***	0.387**	0.588***	-0.452**				
		Shrub cover	-	-	-	-	-	-				
		Tall herb cover	-	0.305*	-	-0.324*	0.306*	-0.832***				
		Herb cover	-	-	0.283*	-	0.397**	-0.363**				
		Moss cover	-	-	-0.273*	-	-	-				

		Plant community	Elevation (m)	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover
Topsoil	Soil group	-0.538***	-	-0.451**	-0.393**	-0.382**	-0.479***	-	-0.397**	-	-	-0.366**	-
	MEAN	0.419**	-	0.283*	0.368**	-	0.395**	-	-	-	-	-	-
	MINDOM	-	-	-	-	-	-	-	-	-	-	-	-
	MAXDOM	0.508***	-	0.420**	0.353**	0.384**	0.344*	-	0.383**	-0.273*	-	-	-
	MODOM	-	-	-	-	-	-	-	-	-	-	-	-
	MEDOM	-	-	-	-	-	-	-	-	-	0.294*	-	-
	Range	-0.653***	-	-0.493***	-0.448**	-0.410**	-0.460***	-	-0.433**	0.383*	-	-	-
	Heterogeneity	-0.502***	-	-0.405**	-0.335*	-0.375**	-0.331*	-0.489*	-0.376**	0.288*	-	-	-
	Soil depth	0.524***	-	0.460***	0.440**	0.374**	0.513***	-	0.328*	-	-	0.353**	-
	pH	-	-	-	-	-	-	-	-	-0.360**	-	-	-
	SMC	-	-	-	-	-	-	-	-	-	-	-	-
	OMC	-	-	-	-	-	-	-	-	-	-0.369**	-	-
	Fine gravel	-	-	-0.270*	-	-	-	-0.268*	-	-	-	-	-
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	-	
Medium sand	-	-	-	-	-	-	-0.349**	0.305*	-	-	-	-	
Fine sand	-	-	-	-	-	-	-	0.281*	-	-	-	-	
Silt	-	-	-	-	-	-	-	-	-	-	-	-	
Medium gravel	-	-	-	-	-	-	-	-	-	-	-	-	
Fine gravel	-	-	-0.428**	-	-0.290*	-0.449**	-	-	-	-	-	-	
Coarse sand	-	-	-	-	-	-	-	-	-	-	-	-	
Medium sand	-	-	-	-	-	-	-	0.303*	-	-	-	-	
Fine sand	0.288*	-	-	-	0.395**	-	0.445**	-0.384**	0.308*	-	-0.426**	0.331*	
Silt	-	-	-	-	-	-	-	-0.302*	-	0.414**	-	-	

Table 3.18: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the embankment on Tomdachoille Island SSSI. $n = 2$ (two-tail test); critical value = 0.9500; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, - = not significant.

(a)									
	Plant community	Elevation (m)	H'	H'max	J	S	TSR	Herb cover	TSR
	H'	-	-	-	-	-	-	-	-
	H'max	-	0.993**	-	-	-	-	-	-
	J	-	-	-	-	-	-	-	-
	S	-	0.994**	-	-	-	-	-	-
	TSR	-	-	-	-	-	-	-	-
	Tree cover	-	-	-	-	-	-	-	-
	Shrub cover	-	-0.998**	-0.996**	-	-0.998**	-	-	-
	Tall herb cover	-	-	-	-	-	-	-	-
	Herb cover	-	-	-	-	-	-	-	-
	Moss cover	-	-	-	-	-	-	-	0.958*

(b)													
	Plant community	Elevation (m)	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover	Soil group
	Soil group	-	-	-	-	-	-	-	-	-	-	-	-
	MEAN	-0.996**	-	-	-	-	-	-	-	-	-	-	-
	MINDOM	-	-	-	-	-	-	-	-	-	-	-	-
	MAXDOM	-0.981*	-	-	-	-	-	-	-	-	-	-	-
	MODOM	-	-	-	-	-	-	-	-	-	-	-	-
	MEDOM	-	-	-	-	-	-	-	-	-	-	-	-
	Range	-	-	-	-	-	-	-	-	-	-	-	-
	Heterogeneity	0.981*	-	-	-	-	-	-	-	-	-	-	-
	Soil depth	-	-	-	-	-	-	-	-	-	-	-	-
	pH	-	0.978*	0.995**	-	0.969*	-	-	-0.982*	-	-	-	0.962*
	SMC	-	-	-	-	-	-	-	-	-	-	-	-
	OMC	-	-	-	-	-	-	-	-	-	-	-	-
	Medium gravel	-	-	-	-	-	-	-	-	-	-	-	-
	Fine gravel	-	-	-	-	-	-	-	-	-	-	-	-
	Coarse sand	-	-	-	-	-	-	-	-	-	-	-	-
	Medium sand	-	-	-	-	-	-	-	-	-	-	-	-
	Fine sand	-	-	-	-	-	-	-	-	-	-	-	-
	Silt	-	-	-	-	-	-	-	-	-	-	-	-
	Fine gravel	-	-	-	-	-	-	-	-	-	-	-	-
	Coarse sand	-	-	-	-	-	-	-	-	-	0.970*	-	-
	Medium sand	-	-	-	-	-	-	-	-	-	0.951*	-	-
	Fine sand	-	-	-	-	-	-	-	-	-	-	-	-
	Silt	-	-	-	-	-	-	-	-	-	-	-	-

to increase where there is greater herb cover indicated by the positive correlation between TSR and herb cover. The most notable correlation in Table 3.18b is between soil pH and the diversity indices and soil pH and shrub cover. Diversity increases as the soil becomes more alkaline. Shrub cover tends to be more dense in the more acidic zones.

3.3.8b. Regression

The results for the best subsets regression analysis for the whole data set are given in Appendix 9. The strongest regression models from the analysis are presented in Table 3.19. The analysis shows that the Shannon indices H' and J can be modelled from the environmental variables recorded. The results show that 72.1% of the variation in H' can be explained by the independent variables in the model. The relationship between J and the independent variables is stronger, explaining 85.4% of the variation. The weakest of these models selected is for herb cover. The model suggests that herb cover is determined by geomorphic and pedological variables within the study area. Table 3.19 shows that soil type is strongly explained by soil depth and particle size range.

Regression equations including 26 independent variables explained 62.4-100% of the variation in environmental variables within six landform classes. The regression models derived from each landform class are presented in Tables 3.20 – 3.25 and the best subsets results are given in Appendix 9. Table 3.20 shows the regression model for the backwater. This shows that plant

Table 3.19: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the whole data set.

	Intercept	Land-form	Elevation (m)	Plant community	S	H'	Tree cover	Herb cover	Moss cover	Soil group	Soil depth	pH	MOD-OM	MED-OM	Range	R^2 (%)
H'	0.455		0.0628	0.0015	0.0542			0.0002	0.0029							72.1
J	0.206		0.0078	0.01	-0.0060	0.275	-0.0009	-0.0001					-0.0128	0.0142		85.4
Shrub cover	74.8	1.4										-14.1				96.5
Herb cover	46.7	9.26	3.03							-4.74			-2.18		-0.319	64.9
Soil group	6.11										-0.0251				0.0364	99.8

community development within this landform strongly responds to species richness, tree cover and the degree of soil profile development. Within the abandoned channel there are seven strong regression models (Table 3.21). The models show that plant community diversity indices and floristic variables can be predicted from vegetation characteristics and soil profile depth. Table 3.22 shows six regression models whereby vegetation diversity can be estimated with relatively high confidence using vegetation cover characteristics and particle size indices within the point bar landform. In addition moss cover, which is important in accelerating primary succession within these habitats, can be predicted using particle size characteristics with 90.1% confidence. The substrate class can also be predicted with reasonable accuracy using particle size indices.

Table 3.20: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the backwater.

	Intercept	S	Tree cover	Soil depth	R^2 (%)
Plant community	13.1	-0.0530	-0.0182	-0.0524	100

Within the abandoned point bar landform (Table 3.23), six dependent variables can be modelled with relatively high accuracy. Vegetation characteristics and particle size indices are key variables for prediction with elevation also playing a role in the development of the vegetation. Table 3.24 shows regression models for dependent variables within the floodplain landform. Soil profile characteristics are key predictor variables for species richness. This indicates that the degree of soil development is important in the development of the plant communities supported within this landform. Table 3.25 shows that vegetation structure and abundance, soil type and soil acidity are key predictor variables for plant community diversity within the remnants of the

Table 3.21: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the abandoned channel landform.

	Intercept	S	H'max	Tree cover	Shrub cover	Tall herb cover	Soil depth	R^2 (%)
Plant community	1.18	-0.0930	1.34	0.0663		-0.0526		80.7
S	2.27				3.28			97.7
H	0.205				0.244			80.1
J	0.0039	-0.0039		0.0051	0.0633			100
Tree cover	6.97						2.92	81.9
Tall herb cover	4.02						2.54	88.1
Herb cover	15.7						1.17	80.1

Table 3.22: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the point bar landform.

	Intercept	Plant community	J	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover	Mean	MAX-DOM	MOD-OM	MED-OM	Range	CG	R^2 (%)
Plant community	10.4		4.99			-0.0784		-0.1060	-0.3970	1.09	-0.2170			0.067	76.7
S	35.4	-1.23			-0.0305		0.0985								68.3
H'	0.126			0.129			0.0049						0.001		82.7
J	0.198			0.0262			0.0017						4E-04		72.6
Moss cover	1.18											1.15	-0.203	1.83	90.1
Soil group	5.75								-0.881			1.22	-0.0203		81.9

CG = coarse gravel

Table 3.23: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the abandoned point bar landform.

	Intercept	Elevation (m)	Plant community	S	H'	J	Tree cover	Tall herb cover	Soil group	Soil depth	SMC	MAX-DOM	MIN-DOM	MOD-OM	Range	R^2 (%)
Plant community	4.75	-0.6470					0.0725					0.285				78.9
S	16.2						-0.1050	0.0812	1.39				1.17	-0.961		66.5
H'	-0.831			0.0694		1.7		-0.0025								88.9
J	0.543		0.0085	-0.0107	0.225		-0.0025									80.4
Tree cover	3.9	-13.4														85.5
Soil group	6.25									-0.0369	0.0424				0.032	82.3

Table 3.24: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the floodplain landform.

	Intercept	S	H'	J	Tree cover	Shrub cover	Soil depth	OMC	MOD-OM	SC	FG	R^2 (%)
Plant community	6.09	-0.0953	5.85	-18.1	0.0176	-0.0265	0.0089					82.5
S	23.4					-0.1680		1.76			0.319	65.4
Soil group	5.68				0.0135				0.084	-0.1490		82.3

SC = small cobble
 FG = fine gravel

Table 3.25: Regression equations for the models with the highest degrees of explanation ($R^2 > 60\%$) within the embankment landform.

	Intercept	S	Tree cover	Shrub cover	Tall herb cover	Soil group	pH	R^2 (%)
S	67.0			-0.4000			-5.0	99.8
H'	1.33	0.0375						98.7
J	0.846	0.0041	0.0009		-0.0019	-0.0293		62.4

embankment. Very strong models are produced for estimating species richness and H'.

3.3.9. ANOVA

The ANOVA results for differences in mean values of environmental variables between the landform classes are presented in Table 3.26. The results show that the means for every variable with the exception of OMC are significantly different between the landforms. All values are significant at $p < 0.001$ level except for pH which is significant at $p < 0.01$. Therefore the null hypothesis of equal means can be rejected with confidence and the alternative hypothesis stating that the mean value of properties between landform type are significantly different.

The graphs in Figure 3.14 show how the mean values of the environmental variables differ between landforms. The graphs show that there is an overall increase in each of the variable mean values with an increase in landform class. This indicates that greater diversity exists along an aquatic-to-terrestrial

Table 3.26: Results of analysis of variance (ANOVA) of environmental variables between the landform classes on Tomdachoille Island SSSI.

a) Elevation

	Sum of Squares	df	Mean Square	F	p
Between groups	71.58	5	14.315	22.405	0.000
Within groups	88.17	138	0.639		
Total	159.75	143			

b) H'

	Sum of Squares	df	Mean Square	F	p
Between groups	18.64	5	3.728	9.508	0.000
Within groups	54.11	138	0.392		
Total	72.75	143			

c) H'max

	Sum of Squares	df	Mean Square	F	p
Between groups	32.95	5	6.589	19.439	0.000
Within groups	46.78	138	0.339		
Total	79.73	143			

d) J

	Sum of Squares	df	Mean Square	F	p
Between groups	1.34	5	0.267	10.145	0.000
Within groups	3.63	138	2.63E-02		
Total	4.97	143			

e) S

	Sum of Squares	df	Mean Square	F	p
Between groups	4349.12	5	869.824	11.205	0.000
Within groups	10712.44	138	77.626		
Total	15061.56	143			

f) TSR

	Sum of Squares	df	Mean Square	F	p
Between groups	8765.3	5	1753.061	8.099	0.000
Within groups	29871.64	138	216.461		
Total	38636.94	143			

g) Tree cover

	Sum of Squares	df	Mean Square	F	p
Between groups	45093.71	5	9018.742	9.007	0.000
Within groups	138172.73	138	1001.252		
Total	183266.44	143			

h) Shrub cover

	Sum of Squares	df	Mean Square	F	p
Between groups	8438.53	5	1687.706	9.783	0.000
Within groups	23807.22	138	172.516		
Total	32245.75	143			

i) Tall herb cover

	Sum of Squares	df	Mean Square	F	p
Between groups	114851.19	5	22970.237	28.901	0.000
Within groups	109679.31	138	794.778		
Total	224530.49	143			

j) Herb cover

	Sum of Squares	df	Mean Square	F	p
Between groups	94257.96	5	18851.591	50.053	0.000
Within groups	51975.79	138	376.636		
Total	146233.75	143			

k) Moss cover

	Sum of Squares	df	Mean Square	F	p
Between groups	22891.57	5	4578.315	14.365	0.000
Within groups	43982.4	138	318.713		
Total	66873.97	143			

l) Soil group

	Sum of Squares	df	Mean Square	F	p
Between groups	217.58	5	43.516	12.198	0.000
Within groups	492.31	138	3.567		
Total	709.89	143			

m) Soil depth

	Sum of Squares	df	Mean Square	F	p
Between groups	197852.01	5	39570.401	83.435	0.000
Within groups	65448.41	138	474.264		
Total	263300.42	143			

n) pH

	Sum of Squares	df	Mean Square	F	p
Between groups	1.51	5	0.301	4.063	0.002
Within groups	7.11	96	7.41E-02		
Total	8.62	101			

o) SMC%

	Sum of Squares	df	Mean Square	F	p
Between groups	15217.88	5	3043.575	30.428	0.000
Within groups	9402.25	94	100.024		
Total	24620.12	99			

p) OMC

	Sum of Squares	df	Mean Square	F	p
Between groups	57.81	5	11.562	1.981	0.088
Within groups	548.51	94	5.835		
Total	606.32	99			

q) MEAN

	Sum of Squares	df	Mean Square	F	p
Between groups	326.02	5	65.204	19.547	0.000
Within groups	430.31	129	3.336		
Total	756.33	134			

r) MINDOM

	Sum of Squares	df	Mean Square	F	p
Between groups	527.87	5	105.574	19.228	0.000
Within groups	708.28	129	5.491		
Total	1236.15	134			

s) MAXDOM

	Sum of Squares	df	Mean Square	F	p
Between groups	483.85	5	96.77	31.374	0.000
Within groups	397.89	129	3.084		
Total	881.73	134			

t) MODOM

	Sum of Squares	df	Mean Square	F	p
Between groups	1075.62	5	215.123	24.567	0.000
Within groups	1129.6	129	8.757		
Total	2205.22	134			

u) MEDOM

	Sum of Squares	df	Mean Square	F	p
Between groups	285.06	5	57.014	21.297	0.000
Within groups	345.34	129	2.677		
Total	630.41	134			

v) Range

	Sum of Squares	df	Mean Square	F	p
Between groups	599929.76	5	119985.953	24.076	0.000
Within groups	642899.16	129	4983.714		
Total	1242828.93	134			

w) Heterogeneity

	Sum of Squares	df	Mean Square	F	p
Between groups	271	5	54.2	11.925	0.000
Within groups	586.3	129	4.545		
Total	857.3	134			

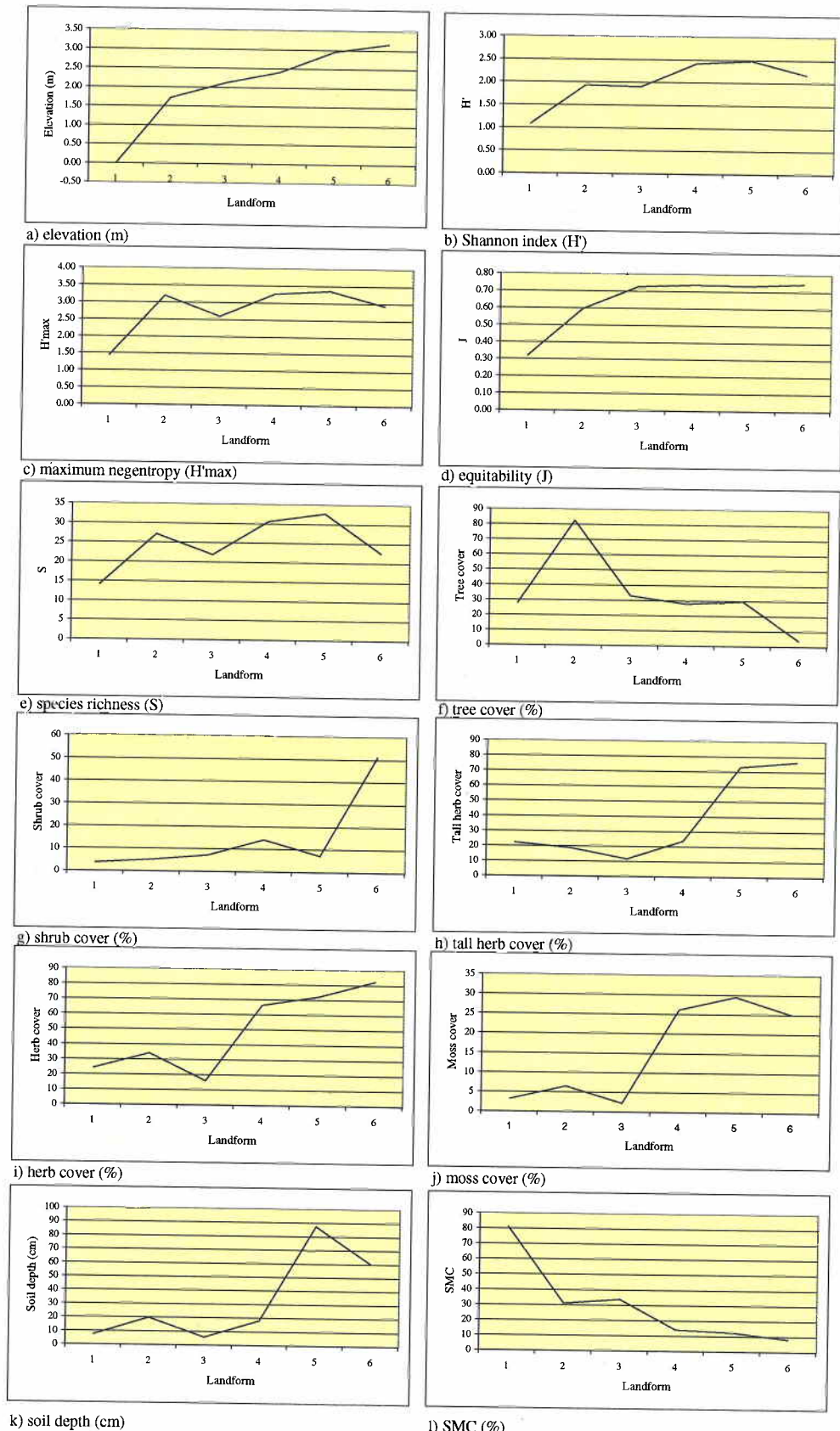


Figure 3.14: Variation in mean values of environmental variables within the landform classes on Tomdachoille Island SSSI.

gradient created by the landforms. In contrast, tree cover and soil moisture content decrease dramatically between the landform classes.

3.3.10. Spatial variance analysis- geostatistics

3.3.10a. Semivariance and spatial dependence

The results of semivariance analysis between significantly correlated floristic and pedological indices and elevation for the whole data set are presented in Table 3.27. Semivariograms for elevation and biodiversity indices are presented in Figure 3.15 and semivariograms of the pedological properties are given in Figure 3.16.

The elevation semivariogram shows strong non-stationarity within the data by the decline in semivariance once *sill variance* is achieved. This shows distinct groupings of topographic features the study area. Semivariance analysis for biodiversity indices produced strong models with a good fit illustrated in Figure 3.15c-j. The isotropic models are stronger than the anisotropic models. The anisotropic models indicating that spatial patterns vary along different orientations within the study area are elevation, H'_{\max} and J. Table 3.27a shows the strength of these models by the high R^2 and low RSS values. The model for elevation is considerably weaker than the other semivariance models. The range of spatial dependence shows that the scale of variation for elevation and diversity indices is relatively small. The range for species richness approximates with that of elevation. H' and J show smaller scales of

Table 3.27: Nugget, sill, range, regression coefficient (R^2) and reduced sum of squares (RSS) for the isotropic (a) and anisotropic (b) semivariogram models computed using the whole data set from Tomdachoille Island SSSI.

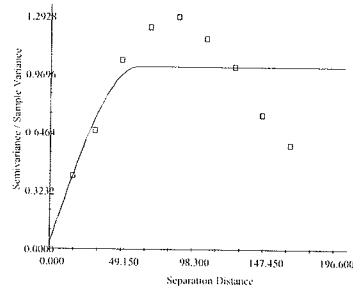
* = log normal transformation; active lag = 196.66; uniform interval = 19.66.

a)

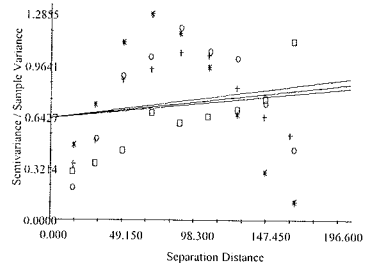
Variable	Model	Nugget variance	Sill variance	Range (m)	R^2	RSS
Elevation (m) *	Spherical	0.007	1.054	69.00	0.64	0.268
S	Spherical	0.200	1.00	70.20	0.97	0.010
H'_{\max}	Exponential	0.460	1.186	176.70	0.87	0.040
H'	Spherical	0.183	1.012	45.50	0.83	0.032
J	Spherical	0.137	1.024	52.30	0.82	0.050
Soil depth *	Spherical	0.383	1.237	156.50	0.99	0.008
SMC *	Spherical	0.171	0.997	33.10	0.45	0.091
MEAN	Spherical	0.525	1.109	121.70	0.97	0.007
MINDOM	Spherical	0.526	1.108	115.60	0.97	0.009
MAXDOM	Exponential	0.312	1.225	168.90	0.99	0.003
MODOM	Spherical	0.442	1.076	9.70	0.96	0.010
MEDOM	Spherical	0.538	1.077	104.50	0.97	0.007
Range	Exponential	0.292	1.180	144.60	1.00	0.001
Heterogeneity	Exponential	0.466	1.054	79.20	0.97	0.003

b)

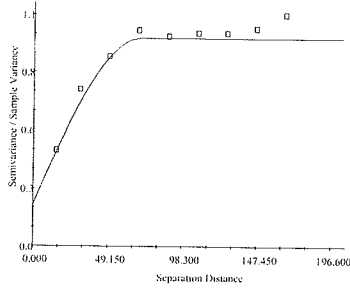
Variable	Model	Nugget variance	Sill variance	Major range (m)	Minor range (m)	R^2	RSS
Elevation (m) *	Spherical	0.001	1.521	107.30	107.40	0.48	7.620
S	Spherical	0.00	1.400	140.50	140.60	0.70	3.004
H'_{\max}	Spherical	0.641	2.600	442.00	1089.00	0.71	1.773
H'	Exponential	0.001	1.420	151.56	205.41	0.43	3.034
J	Spherical	0.639	3.434	585.00	2200.00	0.44	2.513
Soil depth *	Exponential	0.396	1.996	517.50	608.10	0.74	1.189
SMC *	Exponential	0.830	2.319	738.00	7059.00	0.42	1.356
MEAN	Exponential	0.623	2.112	873.30	1046.10	0.69	0.815
MINDOM	Spherical	0.631	2.464	389.00	1046.00	0.74	1.222
MAXDOM	Spherical	0.550	2.285	411.90	683.80	0.68	0.952
MODOM	Spherical	0.680	2.126	491.70	836.20	0.60	1.152
MEDOM	Exponential	0.001	1.349	154.56	157.44	0.65	1.564
Range	Spherical	0.551	2.814	390.00	1205.00	0.66	1.399
Heterogeneity	Spherical	0.716	3.117	487.00	2602.00	0.52	1.955



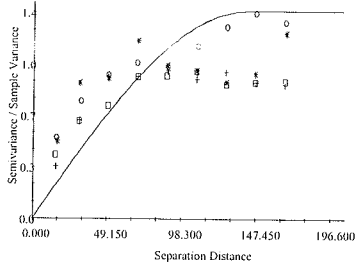
a) Elevation - isotropic



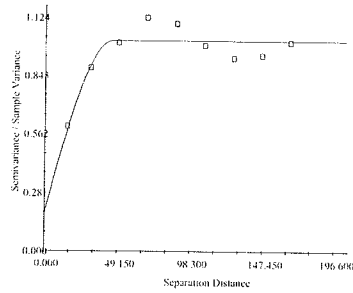
b) Elevation - anisotropic



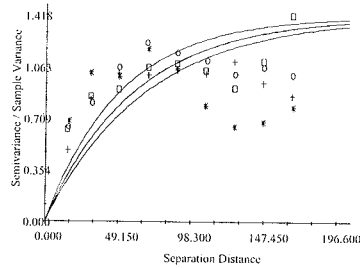
c) S (species richness) - isotropic



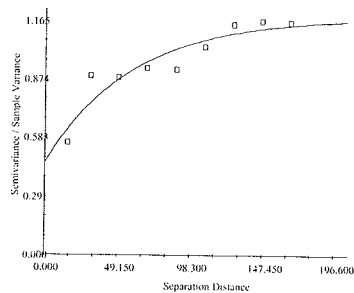
d) S (species richness) - anisotropic



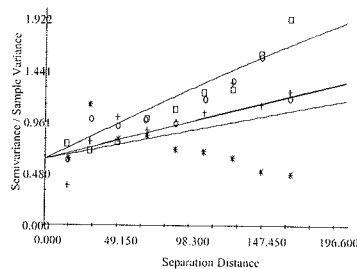
e) H' (Shannon index) - isotropic



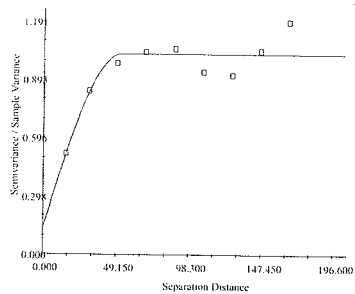
f) H' (Shannon index) - anisotropic



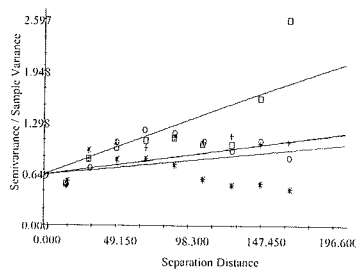
g) H'max (maximum negentropy) - isotropic



h) H'max (maximum negentropy) - anisotropic

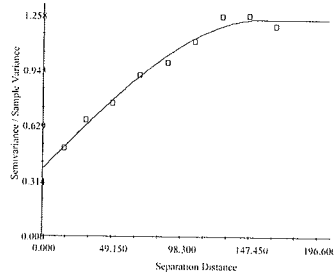


i) J (Equitability index) - isotropic

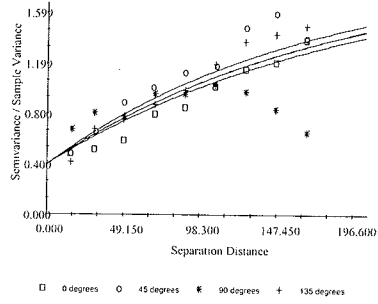


j) J (Equitability index) - anisotropic

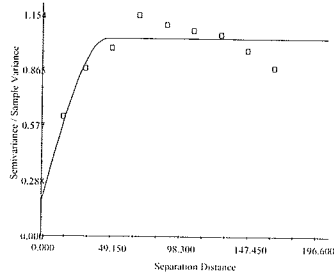
Figure 3.15: Isotropic and anisotropic semivariograms for elevation and biodiversity indices holding a significant correlation with elevation on Toi Separation distance (m).



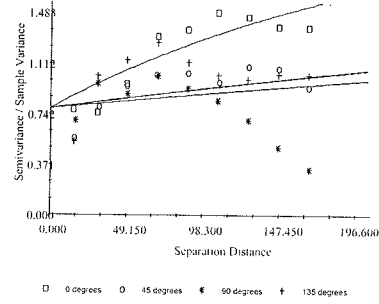
a) Soil depth (cm) - isotropic



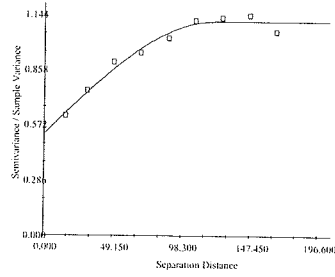
b) Soil depth (cm) - anisotropic



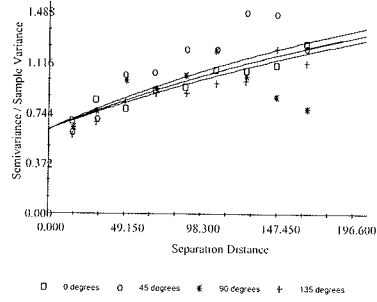
c) SMC (%) - isotropic



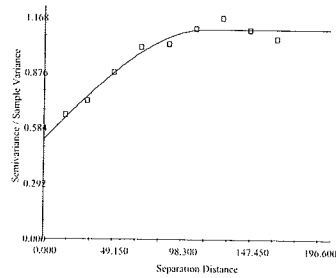
d) SMC (%) - anisotropic



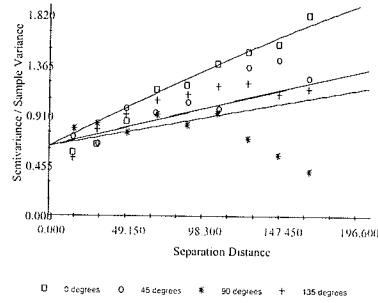
e) MEAN - isotropic



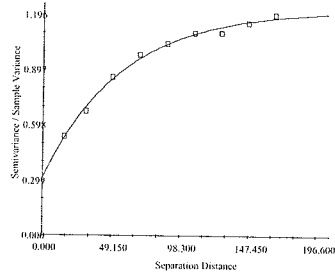
f) MEAN - anisotropic



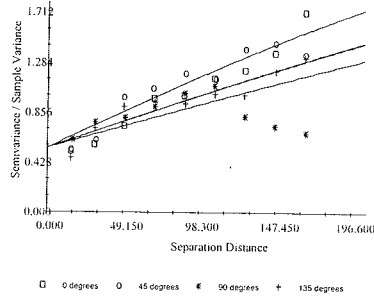
g) MINDOM - isotropic



h) MINDOM - anisotropic



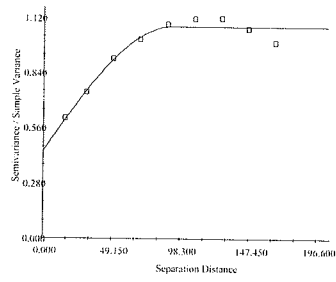
i) MAXDOM - isotropic



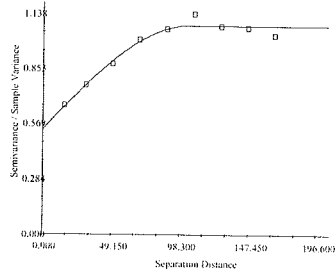
j) MAXDOM - anisotropic

Figure 3.16: Isotropic and anisotropic semivariograms for pedological variables and indices holding a significant correlation with biodivers Island SSSI. Separation distance (m).

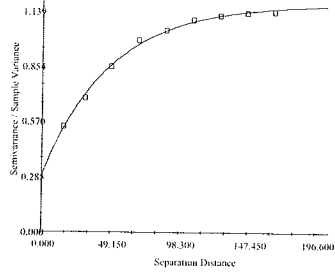
Continued overleaf



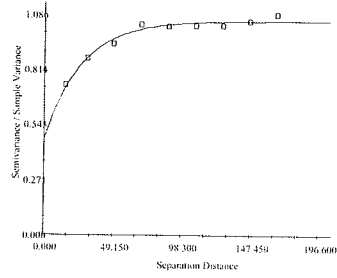
k) MODOM - isotropic



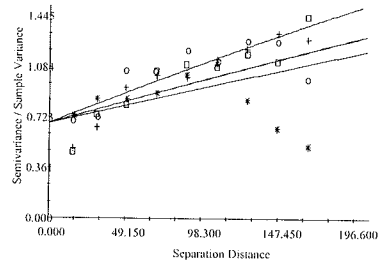
m) MEDOM - isotropic



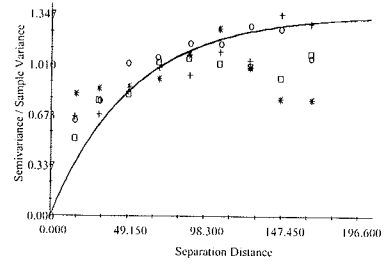
o) Range - isotropic



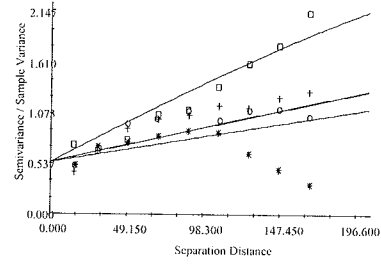
q) Heterogeneity - isotropic
Continued from previous page.



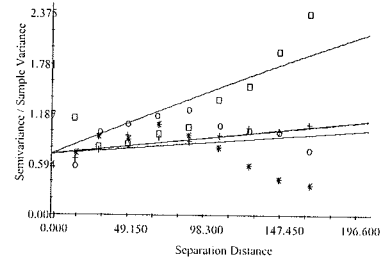
j) MODOM - anisotropic



n) MEDOM - anisotropic



p) Range - anisotropic



r) Heterogeneity - anisotropic

spatial dependence in comparison to elevation. H'_{\max} shows a considerably higher scale of spatial dependence within the study area. *Nugget variance* is low for these variables indicating little localised variation in the property about the sample point. This gives greater confidence in the kriging results as less spatial variation needs to be accounted for in the calculations. *Sill variance* is achieved at similar scales of semivariance for the biodiversity and elevation variables.

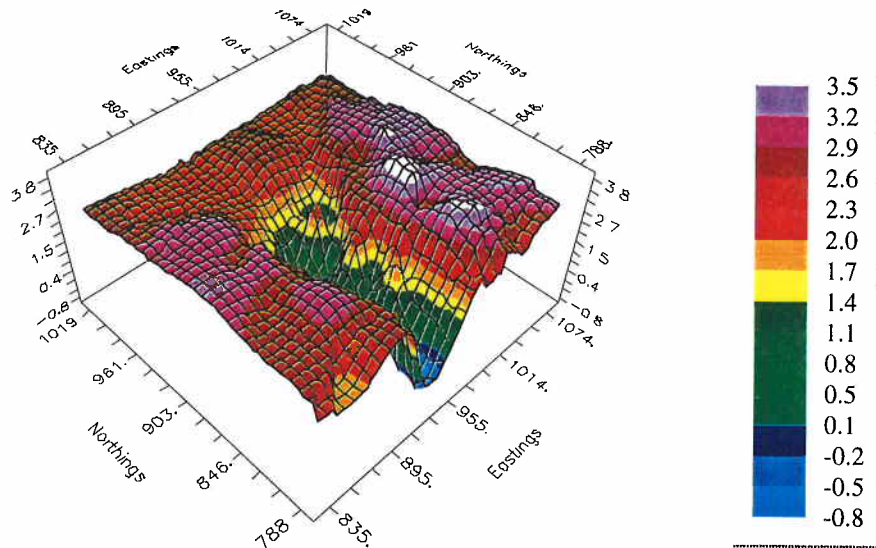
The anisotropic models for biodiversity and elevation are weaker, shown by lower R^2 and higher RSS values in Table 3.27b. The models showing distinct anisotropy are elevation, H' , H'_{\max} and J. The range of spatial dependence of H' and J varies considerably along different orientations across the study area. *Nugget variance* is generally very low for anisotropic analysis of biodiversity and elevation. Similar levels of *sill variance* occur between elevation, and H' .

Previous correlation analysis showed that soil properties are significantly correlated with biodiversity indices. These results address the second hypothesis posed for geostatistical analysis that biodiversity responds to pedo-variation within floodplain environments. Figure 3.16 and Table 2.37a show that very strong isotropic semivariogram models are fitted to the pedological variables, indicated by the high R^2 and low RSS values. The range of spatial dependence of soil properties is generally higher than for geomorphic and biodiversity properties. Where the range is notably greater, the *sill variance* is also higher than for elevation and biodiversity indices. A degree of congruence exists between particle size heterogeneity and the biodiversity indices.

The anisotropic semivariograms in Figure 3.16d, f, h, j, l, p and r show that semivariance of the given property varies along different orientations within the study area. This is supported in Table 3.27b where these variables have large contrasts in the major and minor range of spatial dependence. *Nugget variance* for anisotropic pedological properties is relatively low. *Sill variance* is generally higher than for the biodiversity indices. Congruence occurs between anisotropic semivariograms for MEDOM particle size index and biodiversity indices S and H'.

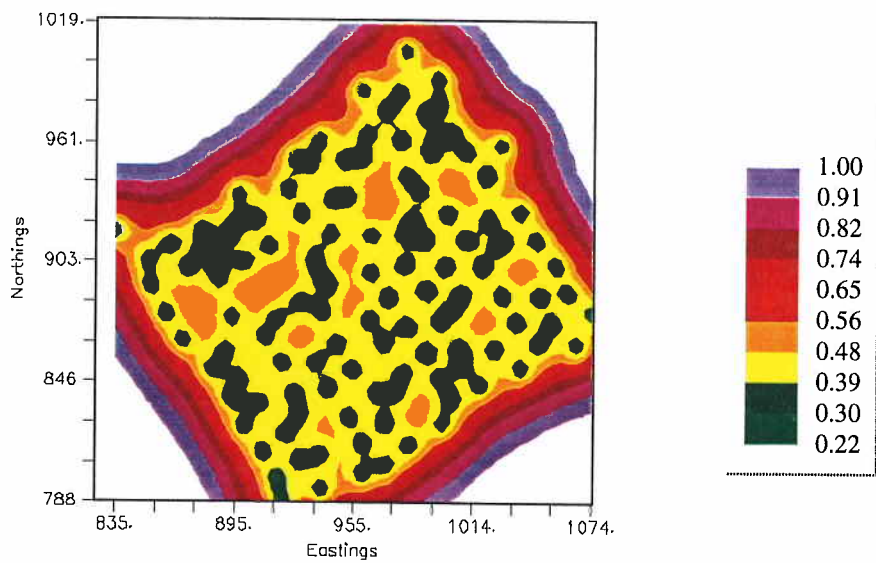
3.3.10b. Kriging

The results of the kriging analysis for selected variables within the whole study area are presented in Figures 3.17 – 3.23. The kriging maps presented are for the variables for which strong models of spatial variance were calculated using semivariance analysis. Variance (measured by standard deviation) of the estimated values within the study area is very low for all variables modelled. Variance only becomes high outside the boundary of the study area. This indicates that sample intensity is sufficient for confidence to be placed in the interpolated values. In comparing Figures 3.18 and 3.19 with Figure 3.17 a loose congruence can be seen between high species richness and elevation peaks and low species richness tends to occur in the lower lying areas. No congruence in the pattern of species richness and evenness can be seen with soil depth, shown in Figure 3.21. However an opposite trend can be seen in the pattern of species richness in Figure 3.18 and the distribution of



a)

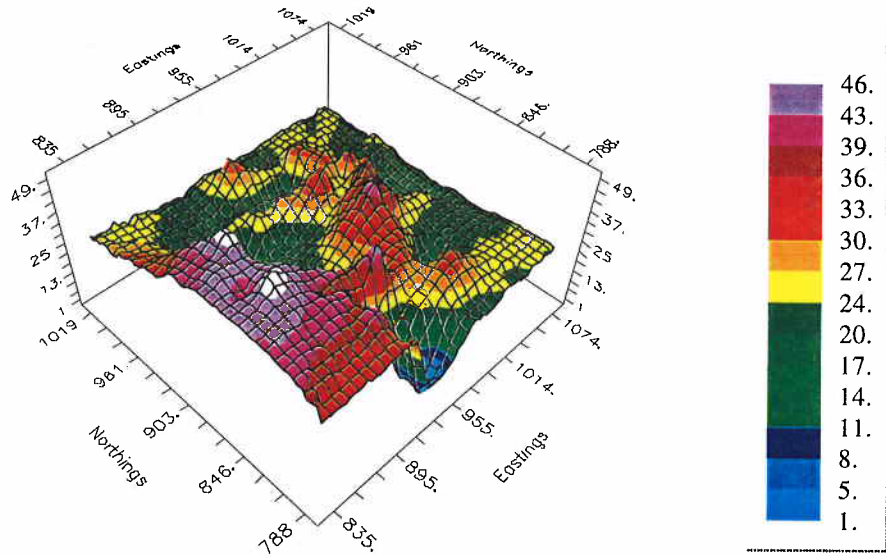
Legend



b)

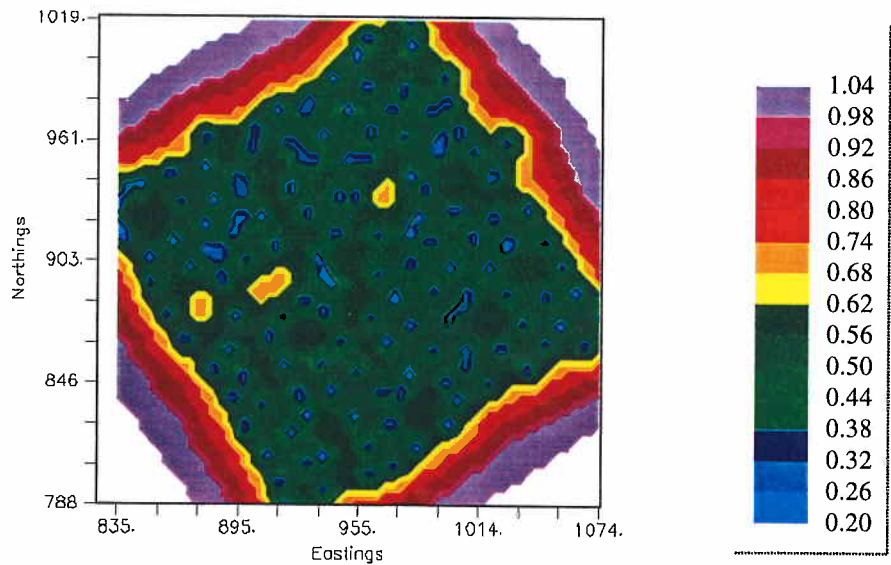
Legend

Figure 3.17: Block kriging maps of elevation (m) calculated using information derived from semivariance analysis on Tomdacheuille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.



a)

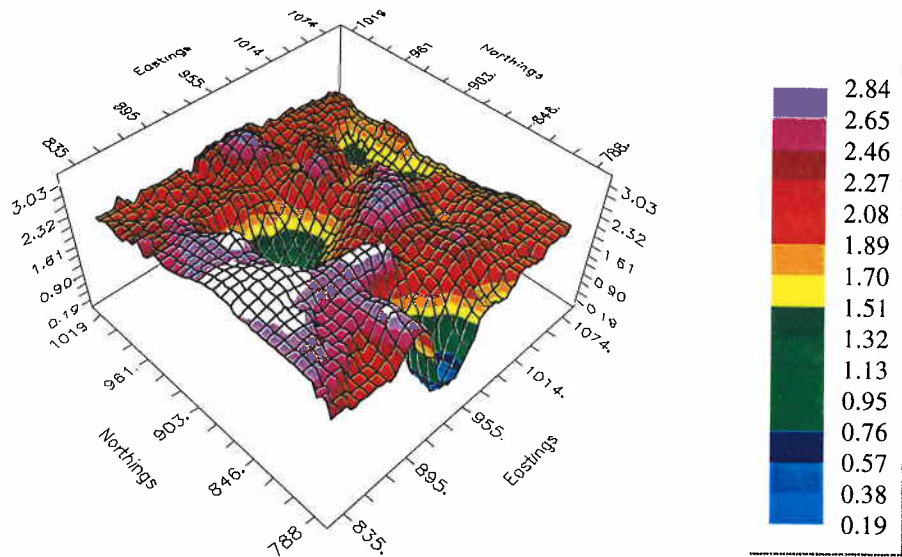
Legend



b)

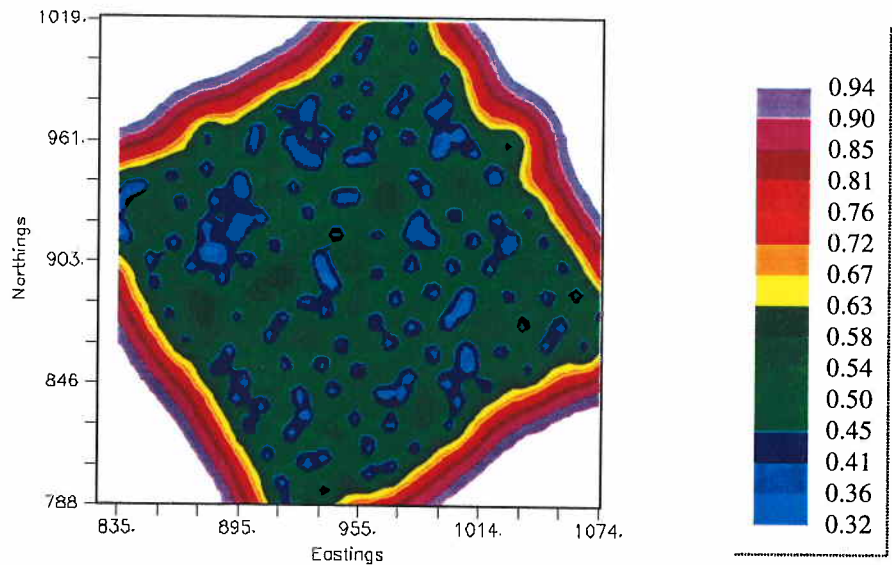
Legend

Figure 3.18: Block kriging maps of species richness count (S) calculated using information derived from semivariance analysis on Tomdacheille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.



a)

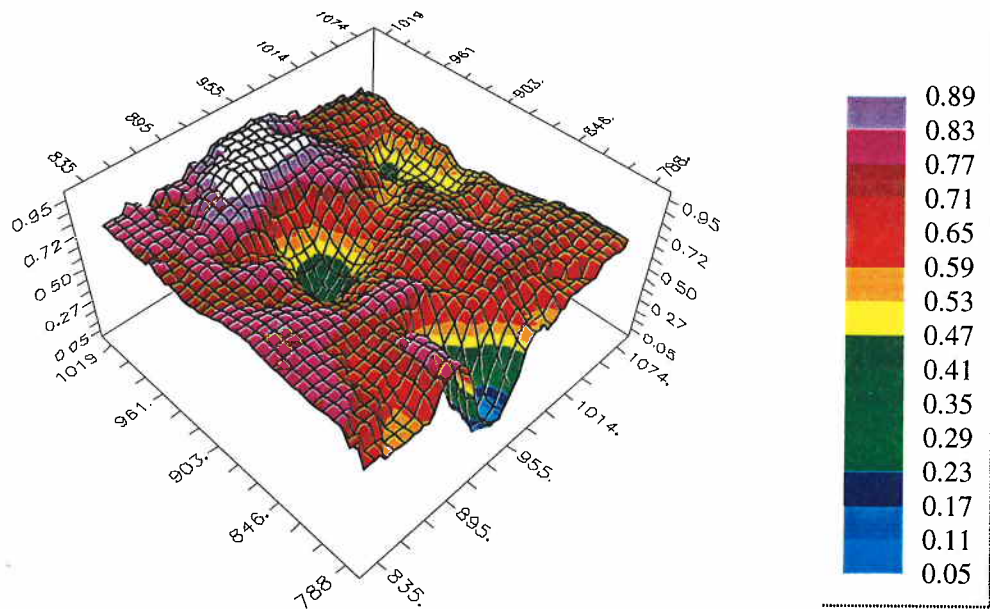
Legend



b)

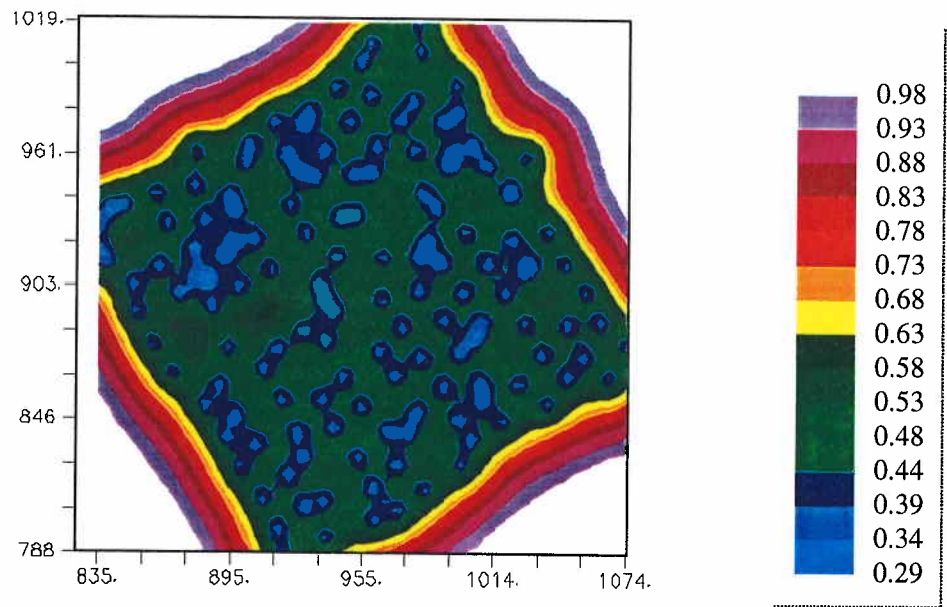
Legend

Figure 3.19: Block kriging maps of the Shannon index (H') calculated using information derived from semivariance analysis on Tomdachoille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.



a)

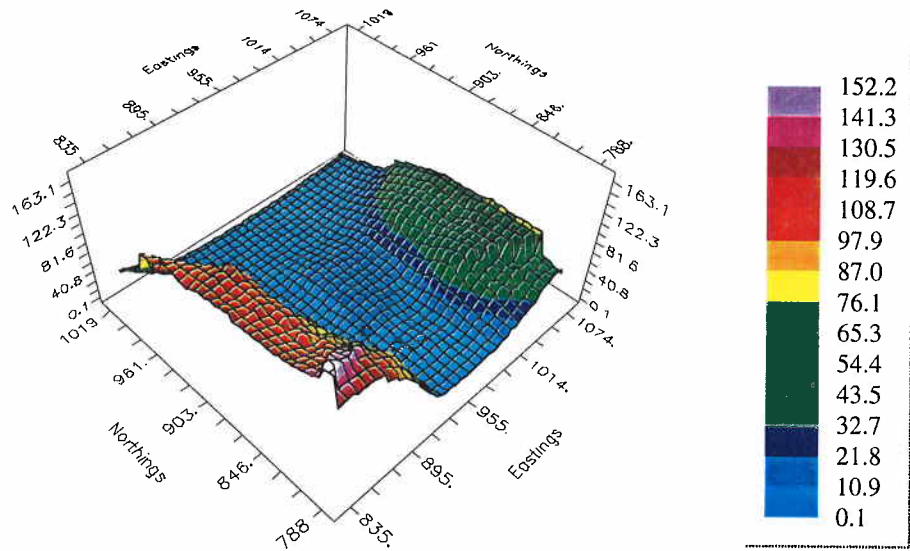
Legend



b)

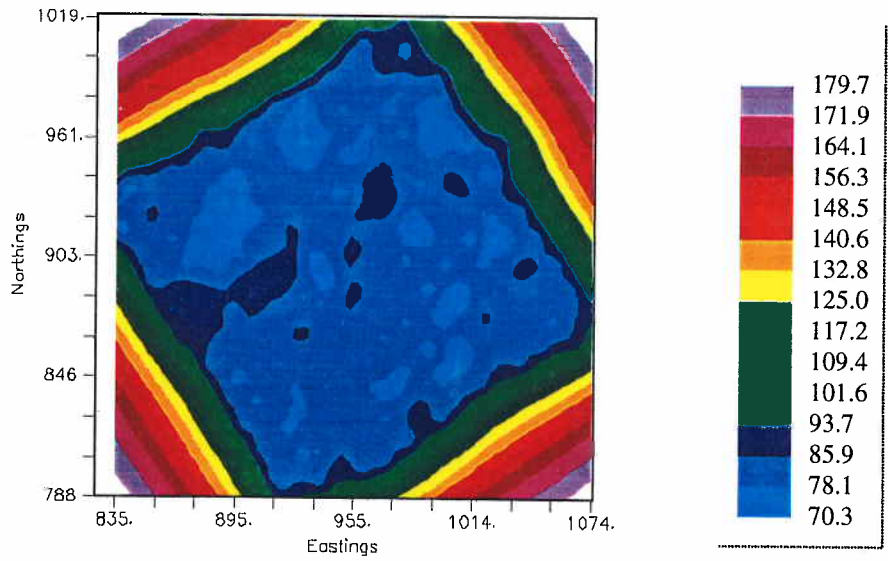
Legend

Figure 3.20: Block kriging maps of equitability (J) calculated using information derived from semivariance analysis on Tomdachoille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.



a)

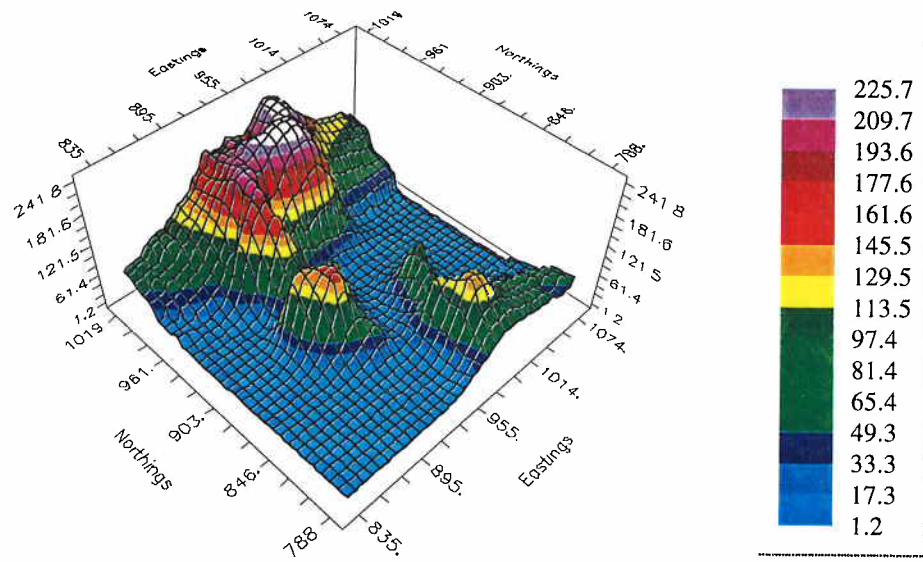
Legend



b)

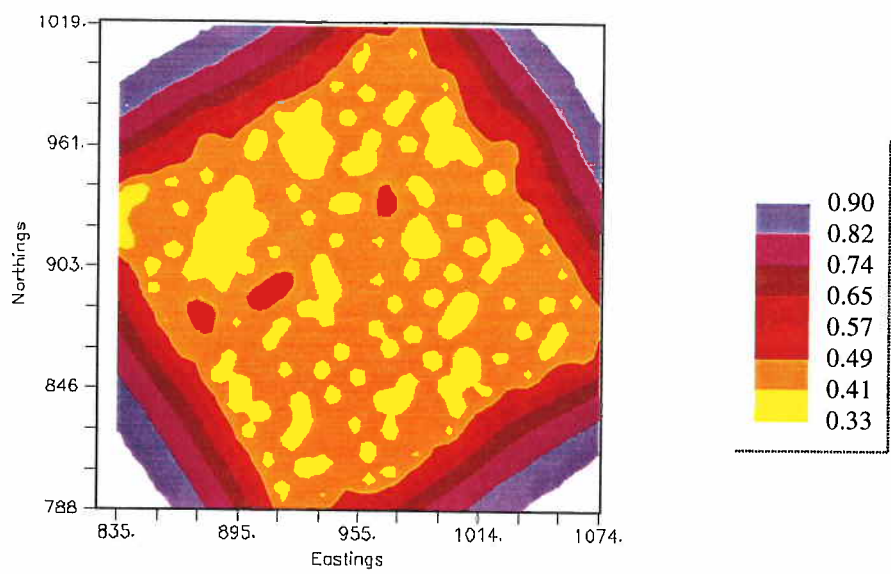
Legend

Figure 3.21: Block kriging maps of soil depth (cm) calculated using information derived from semivariance analysis on Tomdachoille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.



a)

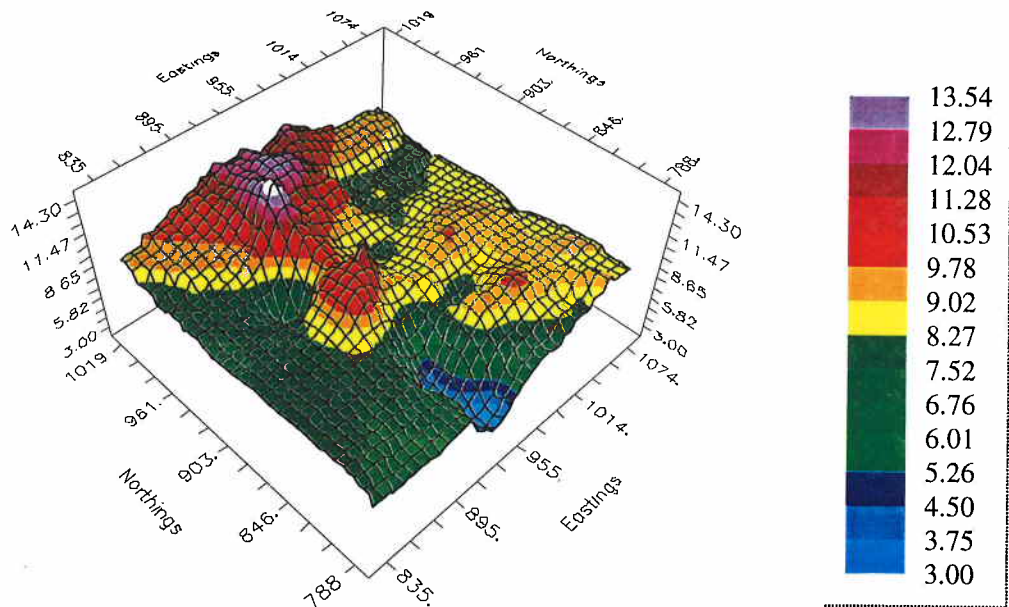
Legend



b)

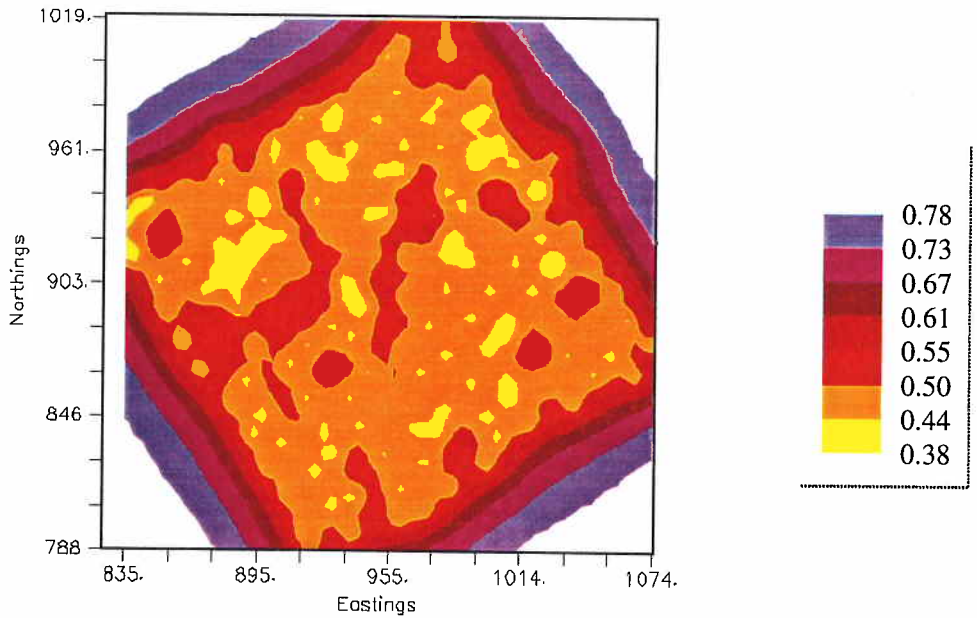
Legend

Figure 3.22: Block kriging maps of particle size range calculated using information derived from semivariance analysis on Tomdacheille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.



a)

Legend



b)

Legend

Figure 3.23: Kriging maps of particle size heterogeneity calculated using information derived from semivariance analysis on Tomdachoille Island SSSI, a) interpolated values, b) standard deviation of interpolated values.

particle size range in Figure 3.22 where areas with great heterogeneity in particle size classes coincide with zones of low species richness.

3.4. Discussion

Channel change has been active along the River Tummel throughout history. The geomorphic dynamics of the system, together with some human influence, have left a legacy of landforms across the valley floor which play an important role in creating the spatial patterns of pedological and floristic diversity. In addition, other research has shown that floodplain environments provide important habitats for fauna and invertebrates (Hughes, 1997). This chapter primarily deals with the current spatial patterns of diversity within the vicinity of Tomdachoille Island SSSI therefore discussion on the wider patterns of diversity and the temporal dimension will be discussed in Chapter 5.

3.4.1. Spatial patterns of succession on Tomdachoille

The geomorphic and pedological patterning of the study area have given rise to the development of thirteen plant communities within a 3.5 ha area. These communities show various stages of succession and development from early colonisers of frequently inundated zones through to mature *Betula* woodland which will only be inundated during large-scale flooding events. The results revealed distinct patterns of succession within the study area. A conceptual model of the stages of succession at Tomdachoille is presented in Figure 3.24 and the stages of plant succession showing the range of habitat types present at

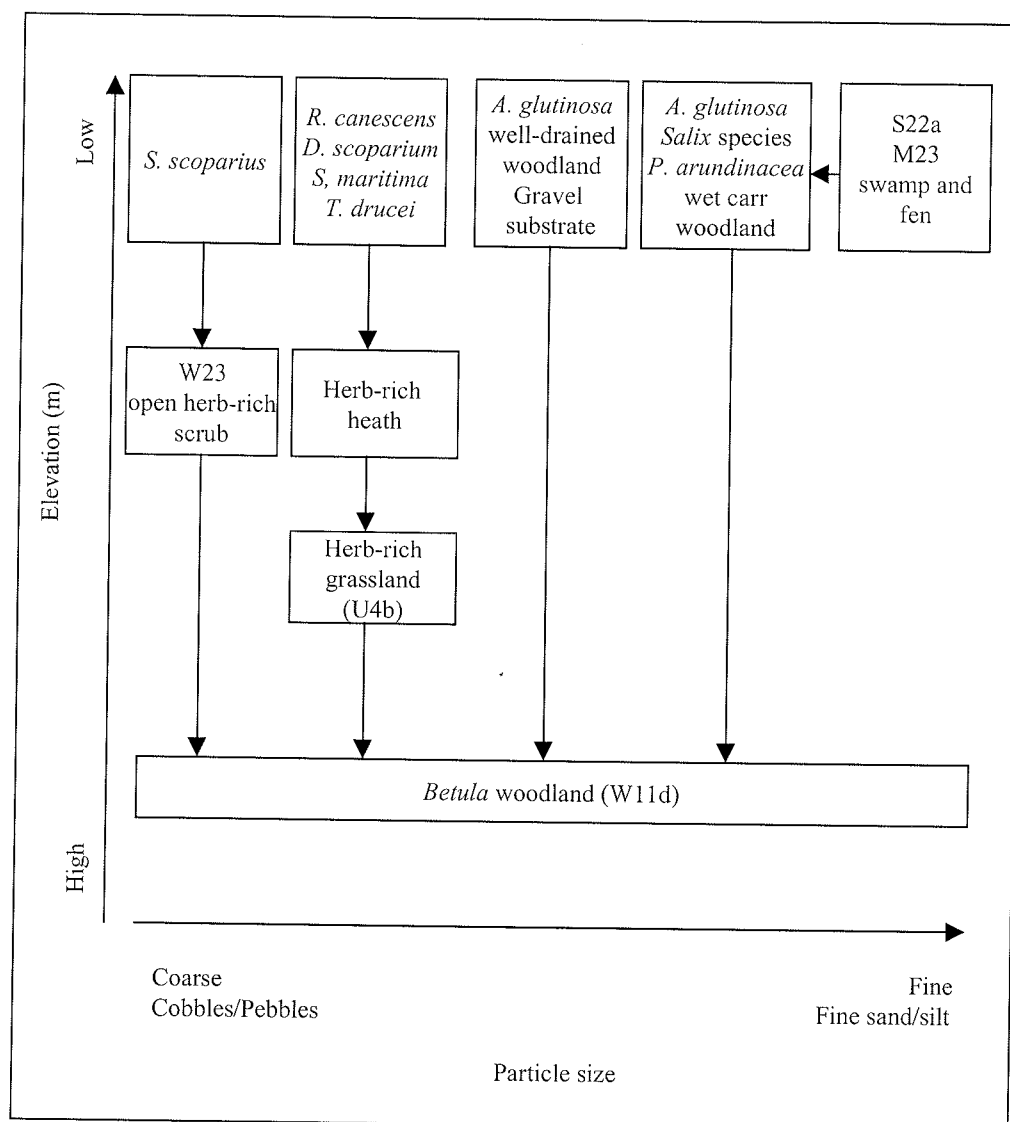


Figure 3.24: Conceptual model of the stages of vegetation succession in relation to elevation and particles size gradients within the Tomdachoille Island SSSI study area.

Tomdachoille are illustrated in Plate 3.2. The poorly colonised bare gravel habitats appear to be initially colonised by *Salix* species and *S. scoparius*. The succession patterns of community development observed are in agreement with the observations of Coates (1915). Greater stability and less frequent inundation are indicated by the presence of bryophytes. Once bryophytes are



a) Point bar with early colonisers and coarse woody debris.



b) Point bar with *Ulex europaeus* and *Sarothamnus scoparius* scrub invasion with carr woodland in the background.

Plate 3.2: Vegetation communities within various landform features on Tomdachoille Island SSSI study area. (Continued overleaf).



c) Abandoned point bar with extensive bryophyte and *Thymus drucei* cover.



d) Carr woodland within an abandoned channel.



e) Wet carr woodland along a cut-off channel.



f) A mosaic of habitat types along a backwater at Tomdachoille.



g) U4b herb-rich meadow with CWD and *Betula* woodland in the background.

established, finer sediment is trapped within the moss-matt produced. This enhances the moisture retention capacity locally and enables other early colonisers to exploit the habitat within the moss patch. Areas of relative stability within the gravel habitats are therefore important for succession to proceed. Bryophyte colonisation appears to be crucial to further development of the community. A clear progression is seen within the study area from bare gravel to bryophyte colonisation through to the herb rich community present on the abandoned point bar. This can be inferred from the TWINSPAN grouping of D5 quadrat with the abandoned gravel bar samples suggesting that the successional pathway is similar. This community then develops into herb rich meadows within the newly developing floodplain zone.

Further successional links are suggested with the grouping of quadrat G3 with the *Arrhenatherum elatius* meadow. This quadrat is in proximity to the U4b herb-rich meadow and W11d *Betula* woodland community. The incorporation of agricultural land into the semi-natural floodplain as a result of channel change at Tomdachoille has led to the development of MG1e community which typically thrives once grazing ceases (Grime *et al.*, 1990). This community typically progresses to broadleaf woodland thus the grouping with G3 suggests floristic similarity to the understorey and field layer of W11d and U4b.

Other pathways of succession on the unvegetated gravel are for riparian woodland development. Carr woodland within the study area forms a linear corridor following the line of the backwater and the abandoned channel.

Proximity to the water table seems crucial due to the water requirements of tree species. The type of carr woodland that develops appears to be closely related to the substrate characteristics. Distinct riparian communities are present adjacent to each other within the study area. The key difference being substrate texture where one community is developing on gravel substrate at the outskirts of the abandoned channel, and the other community is at a lower elevation with sandy substrate and an intricate network of streams. Other studies have shown that elevation and soil/substrate texture are important determinants in the establishment and patterns of development of riparian communities (e.g. Nilsson *et al.*, 1989; Van Splunder, 1998). Nilsson *et al.* (1991) also found a positive correlation between species richness and substrate heterogeneity within riparian communities. This supports the hypothesis that increasing habitat heterogeneity within floodplain environments results in an increase in species diversity locally. Nilsson *et al.* (1991) found that vegetation cover increases with an increase in substrate fineness in floodplain zones. This is consistent with the findings of this research. From this it can be inferred that the moisture retention capacity of the soil/substrate is critical in the more advanced stages of succession. The presence of a fine matrix within the gravel is essential for the establishment of vegetation (c.f. Sneddon and Randall, 1993). This is due to the improved moisture retention capacity of the gravel where finer substrate is present. The fine matrix acts as a reservoir, which is vital for successful germination of seeds. Sneddon and Randall (1993) found that the primary controls on the development and maintenance of vegetation in gravel habitats to be the mobility, matrix and moisture conditions of the substrate.

3.4.2. Spatial patterns and relationships between the landscape components

Nilsson *et al.* (1989) found that the correlation between species richness and substrate heterogeneity is consistent with the hypothesis of Ward and Stanford (1983) that species diversity and environmental heterogeneity should be closely related along rivers. The correlations between the plant species diversity indices confirm the hypothesis that geomorphic heterogeneity is related to plant community development. All correlations are strongly positive and show that diversity measures are greater within the more stable landforms which are infrequently disturbed by flood events.

The analysis revealed the environmental variables explaining the variation in the patterns of species distribution within the study area. Among these variables elevation and pedological properties are shown to play a role in the pattern of species distribution. Floristic patterns vary depending upon elevation of the site, but also in response to a steep substrate environmental gradient. Substrate texture varies from coarse textured gravel including small boulders and large cobbles to shallow immature soils in the very early stages of pedogenesis, through to relatively deep well sorted profiles of fine sands over relatively short distances. Floristic patterns and the structure of the plant communities are also shown to influence species distribution. Tree cover and tall herb cover significantly influence patterns of species distribution. This can be attributed to the distinct vegetation types and flood-tolerant species that colonise riparian woodland communities. Dense carr woodland will also exclude shade-intolerant species. Tall herb cover indicates greater stability and

where it is dense also indicates a longer period of development. The species occurring where there is dense tall herb cover will be less tolerant to disturbance. This is illustrated on the ordination diagram in Figure 3.3 where species locations are clustered around the zones of higher elevation with deeper soils, finer substrate texture and a high cover of tall herbs. Other species clusters are found where there is greater particle size heterogeneity, unvegetated gravel and substrate size is typically relatively coarse. Another group of species are distributed along gradients of dense tree cover associated with carr woodland, bare soil and open water.

Overall this analysis has shown that the plant communities and substrate types are related to elevation and landform class. An increase in elevation across the study area tends to lead to an increase in the floristic variables except for tree cover, soil depth and particle size index scores. Floristic variables also tend to be positively correlated with these pedological variables. Plant community type and species diversity indices tend to be correlated to elevation and soil properties, in particular particle size and soil depth, within all of the landform classes. Within the point bar landform, substrate characteristics are related to elevation where finer more sorted substrate tends to occur within the depressions. In turn, plant community type and vegetation cover is related to particle size. The overall patterns throughout the study area are for plant community type and floristic diversity indices to be related to elevation and soil properties. Tree cover within the floodplain tends to decrease with an increase in elevation. This is consistent with the findings of Baker (1990) and is the result of dense carr woodland colonising low lying areas of alluvial

landscapes. Analysis of variance shows that there are distinct differences in the vegetation and pedological assemblages between the different landform classes. This further supports the hypothesis that geomorphological diversity is the key to overall landscape diversity as it produces botanical and pedological heterogeneity within the valley floor. Diversity within the study area tends to increase along an aquatic-terrestrial gradient.

Despite the results showing that diversity is greater in the perpendicular orientation to the main channel, the correlation results revealed that the diversity indices hold significant correlations with each other in the parallel dimension. In the perpendicular direction, high geodiversity measured by the Shannon index equates with higher H'_{\max} pedodiversity. The relationships between the diversity indices in the parallel orientation are very highly correlated to each other suggesting that biodiversity and pedodiversity are responding to geodiversity, and in turn biodiversity is related to pedodiversity within the study area.

Several strong regression models were derived from the analysis which will be tested for their predictive capacity along other reaches of the river. It is anticipated that several environmental variables can be predicted with reasonable confidence from key environmental predictors. Within the landform classes, very strong regression models have been derived for the floristic diversity indices. Substrate properties being predictor variables in many of the regression models for predicting species diversity. Regression analysis has shown that the environmental variables, in particular floristic

properties, are responding to pedological and geomorphological characteristics of the study area.

Geostatistical analysis revealed that spatial dependence within the study area varies from 9.7-176.7m for isotropic analysis. The range of spatial dependence for elevation, species richness, and to an extent, particle size heterogeneity, show similarity. These variables show spatial independence is achieved at around 70m. The Shannon index (H' and J) show spatial dependence over slightly shorter distances, however both also show anisotropic variation. Although it can be argued that a degree of congruence exists between elevation, species richness and particle size heterogeneity, the model for elevation is weak due to the pattern of semivariance and the fact that it displays anisotropy. However, the relationship between species richness and particle size heterogeneity can still be reinforced with the semivariance analysis results.

Despite the weak model of semivariance for elevation, the kriging results show a fairly accurate representation of the floodplain morphological structure. Overall the estimated values are predicted with low variance thus giving confidence in the results. The maps produced can therefore be seen as a reasonably accurate portrayal of the spatial distribution of the environmental variables analysed. The kriging maps for species richness and particle size range support the hypothesis that species distribution patterns within floodplain environments is related to substrate heterogeneity as a distinct

pattern exists where low species richness tends to coincide with high particle size range.

3.4.3. Spatial patterns of landscape diversity within the Tomdachoille study area

The diversity results support the view that a suite of habitat types is essential for maintaining species richness within alluvial valley floor environments. Although the point bar and its associated plant communities have a low species richness, this feature provides a suitable habitat for rare species which tend to colonise the more elevated parts of the point bar which are less likely to be inundated annually. Where a shifting mosaic of habitats exists the results have illustrated that species richness within point bars increases dramatically over very short time-scales when the feature is isolated from the main channel. From the results it can be inferred that species richness within the now abandoned point bar has increased from approximately 79 species to 93 species in 25 years. However, frequent disturbance does not indicate poor species richness, as illustrated in Table 3.6c. These results show that not only do the highest counts of rare species occur within the landforms most prone to inundation, but also that very high species richness occurs within the abandoned channel. The key variables influencing the dense vegetation within this landform are substrate texture and open water (streams and pools) providing a suitable habitat for species intolerant of drought conditions and tolerant of shade. This landform was created approximately 25 years ago when the river changed course and it now hosts 143 species within the dense carr

woodland that has developed. This landform has the second highest species richness within the study area with the most mature areas of the floodplain having the highest species richness.

The spatial patterns of species richness and their association with landform support the need to preserve and rehabilitate semi-natural floodplain environments. In a culture where development and land management typically cause a decline in species richness, this study area shows distinct trends for species recruitment over time due to the spatial patterns of habitat types creating a variety of vegetation types at different stages of succession. The importance of geomorphic heterogeneity is emphasised in the results by the rapid increase in the number of species unique to the landforms, where 89 species are unique to one landform class. Further analysis of these findings revealed that all of the landform classes have unique species, thus contributing to higher landscape diversity. The Shannon index results show that overall diversity is relatively high in most communities within the study area. The riparian communities score among the lowest on the Shannon index. These communities are W6 and W7a and both occur within the abandoned channel landform. This shows that internal heterogeneity within the landform features also contributes to higher landscape diversity because although these communities score low on the Shannon index, when combined these communities provide high species richness within the landform they inhabit. This emphasises the role of pedodiversity in promoting species richness. A steep environmental gradient of substrate texture exists within this landform creating high pedodiversity, which in turn produces high botanical diversity.

The CANOCO results suggest that the point bar and inundation zones are species poor with low diversity based on the N_2 statistic. The samples within these zones may not be species rich however, they do contain rare species at a higher frequency than the other landform classes. The N_2 statistic revealed the samples within the floodplain zones to be of the highest diversity. This is the case in terms of the count of species. These results show that the mosaic of habitats is important in the maintenance of overall landscape diversity because landforms that are species poor do tend to contain a higher number of rare species. The analysis of species tolerance showed that *Myosotis sylvatica* and *Teesdalia nudicaulis*, which are both rare species occurring in the floodplain and point bar landforms respectively, have low tolerance and are therefore very site specific. Efforts should be made to preserve the suitable habitats for these species to maintain their presence within the county.

Channel abandonment has also enabled the development of swamp and marsh communities thus enhancing local landscape diversity. The pattern of carr woodland also emphasises the importance of channel change in maintaining diversity of plant communities within floodplain river systems. Carr woodland is now a rare feature nationally, being recorded as extensive at 0% of Scottish rivers and present at only 2% of Scottish rivers and the occurrence of *A. glutinosa* is only extensive at 4% of rivers in eastern Scotland (Raven *et al.*, 1998). *A. glutinosa* is also reported to occur in less than 1% of the total cover of British woodland (Grime *et al.*, 1990). When putting the patterns of habitat features and diversity present within the study area in the context of Scottish

rivers, it is evident that this area is of national importance in the habitat types it supports.

Lateral migration and channel change also enhances the diversity of the fluvial landscape. Differing patterns of diversity are observed along different orientations of the floodplain showing the spatial heterogeneity that exists along an aquatic-terrestrial environmental gradient. Bio- and pedo-diversity are both shown to be greatest in the transverse orientation to the main channel. This indicates that distance from the channel influences the patterns of diversity that evolve. The unstable landform classes have greater internal heterogeneity in terms of bio- and pedo-diversity, in particular particle size. In terms of the whole study area, relatively high heterogeneity is observed for species richness, soil depth, soil moisture content and particle size range. The heterogeneity of the soil properties being of key importance in providing an array of differing local habitats which lead to diversity among plant communities.

The small study area hosts 17 rare species including some very rare species both locally and nationally in the UK context. These species include *P. veris* which is now rare in meadows in the UK due to agricultural practices (Grime *et al.*, 1990). However the Rivers Tummel, Tay and Garry provide suitable habitats for this species and its occurrence is recorded as occasional within the county (Smith *et al.*, 1992). The results revealed that the maintenance of a mosaic of fluvial landforms is crucial to the persistence and preservation of rare and very rare species of flora. Many of the rare species within the point

bar and abandoned point bar landforms have not been recorded in Perthshire since 1970. This emphasises the importance of these features in maintaining diversity at the county level. The landforms these rare and very rare species have colonised have been modified by channel change in the post 1971 period at Tomdachoille. This has created areas of the point bar landforms that are inundated at a lower frequency thus enabling early stages of succession to proceed. A summary of the species present within the study area which are in decline in the UK context are summarised in Table 3.28.

Table 3.28: Summary of species present in abundance at Tomdachoille that are undergoing a decline in abundance in the UK context (taken from Grime *et al.*, 1990).

Species name	Reason for decline
<i>Filipendula ulmaria</i>	Decreasing due to the loss of wetlands
<i>Galium cruciata</i>	Poor coloniser, mainly riverbanks
<i>Galium verum</i>	Restricted to semi-natural and ancient habitats
<i>Lotus corniculatus</i>	Agricultural pressure
<i>Potentilla sterilis</i>	Plant of ancient woodland, poor coloniser
<i>Primula veris</i>	Declining through ploughing of pasture and decrease in grazing pressure in semi-natural grasslands
<i>Ranunculus acris</i>	Easily controlled and slow to establish, confined mainly to permanent pasture
<i>Rhinanthus minor</i>	Habitat destruction
<i>Thymus drucei</i>	Land use practices in lowlands

3.5. Summary

The aim of this chapter was to interrogate landscape diversity and investigate the relationships between landscape components and the spatial patterns of diversity. From the analysis, linear statistical models of the controls on the patterns of diversity have been produced and are to be tested along other reaches. In addition, a conceptual model of the pathways of plant succession based on variations in particle size and elevation is to be validated at the other study areas.

Overall the results of the diversity analysis suggest that the landforms are the basic unit of the landscape. This is indicated by the lower variation between classes in the diversity indices of the plant communities and soil/substrate groups when the data was grouped by landform in comparison to grouping the data by plant community or soil/substrate type. Although no distinct pattern can be derived between the distribution of plant communities and soil/substrate class, the results have indicated that particle size is an important factor in influencing the spatial patterns of species assemblages across the study area. The variation in the diversity of landforms within the soil/substrate groups suggests that soil type does not directly respond to the landform class on which it is developing and other factors come into play. The results show considerable substrate heterogeneity within the landform classes. This heterogeneity seems to influence the patterns of plant communities that colonise. Thus not only do the landforms increase pedorichness within the landscape, but also the spatial patterns of the landforms and soil/substrate

types enhance biodiversity within the landscape. Thus landscape diversity is dependent upon the degree of heterogeneity of these three key landscape components.

Following the study at Tomdachoille Island, further research was planned for other reaches of the River Tummel in order to validate the models produced. In addition relationships between diversity, environmental variables and the spatial pattern of diversity were also studied within the other study areas.

Chapter 4: Validation of the relationships between the components of landscape diversity along other reaches of the River Tummel.

4.1. Introduction

Additional reaches along the river which have a history of channel change and a mosaic of landform and habitat types were selected for testing the relationships between the components creating landscape diversity within alluvial valley floors. Sampling intensity was reduced partly due to logistics but also as a result of high water levels throughout the year for the following two field seasons. Many areas of the gravel islands were inundated or access was hazardous throughout the summer months either as a result of deep high velocity water or due to nesting terns on the mid-channel bars.

4.2. Methodology

4.2.1. Criteria for the selection of study areas

Additional study areas were selected based upon geomorphic criteria outlined in Appendix 2. The geomorphic landforms within the study areas were mapped from aerial photography from 1994 and field investigation. NVC Phase 1 Habitat Survey was also carried out from aerial photographs from 1994 and the habitat map derived was validated in the field. The results in Chapter 3 revealed that the geomorphic landforms are the basic unit of the landscape influencing the spatial patterns of plant community and substrate

heterogeneity within the valley floor. Therefore field sampling was stratified within the various landforms mapped within the study areas. Sampling was further stratified so that sample points were located within the plant communities mapped from NVC Phase 1 Habitat Survey within the landform classes. Samples were located along transects running parallel and perpendicular to the main channel. Transects were positioned parallel and perpendicular to the channel in order to assess the degree of spatial variation in relation to orientation to the channel. Transects were located randomly within each habitat type and samples were located randomly along transects. By adopting this approach, the major sources of variation within the study area have been identified prior to sampling thus the overall pattern of variability within the study area has been incorporated (Kent and Coker, 1992). This sampling strategy also ensures that all areas of major variation are sampled equally. This approach was not adopted for the initial study at Tomdachoille as the patterns of variation were unknown and could only be inferred from visual interpretation of the landscape character. This however introduces bias into the results. The analysis revealed that the landscape pattern is governed by geomorphic patterns and that variation exists within the plant community types. These results support the need for stratifying sampling when studying the spatial patterns of diversity within alluvial valleys.

A map of the additional study areas where access was feasible during the following field seasons is presented in Figure 4.1. The landforms sampled are point bar (opposite Tomdachoille Island SSSI, Figure 3.1) and Ballinluig

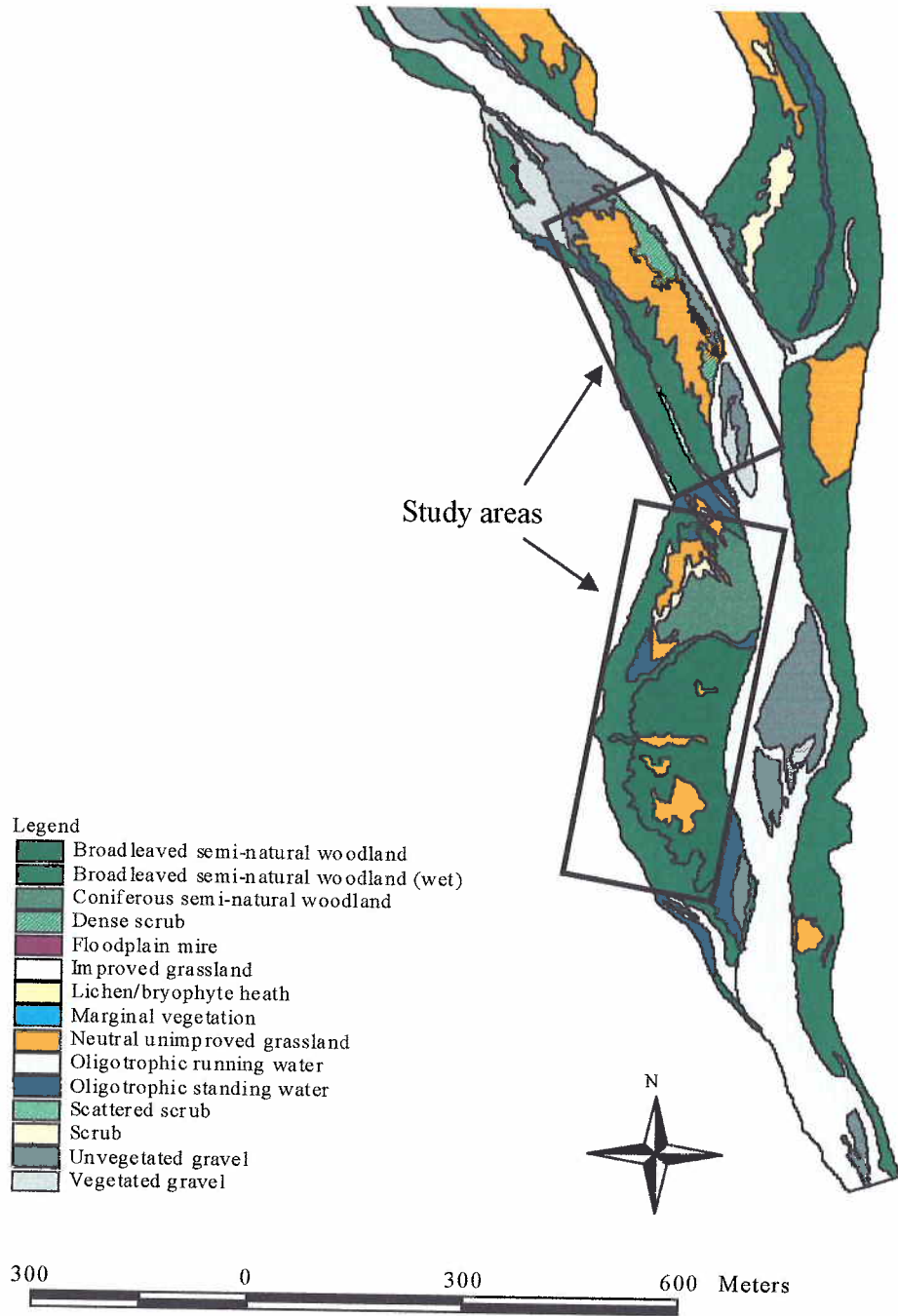


Figure 4.1: NVC Phase 1 Habitat Survey map of Ballinluig Island study area.

Island SSSI. Ballinluig Island SSSI incorporated a suite of landforms including floodplain, abandoned channel, and backwater. The gravel areas at Ballinluig were inundated during the field season and the mid-channel bars inaccessible and so were not included in the sampling. However, these areas are included in the temporal analysis of diversity patterns in chapter 5.

4.2.2. Field sampling strategy

Sample points were located randomly along randomly located transects running parallel and perpendicular to the main channel within the habitat types found within each landform class. A minimal sampling interval of 50m was chosen by utilising information on spatial dependence from geostatistical analysis of data from Tomdachoille Island. This was done to improve statistical analysis of the data as most tests assume that the data is not spatially autocorrelated. Field data collected at each sample point was consistent with the sampling undertaken at Tomdachoille Island SSSI. Field data was also analysed in accordance with the methodology stated in Chapter 3. Regression equations derived in Chapter 3 were tested on the data derived from the additional study areas in order to test their predictive capacity. The differences between actual and predicted values were analysed using paired t-test. The hypotheses for the test are given below:

H_0 = predicted and actual values are equal

H_1 = predicted and actual values are not equal.

The test was performed with the aim of accepting the null hypothesis that the values are equal.

4.3. Results

4.3.1. Historical data interpretation

Historical changes in the planform of the river are described in Chapter 1 and further details are given in Winterbottom (1995). The aerial photographs presented in Plate 1.2 demonstrate the patterns of channel change and plant community development in the vicinity of Ballinluig over the past 50 years. The patterns of temporal change are presented and discussed in greater detail in Chapter 5. Channel change has occurred within this reach following the floods of 1990 and 1993. This flooding caused reworking of the gravel overriding existing vegetation on the gravel island opposite Tomdachoille and causing the channel to erode the point bar at Ballinluig Island. This led to the creation of a mid-channel bar and the river is now eroding the banks of Ballinluig Island SSSI.

4.3.2. Vegetation classification and description

The NVC Phase 1 Habitat Survey map is presented in Figure 4.1 of the Ballinluig reach of the river. The NVC Phase 1 Habitat Survey map of the point bar opposite Tomdachoille Island is given in Figure 3.1. The habitat map shows that the Ballinluig reach of the River Tummel is dominated by broad-leaved semi-natural woodland. These woodland patches form semi-continuous longitudinal patches along the river corridor. The broad-leaved woodland is interspersed with patches of semi-natural neutral unimproved grassland and

semi-natural coniferous woodland. The coniferous woodland is composed of *P. sylvestris* with its seed source being derived from the coniferous plantation spanning the valley walls of this section of the Tummel valley on the right side of the river. Other habitat types present are dense scrub dominated by *S. scoparius*, oligotrophic standing water within the cut-off channels, oligotrophic running water and a floodplain mire is present within the wet woodland opposite Ballinluig Island SSSI. Vegetated and unvegetated gravel habitats are additional features. It is these areas which were either inaccessible or inundated during the field seasons.

4.3.2a. TWINSPAN interpretation

The dendrogram showing the divisions of the samples by species in the TWINSPAN routine is given in Figure 4.2. At the first level of divisions the samples are split separating the grassland and heath vegetation types from the wooded communities. The indicator species on the positive arm of the division are *B. pubescens*, *S. sylvatica* and *G. aparine*. The strength of the split is strong, indicated by the high eigenvalue.

The following paragraphs explain the divisions on the negative arm of the dendrogram only. The negative split at the second level of divisions is very strong, with an eigenvalue of 0.632, separating out the gravel bar community upstream from the grassland communities on Ballinluig Island SSSI. The negative group at the second level of divisions forms the end group. The

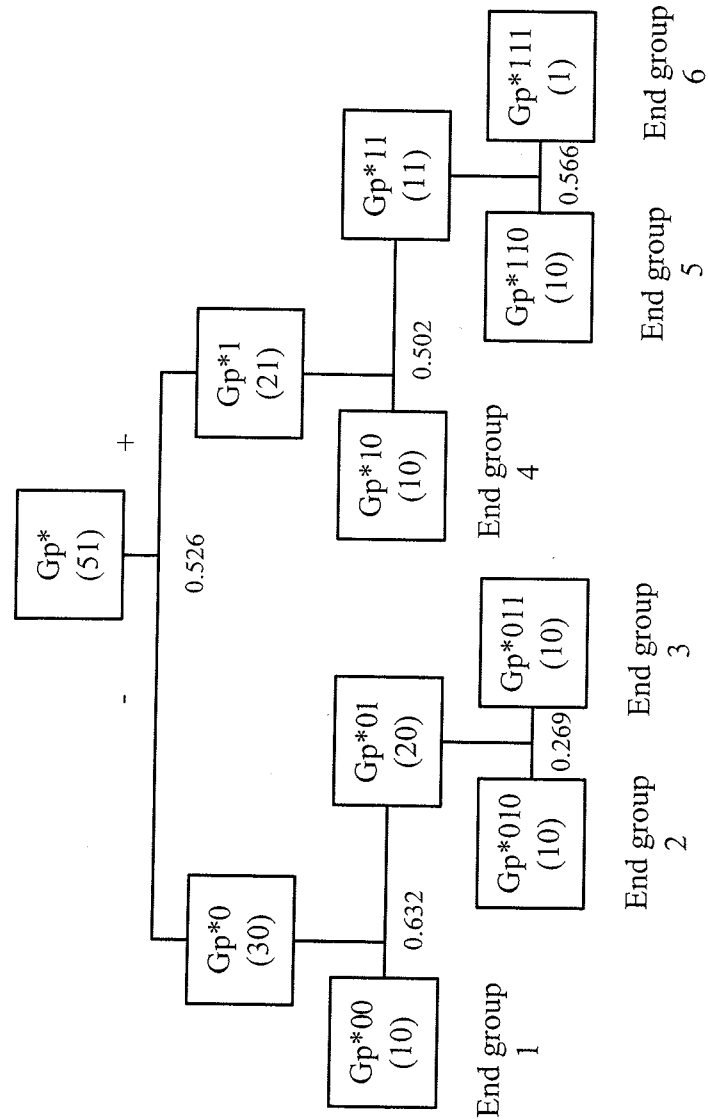


Figure 4.2: Dendrogram showing the sample divisions by species from TWINSpan analysis. Eigenvalues indicate the strength of the split at each level, the figures in brackets indicate the number of samples in each group. The negative branches are split to the left and the positive branches are to the right.

positive group produced from this split is divided once more. The strength of the split is quite weak however, but accepted as separate communities due to the negative indicator species being *S. scoparius*, an abundant scrub species which is absent in the other group of samples. Level three of the divisions on the negative arm of the dendrogram is accepted as the final level.

The following paragraphs describe the divisions of the groups of samples on the positive arm of the dendrogram. Group*1 is further divided with a relatively high eigenvalue of 0.502, with *A. odoratum* being the negative indicator species. This has separated out the woodland community on the negative side of the split from the wetter woodland communities. The second level of divisions is accepted as the final end group for the negative side of the split. The remaining 11 samples in group*11 is split once more to produce 2 end groups. Again the split is strong, with negative group indicator species being *A. glutinosa* and *A. pseudoplatanus*, and the positive group indicator species being *A. capillaris* and *Barbarea vulgaris*.

4.3.2b. Community classification

A total of six vegetation types were identified by the TWINSpan analysis. The end groups were entered into TABLE routine within the VESpan program to produce constancy tables of the floristic data. Data were prepared in TABLE for analysis in the MATCH routine for allocating the groups to a British Plant Community type. The constancy tables produced in the TABLE routine for each plant community type are given in Appendix 10. These tables

show the floristic composition of the communities along with a summary table of the environmental variables. The best fitting British Plant Communities for each end group are presented in Table 4.1. The results from the MATCH routine were used as an aid to classifying the vegetation types within the study areas. Descriptions of the floristic characteristics of these habitats are given in the British Plant Community publications (Rodwell, 1991a; 1991b; 1992; 1995a). The MATCH routine failed to allocate a suitable vegetation type to the gravel and backwater habitats because these communities have not been sampled in the British Plant Community system. Habitat names for these communities have been given according to the dominant and most abundant species characteristic of the community. A vegetation map of the area is given in Figure 5.8d in Chapter 5.

4.3.3. Floristic relationships with environmental variables

The results of the forward selection of environmental variables in the CANOCO routine are given in Table 4.2. The table shows the cumulative variance of each variable in explaining the pattern of species distribution, and the order in which the significant variables ($p < 0.05$) were included into the model. A summary of the CANOCO output is given in Table 4.3. The total inertia is a measure of the total variance in the species data (3.177). The eigenvalues are a measure of the importance of an ordination axis. The species-environment correlations are a measure of the strength of the relationship between the species and environment for a given axis, with axes 1 and 2 having high values (0.976 and 0.942 respectively). The cumulative

Table 4.1.a: The 'best fitting' British Plant Community allocated to the vegetation types on Ballinluig Island SSSI.

End group	British Plant Community	British Plant Community name	MATCH coefficient
2	MG5b	<i>Cynosurus cristatus-Centaurea nigra</i> grassland, <i>Galium verum</i> sub-community	42.7
3	U4b	<i>Festuca ovina-Agrostis capillaris-Galium saxatile</i> grassland, <i>Holcus lanatus-Trifolium repens</i> sub-community	41.4
4	W11c	<i>Quercus petraea-Betula pubescens-Oxalis acetosella</i> woodland, <i>Anemone nemorosa</i> sub-community	39.0
5	W7	<i>Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum</i> woodland	45.1

Table 4.1.b: Plant Community types on the gravel bar.

End group	British Plant Community	British Plant Community name	MATCH coefficient
1	SHpc	<i>Senecio jacobaea-Chamerion angustifolium-Silene uniflora-Impatiens glandulifera</i> gravel community	N/A
6	M23	<i>Mentha aquatica-Phalaris arundinacea-Juncus effusus-Filipendula ulmaria</i> backwater community	N/A

Table 4.2: Forward selection of significant environmental variables ($p < 0.05$) in CANOCO. The total variance describes the cumulative variance each property explains when added to the model. The variables are presented in the order they were included into the model.

Variable	Total variance	p-value
Tree cover	0.46	0.005
MINDOM	0.83	0.005
Open water (%)	1.04	0.005
Unvegetated gravel	1.14	0.005
MAXDOM	1.24	0.005
SMC (%)	1.33	0.005
Elevation (m)	1.41	0.005
Dead wood (%)	1.49	0.005
Shrub cover	1.57	0.005

Table 4.3: Summary statistics of the CANOCO results for the first 4 ordination axes.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.500	0.454	0.225	0.121	3.177
Species-environmental correlations	0.976	0.942	0.918	0.852	
Cumulative percent variance:					
Of species data	15.7	30.0	37.0	40.8	
Of species-environment relation	31.9	60.9	75.2	82.9	
Sum of all unconstrained eigenvalues					3.177
Sum of all canonical eigenvalues					1.566

percent variance of the species-environment relation shows that 60.9% of the variation in the species distribution is explained by the environmental variables in the first two axes. The resulting ordination diagram produced when plotting the species scores with the biplot scores of environmental variables is given in Figure 4.3.

The analysis shows that nine environmental variables are significantly correlated to the pattern of species distribution. The direction of the greatest influence the variables have upon the species distribution is denoted by the direction and length of the arrows on the ordination diagram. On the lower left-hand side of the ordination, the species and habitats are occurring in areas of relatively high elevation and in well-drained conditions. Key species in the lower left-hand section of the diagram that are highly correlated to increasing elevation are grassland species, namely *A. odoratum*, *F. ovina* and *H. lanatus*. The diagram also indicates that there is a high proportion of shrub cover, typically that of scrub species such as *S. scoparius*. Substrate texture is finer where these species and habitats occur. The upper left-hand section of the diagram shows the distribution of species typical to the gravel habitat in relation to environmental variables. The species that is highly correlated to the axes is *H. matronalis*. These species occur where there is a relatively high proportion of unvegetated gravel substrate, which is well drained due to substrate composition. On the lower right-hand side of the ordination, the plant communities respond to an increase in elevation, although the species distribution within these communities is less related to elevation than the grassland habitats. Fine substrate texture and soil moisture content are more

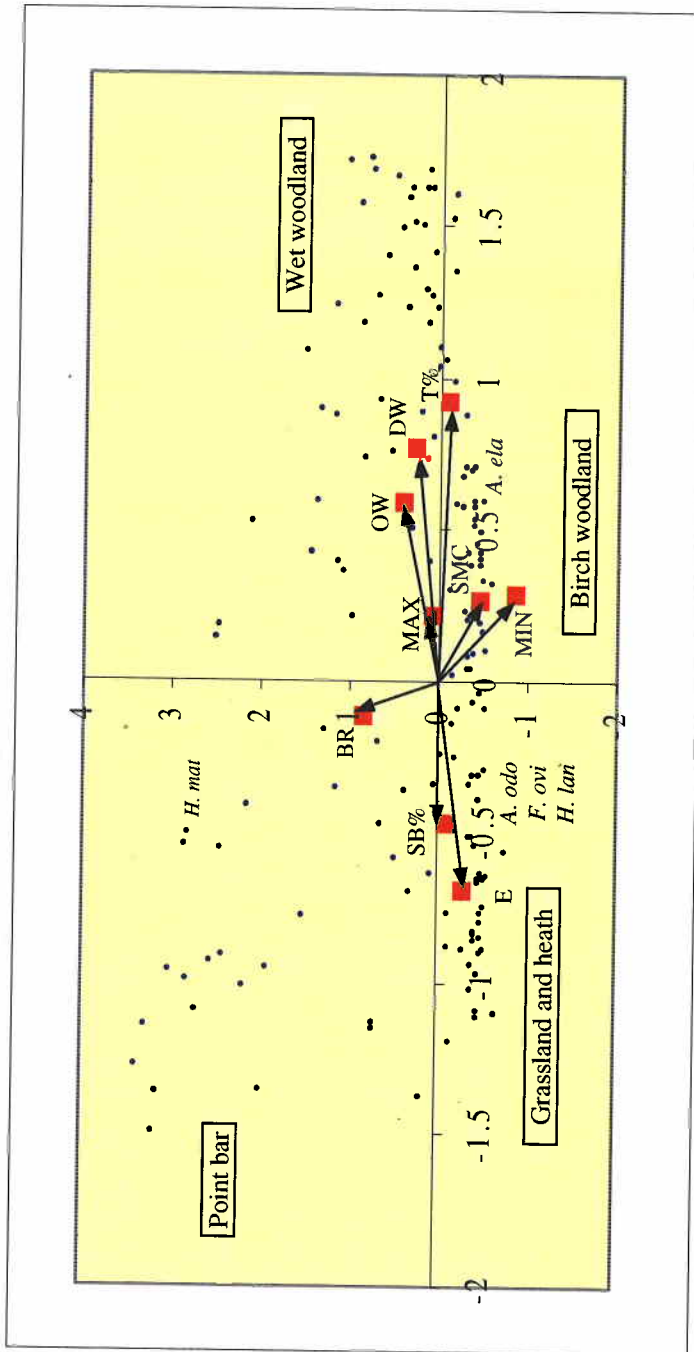


Figure 4.3: Ordination diagram of species and environmental variables within the additional study areas. Environmental variables are denoted by arrows and red squares, the species carrying a high weight for its species score are marked on the diagram.

Legend:

- E: elevation (m)
- OW: open water (%)
- SMC: soil moisture content (%)
- A. ela: *Arrhenatherum elatius*
- H. lan: *Holcus lanatus*
- SB%: shrub cover
- DW: coarse woody debris (%)
- BR: unvegetated gravel (%)
- A. odo: *Arrhenatherum odoratum*
- F. ovi: *Festuca ovina*
- H. mat: *Hesperis matronalis*
- MAX: MAXDOM (particle size index)
- MIN: MINDOM (particle size index)

important environmental variables influencing species distribution in the lower right of the diagram. The increase in soil moisture is likely to be in response to the finer substrate texture which has a greater moisture retention capacity. *A. elatius* is strongly correlated with the environmental variables in this quarter of the ordination. This species is the dominant grass among the field layer of the *Betula* woodland. Low lying zones of the study area are situated within the upper right of the ordination. With a decline in elevation, Figure 4.3 shows that there is an increase in tree cover, coarse woody debris, open water and coarser substrate indicated by MAXDOM. Species typical of wet woodland are plotted in this portion of the ordination and are found within the backwater communities.

The CANOCO routine examines sample heterogeneity as a measure of species diversity using the N_2 statistic, which is the reciprocal of the Simpson diversity measure. A summary of these results are given in Table 4.4 showing those samples with very low diversity and species poor (Table 4.4a), and those samples with high diversity and species rich (Table 4.4b). The samples presented in Table 4.4a are from areas of poorly colonised gravel. The samples in Table 4.4b are from the *Betula* woodland W11c, the carr woodland W7, and MG5b grassland community. Table 4.5 shows summaries of species tolerance analysis in CANOCO. Table 4.5a shows species having a low tolerance ($N_2 < 3$), meaning they tend to be site-specific species which only colonise certain habitats within the study area. Table 4.5b shows species with a high tolerance ($N_2 > 25$); the tolerance level was reduced for this analysis based upon the range of species tolerance within the dataset. The species recorded in

Table 4.4: Sample heterogeneity expressed by N_2 . Showing (a) samples with low N_2 (species poor) and (b) samples with high N_2 (species rich).

(a)		(b)	
Sample	N_2	Sample	N_2
GB1	6.81	W3	32.35
GB2	10.29	W4	31.81
GB4	8.45	W5	31.88
GB5	11.49	W6	31.09
GB6	10.64	W7	36.32
GB7	12.78	W8	35.73
GB8	11.08	W10	32.33
GB10	12.55	WW1	33.04
		SB2	31.18
		SB7	30.27

Table 4.5: Summary of the CANOCO output of species with (a) low tolerance ($N_2 < 3$) and (b) high tolerance ($N_2 > 25$).

(a)		(b)	
Species name	N_2	Species name	N_2
<i>Agrostis capilaris</i>	2.97	<i>Anthoxanthum odoratum</i>	29.18
<i>Alchemilla vulgaris</i>	1.90	<i>Arrhenatherum elatius</i>	27.23
<i>Angelica sylvestris</i>	2.89	<i>Deschampsia cespitosa</i>	28.23
<i>Calluna vulgaris</i>	2.96	<i>Festuca ovina</i>	37.6
<i>Chrysosplenium oppositifolium</i>	2.97	<i>Galium verum</i>	25.77
<i>Climacium dendroides</i>	1.97	<i>Holcus lanatus</i>	29.53
<i>Conopodium majus</i>	3.00	<i>Hylocomnium splendens</i>	26.89
<i>Cynosurus cristatus</i>	2.80	<i>Rhytidiadelphus squarrosus</i>	25.94
<i>Helianthemum chamaecistus</i>	2.80	<i>Teucrium scorodonia</i>	25.99
<i>Hypochoeris glabra</i>	2.89	<i>Veronica chamaedrys</i>	25.02
<i>Juncus articulatus</i>	1.90	<i>Viola riviniana</i>	30.14
<i>Lepidium heterophyllum</i>	2.89		
<i>Luzula sylvatica</i>	1.99		
<i>Mimulus guttatus</i>	1.97		
<i>Rorippa nasturtium-aquaticum</i>	2.89		
<i>Rumex obtusifolius</i>	1.90		
<i>Scrophularia nodosa</i>	3.00		
<i>Scutellaria galericulata</i>	1.90		
<i>Senecio viscosus</i>	1.73		
<i>Stellaria holostea</i>	2.85		
<i>Stellaria media</i>	2.85		
<i>Trifolium pratense</i>	1.90		
<i>Valaria officinalis</i>	1.80		

Table 4.5b are tolerant of environmental variation and occur in many samples and different plant communities within the study area. The species showing low tolerance are typical of the gravel habitats, coarse substrate and areas prone to inundation. Grass species are highly tolerant, along with common herbaceous species and bryophytes.

4.3.4. Soil classification and description

Cluster analysis identified five soil/substrate groups based on soil profile and substrate characteristics. Tables of the soil/substrate groups, showing the values of the variables, summary statistics and the samples belonging to each group, are given in Appendix 11. The soil groups defined by cluster analysis were compared to the substrate types classified within the Tomdacheuille dataset and where groups were found to not be significantly different they were classified as the same group.

Group 1 is composed of gravel substrate with no soil profile development. The substrate texture is highly heterogeneous with a large range of substrate particle size classes. The samples are overall characterised by a coarse texture and are derived from the gravel island habitat.

Substrate group 3 occurs where there sample area is either inundated or the ground has a full matt of vegetation with no soil profile development overlying the gravel deposits, hence no data could be recorded in these circumstances.

Group 5 is composed of samples from woodland communities with considerably deeper soil profiles. Consequently these soils are more freely draining and have a lower pH as a result of leaching of these sandy soils. These soils are still lack distinct soil horizon development. The texture of these soils is dominated by medium and fine sands and is well mixed.

Group 6 is composed of deeper soil profiles, although still immature in development. Profiles are more well-drained than group 7, probably due to the deeper soils. These soils are also notably of a coarser texture which will reduce the moisture retention capacity of the substrate. The samples making up this group are from woodland and grassland communities.

Group 7 is characterised by shallow basic alluvial soils. The samples making up this group are mainly from the grassland communities. These soils have a relatively high soil moisture status and are composed of fine textured material. The organic content of these profiles is also on the whole greater than in the other soil/substrate groups.

4.3.5. Landform classification and description

Four landforms were identified within the study area. The landforms present are backwater, abandoned channel, point bar and floodplain. Floodplain is defined as land either side of the channel from the first major break in slope. Confusion may occur in definition in terraced floodplain environments but generally this approach should work.

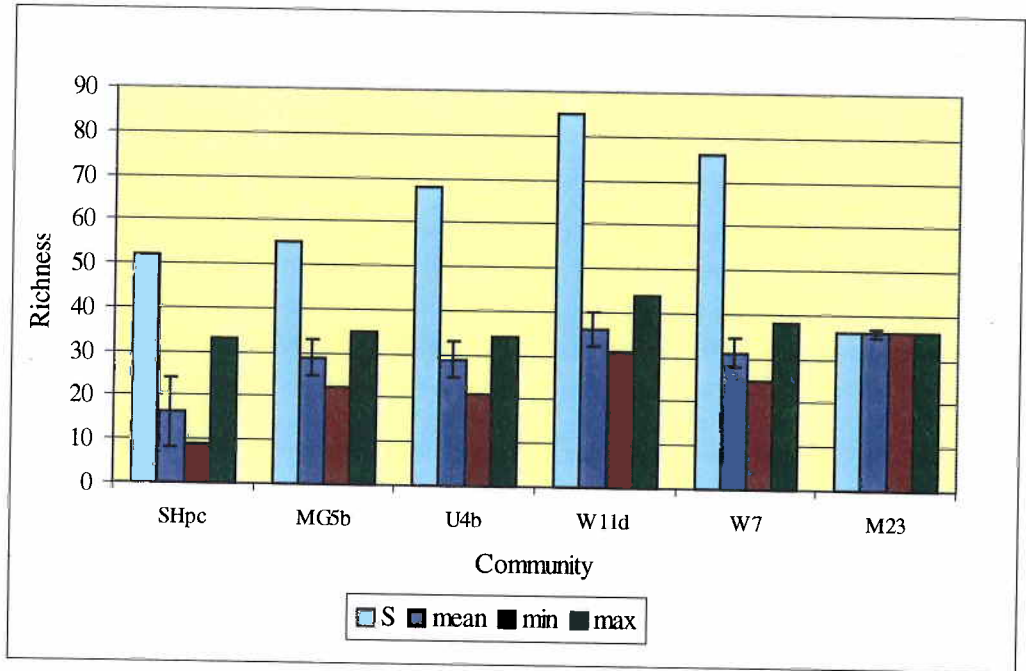
4.3.6. Diversity analysis

The results of the diversity analysis are presented in Figures 4.4-4.8 and Appendix 12. Diversity indices were calculated with the data grouped according to plant community, soil/substrate group, and landform class. In addition differences in diversity along transects perpendicular and parallel to the channel were also examined.

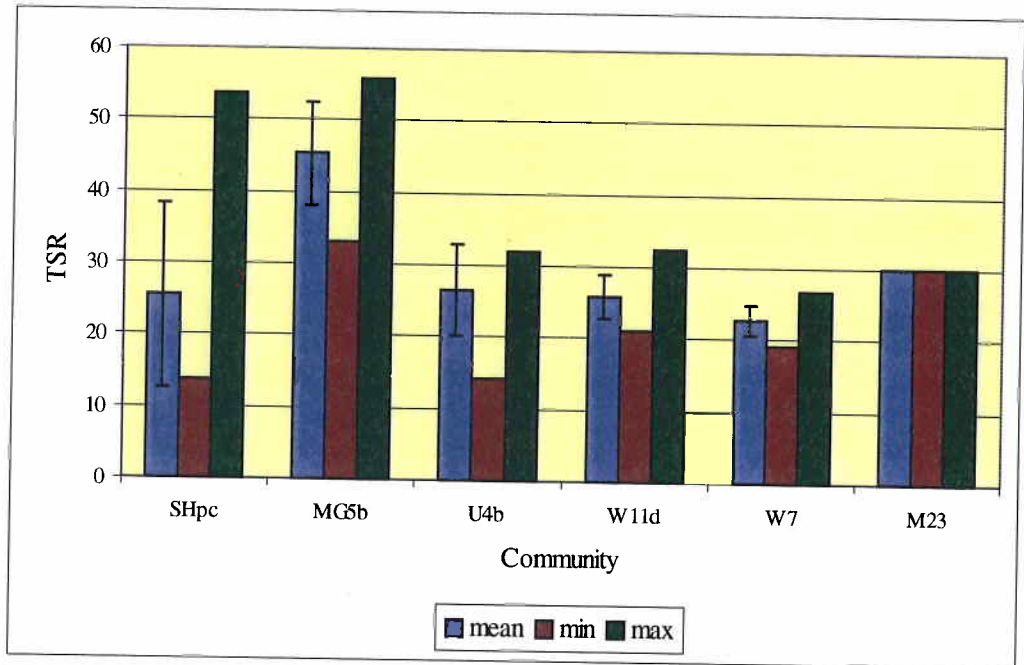
4.3.6a. Data grouped by plant community

4.3.6ai. Richness

Total species richness and summary statistics of species richness within each plant community are presented in Figure 4.4a and Figure 4.4b shows the results of the summary statistics of the TSR index within the study area. In terms of total species richness, Figure 4.4a shows W11c community to be the most diverse, with relatively high mean, minimum and maximum values and a low standard deviation. However this community is also the most extensive of all of the vegetation types thus increasing the likelihood of having a higher species diversity. The W7 woodland and U4b communities are also relatively species rich in terms of the total number of species present. The gravel bar community SHpc is the least diverse of the plant communities present. This is due to poor colonisation of the point bar at present with only localised patches of full vegetation cover existing. Where a full matt of vegetation does cover a



a)



b)

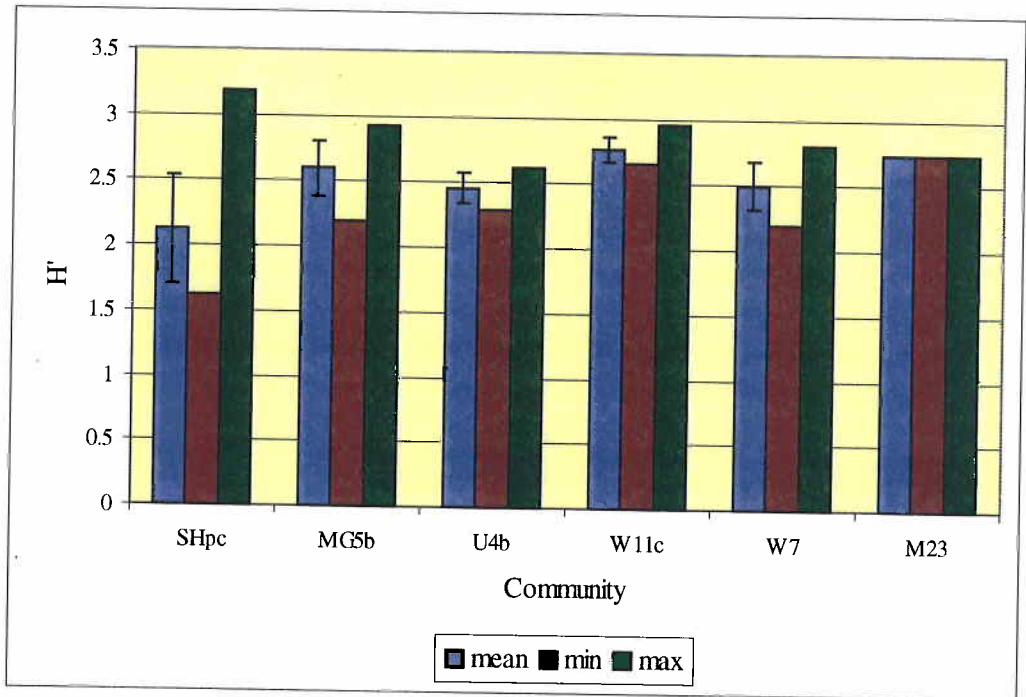
Figure 4.4: Summary statistics of a) total species richness and b) TSR within the plant communities within the Ballinluig dataset.

small area of the point bar, the patch is also generally composed of relatively few species. This community also shows the highest variance in species richness indicated by the standard error bar.

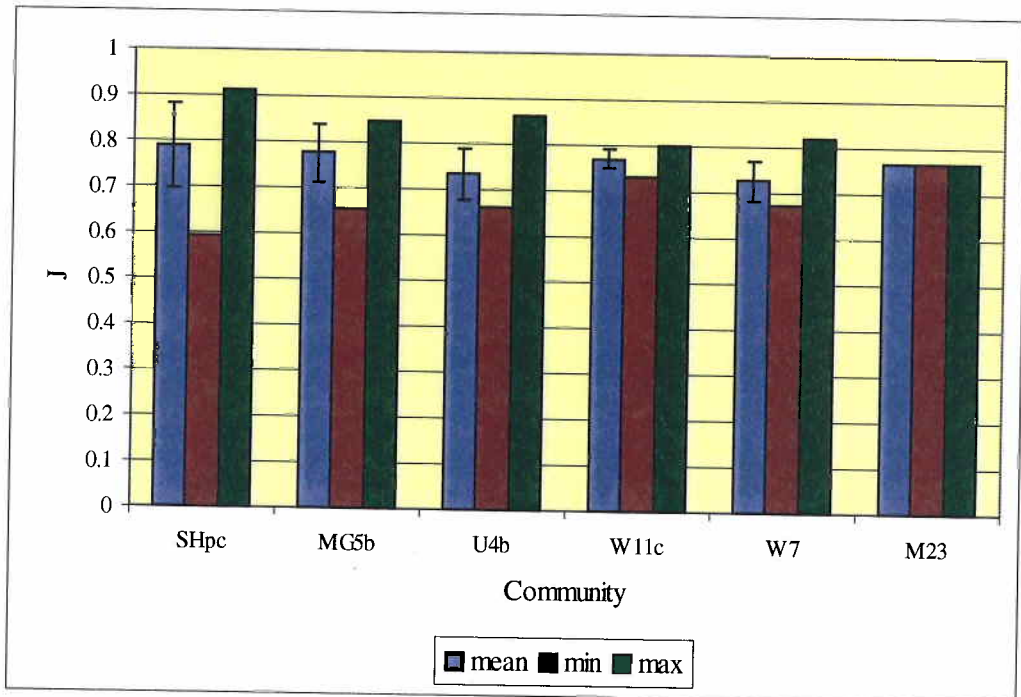
When accounting for sample area, the species richness for each community shows a markedly different pattern. The MG5b habitat is the most diverse, shown in Figure 4.4b. The W11d and W7 communities show little variation in species richness portrayed by TSR. High variance is again demonstrated in the SHpc habitats. A notable difference is the balancing out of the discrepancy between the species richness of the gravel community to the other habitats, where the mean number of species in the SHpc community is now similar to mean species richness in the U4b, W11c and W7 vegetation types.

4.3.6iii. Shannon index H' and J

The variation in diversity indices H' and J between the plant communities are presented in Figure 4.5. Figure 4.5a shows that the *Betula* woodland W11c is the most diverse with the highest mean Shannon index value of 2.8. The variance in species richness within this community is also very low, with a standard deviation of 0.1. The variation in the Shannon diversity index among the other communities is negligible, with the exception again of the gravel habitat, which has a low index value of 2.1 and a relatively high variance of 0.4.



a)



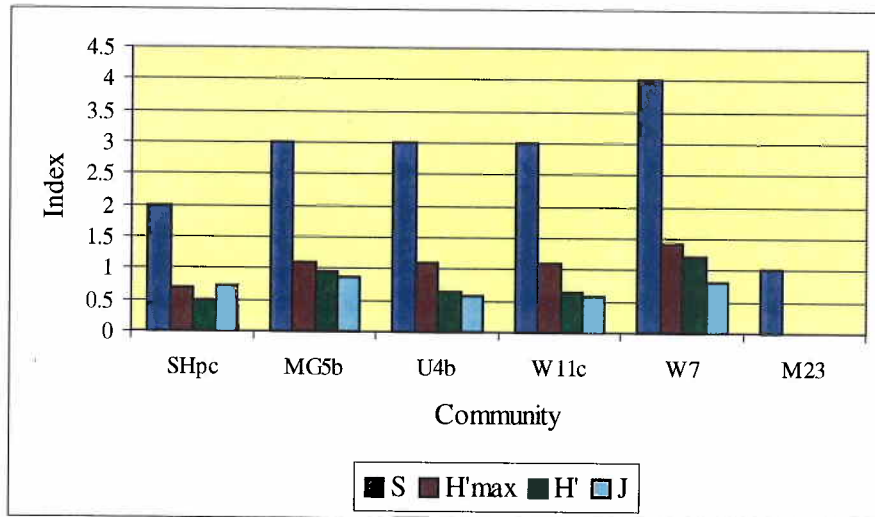
b)

Figure 4.5: Summary statistics showing species diversity in terms of a) Shannon index H' and b) equitability index J within the plant communities within the Ballinluig dataset.

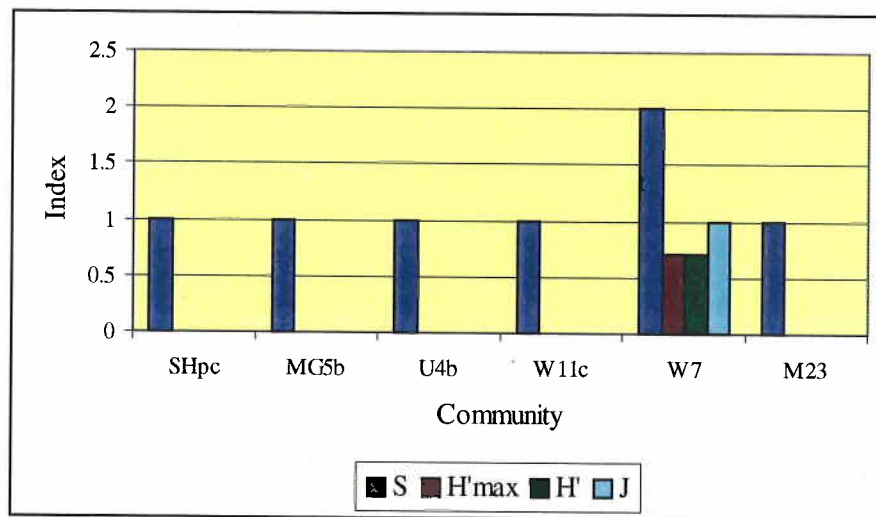
The Equitability index summary statistics describing the evenness of the distribution of the species as a measure of diversity are given in Figure 4.5b. The gravel habitat SHpc is the most diverse in terms of the evenness of the species distribution. The patches of vegetation within this habitat however tend to be composed of very few species with each species having a relatively high abundance. The U4b and the W7 communities have the lowest evenness score showing that there is a considerable level of variation in species abundance within the samples in comparison to the other vegetation types sampled.

4.3.6a.iii. Pedodiversity within the plant communities

Pedodiversity variation within the plant community types is illustrated in Figure 4.6a. The figure shows that pedodiversity within the SHpc community on the point bar holds congruence with the degree of pedological heterogeneity within the point bar in the Tomdachoille dataset. Values of S and H'_{max} within the U4b community at Ballinluig show congruence with pedodiversity within this community at Tomdachoille. Values of the Shannon index H' and J however are lower at Ballinluig within the U4b habitat suggesting differences in the proportion of the soil types present and that the soil types are less evenly distributed within this community. The *Betula* woodland community at Ballinluig has similar levels of H' and J revealing that congruence between species richness and evenness with the W11d community at Tomdachoille. The W7 community has slightly lower species richness in



a)



b)

Figure 4.6: Pedodiversity variation (a) and geodiversity variation (b) within the plant communities within the Ballinluig dataset. S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

comparison to the W7a variant at Tomdachoille Island. This vegetation type however holds similar levels of H'_{\max} , H' and J .

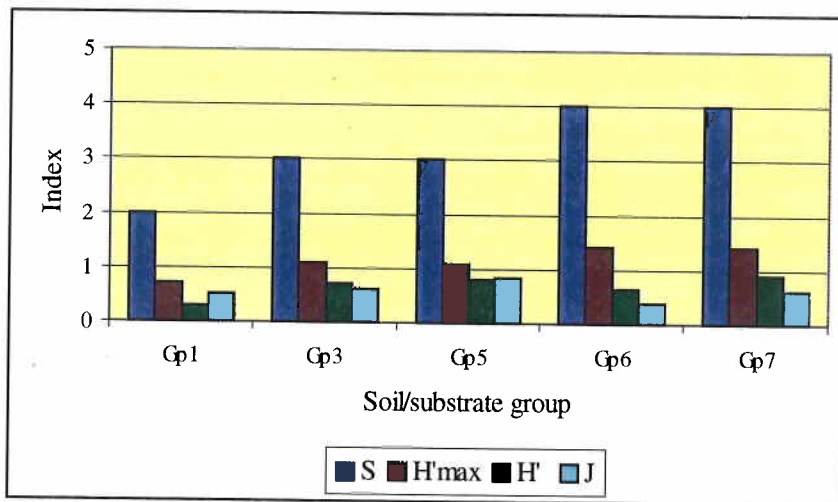
4.3.6aiv. Geodiversity within the plant communities

Figure 4.6b shows that the plant communities within the Ballinluig dataset are generally specific to a given geomorphic unit in contrast to the Tomdachoille data. However it is only the plant communities present at Tomdachoille and absent within the Ballinluig dataset that show greater geomorphic diversity otherwise that similar vegetation types within both datasets occur on only one landform type. The W7 community is the only vegetation type to span more than one landform type. The extent of this community is evenly distributed between the two landforms indicated by the value of J being 1.0.

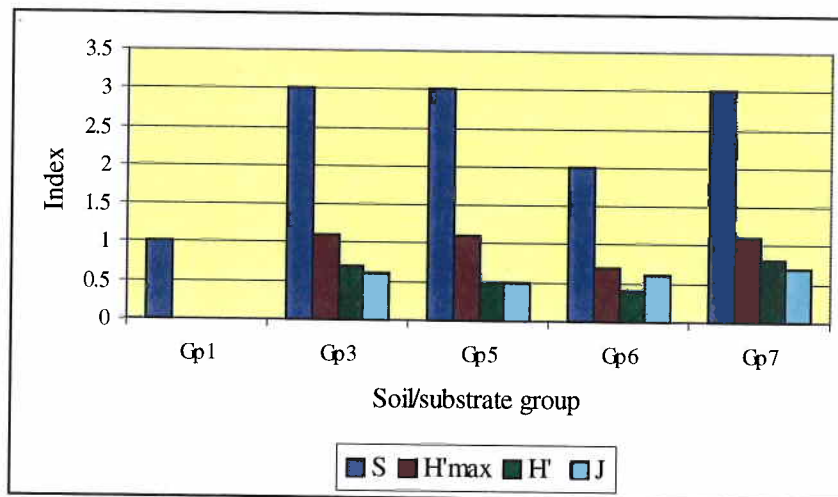
4.3.6b. Data grouped by soil/substrate group

4.3.6bi. Biodiversity within the soil groups

Figure 4.7a shows that there is low biodiversity present within substrate class 1 within the Ballinluig dataset in contrast to Tomdachoille where seven plant communities were present on this substrate type. Again this is a result of the complex spatial patterning being less pronounced within the Ballinluig dataset in contrast to Tomdachoille. Overall plant community diversity within the soil/substrate groups is lower within the Ballinluig dataset in contrast to



a)



b)

Figure 4.7: Biodiversity variation (a) and geodiversity variation (b) within the soil/substrate groups within the Ballinluig dataset. S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

Tomdachoille. This suggests that the spatial patterning of plant communities holds similarities to the spatial organisation of the substrate types.

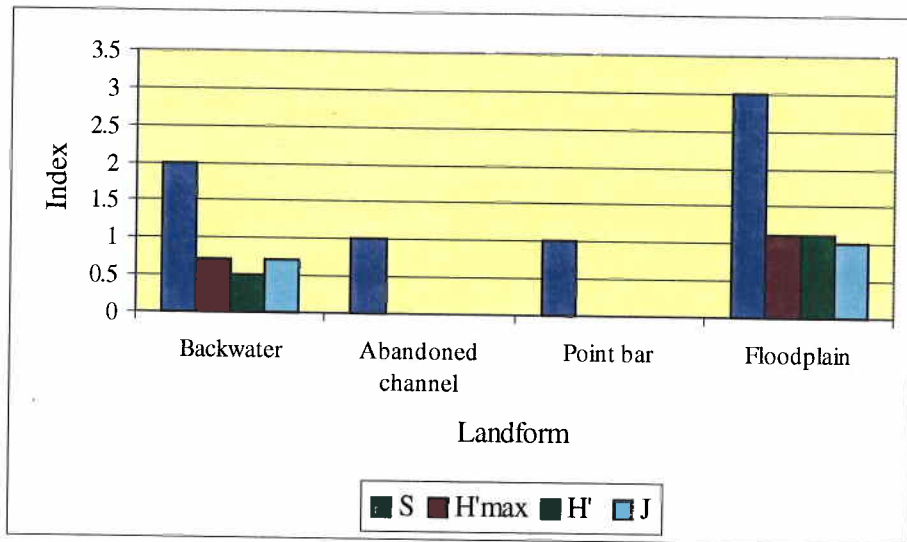
4.3.6bii. Geodiversity within the soil groups

Figure 4.7b shows that geodiversity within the soil groups is relatively low in comparison to Tomdachoille analysis in Figure 3.9b. However, this is possibly due to fewer landforms being present within the Ballinluig dataset. The diversity indices H'_{\max} , H' and J are lower than at Tomdachoille suggesting an uneven distribution of the substrate types between the landform classes.

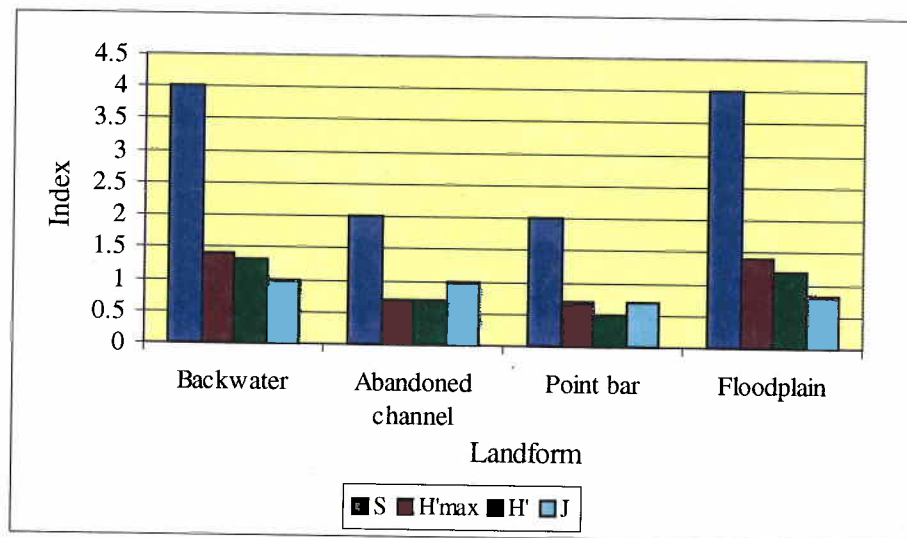
4.3.6c. Data grouped by landform

4.3.6ci. Biodiversity within the landform classes

Figure 4.8a shows that biodiversity is relatively low within the backwater in contrast to diversity levels at Tomdachoille (Figure 3.10a). Fewer plant communities are present and H'_{\max} and H' are also lower are the plant communities have a less even distribution within the landform in comparison to Tomdachoille. Biodiversity within the abandoned channel and point bar landforms is also considerably lower in comparison to Tomdachoille. Within the Ballinluig dataset the plant communities are distributed within a single landform type in contrast to Tomdachoille where some vegetation types are found on more than one geomorphic unit. This is in agreement with the results in Figure 4.6b suggesting that plant communities at Ballinluig are organised



a)



b)

Figure 4.8: Biodiversity variation (a) and pedodiversity variation (b) within the landform classes within the Ballinluig dataset. S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

more in congruence with the geomorphic units of the landscape. The floodplain landform has fewer plant communities in comparison to Tomdachoille, but is still the most floristically diverse landform present within the Ballinluig data. Values of H'_{\max} and H' are slightly lower than at Tomdachoille but J is higher indicating that the vegetation types at Ballinluig are more evenly distributed within the landform than at Tomdachoille.

4.3.6cii. Pedodiversity within the landform classes

Figure 4.8b shows that the backwater landform at Ballinluig is pedologically more diverse than at Tomdachoille (Figure 3.10b) with four different substrate groups present. This substrate heterogeneity provides a range of different niches for species to colonise, however, the results in Figure 4.8a show that biodiversity is lower within the backwater at Ballinluig. Pedological diversity within the abandoned channel and point bar within the Ballinluig dataset are less diverse in contrast to Tomdachoille. Considerably fewer substrate types are present and H'_{\max} , H' and J also have a lower score. Pedorichness within the floodplain zones at Ballinluig is equal to Tomdachoille and similar levels of the other three diversity indices are also observed between the two data sets for the floodplain landforms.

4.3.6d. Diversity variation perpendicular and parallel to the main channel

4.3.6di. Habitat diversity

The results in Table 4.6 show variations in floristic diversity between quadrats parallel and perpendicular to the main channel within each plant community type. The overall trend shows diversity to be greatest in the perpendicular orientation to the main channel within the plant communities. This is in agreement with the findings in Chapter 3 where biodiversity was shown to be greatest along this orientation to the river. The exception to this trend is within the W7 community where diversity is higher parallel to the channel. This may be a result of this transect being less frequently inundated due to the higher elevations thus allowing plant succession to progress more rapidly than in the lower lying and frequently inundated zones. Values for S , H'_{\max} and H' tend to vary within each community along the two orientations to the channel. Despite this, the evenness of the distribution of diversity parallel and perpendicular to the channel are equal with the exception in the W7 community where diversity scores lower on the equitability index perpendicular to the channel. Diversity is possibly higher along the perpendicular axis due to a lower inundation frequency and greater shelter from disturbance.

Table 4.6: Biodiversity parallel and perpendicular to the main channel within the a) W11c b) U4b c) MG5b d) W7 and e) SHpc community. N = number of observations; S = species richness; H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

a)

	Mean				
	N	S	H'_{max}	H'	J
Parallel	4	34.5	3.5	2.7	0.8
St. dev	-	2.6	0.1	0.0	0.0
Perpendicular	6	37.3	3.6	2.8	0.8
St. dev	-	4.3	0.1	0.1	0.0

b)

	Mean				
	N	S	H'_{max}	H'	J
Parallel	5	28.8	3.4	2.5	0.7
St. dev	-	2.9	0.1	0.1	0.0
Perpendicular	5	29.0	3.4	2.4	0.7
St. dev	-	5.1	0.2	0.1	0.1

c)

	Mean				
	N	S	H'_{max}	H'	J
Parallel	6	28.8	3.3	2.6	0.8
St. dev	-	4.8	0.2	0.2	0.1
Perpendicular	4	29.0	3.4	2.6	0.8
St. dev	-	3.6	0.1	0.2	15.3

d)

	Mean				
	N	S	H'_{max}	H'	J
Parallel	5	32.2	3.5	2.6	0.8
St. dev	-	3.4	0.1	0.1	0.0
Perpendicular	5	30.2	3.4	2.4	0.7
St. dev	-	3.0	0.1	0.1	0.0

e)

	Mean				
	N	S	H'_{max}	H'	J
Parallel	6	14.0	2.6	2.0	0.8
St. dev	-	6.7	0.4	0.2	0.1
Perpendicular	4	19.3	2.9	2.4	0.8
St. dev	-	9.3	0.4	0.6	0.1

4.3.6dii. Pedodiversity

The result of pedodiversity variation along transects parallel and perpendicular to the river within the vegetation types is presented in Table 4.7. Pedodiversity is greater in the parallel orientation to the river within the W11c and SHpc communities. The variation in substrate type along this orientation within the point bar community may be a result of the sorting of sediments by the river during high flows creating this longitudinal pattern along the point bar. The W11c community has developed on a former point bar and is a longitudinal feature adjacent to the channel. Therefore this sorting of sediments creating longitudinal variation in substrate type may be inherited from past processes. The pedological variation within the landforms may also be an influential factor in the spatial pattern of vegetation types. Pedodiversity is higher in the perpendicular orientation within the MG5b and W7 communities. Table 4.7c shows that H' and J are slightly higher in the perpendicular axis within the MG5b community showing a more even coverage of the substrate groups in contrast to the parallel directions. This is a result of fewer substrate types being present perpendicular to the river within this community. Pedodiversity is considerably higher in the perpendicular orientation within the W7 community. This is due to greater richness of substrate types being present therefore a higher H' score is derived. In terms of equitability however, there is no difference between the two orientations. Thus overall pedodiversity is greater perpendicular to the river within this community. Table 4.7b shows that pedodiversity is equal in both orientations to the channel within U4b vegetation type.

Table 4.7: Pedodiversity parallel and perpendicular to the main channel within the a) W11c b) U4b c) MG5b d) W7 and e) SHpc community. N = number of observations; S = species richness (number of soil types); H'_{max} = maximum negentropy; H' = Shannon index; J = equitability index.

a)

	N	S	H'_{max}	H'	J
Parallel	4	2	0.7	0.6	0.8
Perpendicular	6	2	0.7	0.5	0.7

b)

	N	S	H'_{max}	H'	J
Parallel	5	2	0.7	0.5	0.7
Perpendicular	5	2	0.7	0.5	0.7

c)

	N	S	H'_{max}	H'	J
Parallel	6	2	0.7	0.5	0.7
Perpendicular	4	2	0.7	0.6	0.8

d)

	N	S	H'_{max}	H'	J
Parallel	5	2	0.7	0.7	1.0
Perpendicular	5	4	1.4	1.3	1.0

e)

	N	S	H'_{max}	H'	J
Parallel	6	2	0.7	0.6	1.0
Perpendicular	4	1	0.0	0.0	0.0

4.3.6diii. Geodiversity

As sampling was undertaken within the discrete vegetation types identified by NVC Phase 1 mapping and the plant communities being unique to a given landform type, it is not possible to analyse geomorphic diversity along the transect sampled.

4.3.7. Species unique to landform units and vegetation types

The number of species unique to each landform type was assessed from the dataset. The results of the analysis are presented in Table 4.8 and the data is presented in Appendix 13. The results in Table 4.8a reveal that a high number of species are unique to one landform unit. This again emphasises the importance of a suite of landform types within fluvial environments for maintaining species richness and diversity. This is also illustrated in Table 4.8c where locally rare species are present in all land unit classes. A decline in the number of species common to the land unit classes is observed with an increase in the number of land unit types with few species being common to all land unit types. Table 4.8b shows the break down of which landforms these species are unique to. Those unique to just one landform class are predominantly within the floodplain zones. This is probably a result of higher species richness within this landform and also as a result of a longer history of development. The landforms that are typically inundated frequently have the next highest number of unique species. There is little difference in the number of species unique to two landform classes between the landform types.

Table 4.8: Count of species unique to the landform classes. Showing a) the number of species encountered in all landform classes through to the number of species unique to one landform class; b) the number of species unique to only one or two landform classes and c) the count of the number of rare species nationally, locally and the total number of species occurring within each landform class within the Ballinluig dataset.

a)

58 species found only in one landform
43 species found only in two landforms
34 species found in three landforms
13 species found in four landforms

b)

Landform	One landform	Two landforms
Backwater	9	25
Abandoned channel	3	19
Point bar	9	19
Floodplain	37	23

c)

Landform	Nationally rare	Locally rare	Locally very rare	Total number of species
Backwater	0	1	0	79
Abandoned channel	0	1	0	58
Point bar	0	2	1	54
Floodplain	3	2	2	107

The data was further analysed to examine the number of species unique to each vegetation type present within the dataset. The results of the analysis are presented in Table 4.9 and Appendix 13b. Table 4.9a shows that a high number of species are unique to one or two plant community types. Relatively few species are common to five of the vegetation types and no species are common to all six plant communities. Table 4.9b shows the ecological importance of carr woodland communities where the W7 vegetation type has the highest number of unique species present. It is also worth noting from the

Table 4.9: Count of species unique to the plant community types. Showing a) the number of species encountered in all plant communities through to the number of species unique to one plant community; b) the number of species unique to only one or two plant communities and c) the count of the number of rare species nationally, locally and the total number of species occurring within each plant community within the Ballinluig dataset.

a)

40 species found in only one plant community
44 species found in only two plant communities
31 species found in only three plant communities
23 species found in four plant communities
10 species found in five plant communities
0 species found in all six plant communities

b)

Plant community	One plant community	Two plant communities
SHpc	8	9
MG5b	3	17
U4b	2	14
W11c	9	20
W7	17	15
M23	3	11

c)

Plant community	Nationally rare	Locally rare	Locally very rare	Total number of species
SHpc	0	2	1	54
MG5b	2	1	2	55
U4b	1	1	1	65
W11c	0	2	0	81
W7	0	1	0	72
M23	0	1	0	36

table that the gravel bar is also important for providing a habitat for unique species and therefore plays an important role in enhancing species richness within the river corridor. The highest numbers of species unique to two plant communities are within the W7 and W11c groups. This is a result of considerable overlap between these two woodland communities which have

species common to each other due to the community structure. Likewise an overlap occurs between the grassland communities MG5b and U4b and the gravel community SHpc and the adjacent M23 vegetation type. Table 4.9c shows that nationally rare species are present within the herb rich grassland communities. This is possibly due to semi-natural grassland being relatively rare within the UK context due to land management practices. Locally rare species are present in all of the vegetation types within the dataset. The ecological value of semi-natural grassland is further supported by the presence of locally very rare species within these communities. Table 4.9c also shows that species richness also increases along a gradient from inundated fen community to gravel bar to grassland, wet woodland and finally the highest species richness within the mature *Betula* woodland.

4.3.8. Relationships between variables- correlation and regression

4.3.8i. Correlation

The results of the correlation analysis between environmental variables and indices within the Ballinluig dataset are presented in Table 4.10. Numerous significant correlations were found between the variables when addressing the hypotheses that species diversity and vegetation composition are related to geomorphic and pedological properties, and in addition, pedological variation is related to geomorphic units. Table 4.10a shows that plant community type is positively correlated with elevation suggesting that geomorphic heterogeneity does influence plant community development and composition. Elevation also

Table 4.10: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the Ballinlugh data set. $n = 49$ (two-tail test); critical value = 0.2732; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

a)													
	Plant community	Landform	Elevation (m)	H'	H'max	J	S	TSR					
Landform	-	-	-	-	-	-	-	-					
Elevation (m)	0.294*	0.606***	-	-	-	-	-	-					
H'	-	0.300*	-	-	-	-	-	-					
H'max	-0.403**	-	-	0.776***	-	-	-	-					
J	-	-	-	0.390**	-	-	-	-					
S	-0.422**	-	-	0.773***	0.981***	-	-	-					
TSR	0.489***	0.371**	0.439**	0.415**	0.377**	-	0.335*	-					
Tree cover	-0.372**	-0.422**	-0.411**	0.325*	0.457**	-	0.495***	-0.377**					
Tall herb cover	-0.455**	-	-	0.511***	0.576***	-	0.545***	-					
Herb cover	-	-	-	-	-	-	-	-					
Moss cover	-0.522***	0.669***	-	-	-	-	0.358*	-					
b)													
	Plant community	Landform	Elevation (m)	H'	H'max	J	S	TSR	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover
Soil depth	-0.493***	0.285*	-	0.448**	0.565***	-	0.610***	-	0.516***	-	0.644***	-	0.279*
pH	-0.379**	0.447**	-	0.542***	0.664***	-	0.624***	-	-	-	0.692***	-	0.438**
SMC	-0.492***	-	-	0.339*	0.490***	-	0.447**	-	0.317*	-	0.552***	-	0.319*
OMC	-0.466**	-	-	-	0.383**	-	0.365**	-	-	-	0.403**	-	0.431**
Unvegetated gravel	0.353*	-0.414**	-	-0.602***	-0.833***	0.302*	-0.778***	0.367**	-	-	-0.675***	-0.366**	-0.434**
Sand drape	-	-	-	-	-	-	-	0.327*	-	-	-	-	-
Leaf litter	-	-0.313*	-	-	0.406**	-	0.419**	-	0.377**	-	-	-	-
MEAN	-	0.318*	-	0.351*	0.542***	-	0.569***	-	0.397**	-	0.308*	0.314*	-
MINDOM	-	-0.331*	-	-	-	0.367*	-	-	-	-	-0.338*	-	-
MAXDOM	0.376*	-0.295*	-	-0.501***	-0.781***	0.407**	-0.709***	-	-0.358*	-	-0.689***	-0.358*	-0.367*
MEDOM	-	-	-	0.356*	0.545***	-	0.572***	-	0.449**	-	0.308*	0.305*	-
MODOM	-0.436**	0.378*	-	0.454**	0.722***	-	0.697***	-	0.338*	-	0.538***	0.427**	0.416**
Range	0.324*	-	-	-0.416**	-0.711***	0.392**	-0.638***	-	-0.339*	-	-0.585***	-0.341*	-0.326*
Heterogeneity	-	-	-	-	-	0.335*	-	-	-	-	-	-	-
Soil/substrate class	-0.346*	0.331*	-	0.472***	0.657***	-	0.590***	-	-	-	0.606***	-	0.376**

holds a strong positive correlation with landform type indicating that the structural mosaic of the geomorphic units is relative to height. Plant community type is related to the species diversity of the communities indicated by the correlation between plant community with H'_{\max} , S and TSR. This relationship indicates that species diversity is greatest in the more mature plant communities and lowest in the gravel habitats. TSR also increases with elevation. The correlation between H' and landform suggests that species diversity is related to geomorphic heterogeneity within fluvial environments. The direction of this relationship shows that species diversity increases along a gradient of reduced frequency inundation. In terms of plant community structure, tree cover is again negatively correlated with landform and elevation showing that tree cover is more dense within the lower lying zones of the study area. This is in agreement with the baseline study and findings by other authors such as Baker (1990) and Van Splunder (1998). Tree cover holds a positive relationship with diversity indices showing that the presence of trees increases diversity levels locally. This is due to either the diverse array of flora wet woodlands support or due to the high diversity associated with mature stands which are present within areas of the floodplain. Tall herb cover and moss cover hold a positive relationship with diversity indices. This emphasises the importance of moss colonisation in promoting vegetation colonisation within the gravel bars.

The results in Table 4.10b show that plant community type is related to the soil properties where mature plant communities tend to occur on the more developed soil profiles. Soil properties are correlated with landform type

revealing that these two landscape features are related. Soil development is greater within the landforms that are less frequently inundated. Floristic characteristics in terms of diversity and vegetation structure are strongly correlated to soil properties. The floristic characteristics tend to increase with greater pedological development of the soil and substrate properties. The results of the correlation analysis between environmental variables and indices within the Ballinluig dataset has proven that floristic diversity and vegetation structure is related to elevation and geomorphic heterogeneity and soil/substrate properties. In addition, soil/substrate characteristics are also related to geomorphic land unit type.

Few significant correlations were found within the backwater landform, shown in Table 4.11. Species diversity indices are correlated with plant community type and vegetation structure. These floristic characteristics are also related to elevation showing the influence of the frequency of inundation and age of development on plant community structure. Table 4.11b shows that substrate size becomes finer with an increase in elevation indicated by the negative relationship with MAXDOM and a positive relationship with particle size range suggesting the presence of finer particles within the substrate mix. Species diversity holds a positive correlation with particle size heterogeneity, probably as a result of finer substrates being present within the matrix. Species structure is also correlated with soil properties where tall herb cover increases with greater soil depth and higher pH. Herb cover holds a negative relationship with OMC, possibly due to more frequent inundation which slows down the rate of decomposition of organic matter under anaerobic conditions.

Table 4.11: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the backwater landform on Ballinluig Island SSSI. $n = 4$ (two-tail test); critical value = 0.8114; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

a)

	Plant community	Landform	Elevation (m)	H'	H' max	J	S	TSR
Landform	-							
Elevation (m)	-0.908*							
H'	0.855*							
H' max	-			0.873*				
J	0.893*			0.941**				
S	-			0.896*	0.998***			
TSR	0.854*			0.934**	0.898*	0.818*	0.924**	
Tree cover	-0.983***		0.965**	-	-	-0.854*	-	
Tall herb cover	-		0.865*	-	-	-	-	
Herb cover	-		-	-	-	-	-	
Moss cover	-		-	-	-	-	-	

b)

	Plant community	Landform	Elevation (m)	H'	H' max	J	S	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover
Soil depth	-									0.943**	-	-
pH	-									0.869*	-	-
SMC	-									-	-	-
OMC	-									-	-0.870*	-
Unvegetated gravel	-									-	-	-
Sand drape	-									-	-	-
Leaf litter	-									-	-	-
MAXDOM	-		-0.986*							-	-	-
Range	-		0.959*							-	-	-
Heterogeneity	-			0.936*	0.960**		0.956*			-	-	-
Soil/substrate class	-									-	-	-

Table 4.12 shows the significant correlations within the abandoned channel on Ballinluig Island SSSI. The analysis yielded very few significant results between environmental properties and indices. Overall the results show that species diversity measured by the Shannon index increases with an increase in the herb layer cover within this landform. Diversity also tends to increase with a fining of the substrate matrix, indicated in Table 4.12b. However, tree cover tends to decrease with a fining of substrate size indicated by its relationship with the MINDOM particle size index.

Table 4.13 shows the results of correlation analysis within the point bar landform opposite Tomdachoille Island SSSI. Again few significant correlations were derived between species diversity indices, vegetation structure and geomorphic variables. Diversity indices are positively correlated with each other as can be expected. Herb cover holds a negative relationship with the equitability index suggesting that species richness increases with an increase in herb cover, however the species present then hold an uneven distribution with one or a few species holding dominance within a more heterogeneous species pattern.

Table 4.13b shows the importance of sand drapes on gravel habitats for increasing species richness locally due to the positive correlation between H' , H'_{\max} , S, and TSR with sand drapes. The equitability index holds a positive correlation with the proportion of unvegetated gravel, which supports the negative relationship between J and herb cover. This is because where there is a high level of unvegetated gravel, substrate size tends to be coarser and fewer

Table 4.12: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the abandoned channel landform on Ballinluig Island SSSI. $n = 3$; critical value = 0.8783; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

a)

	Plant community	Landform	Elevation (m)	H'	H'max	J	S	TSR
Landform	-	-	-	-	-	-	-	-
Elevation (m)	-	-	-	-	-	-	-	-
H'	-	-	-	-	-	-	-	-
H'max	-	-	-	-	-	-	-	-
J	-	-	-	-	-	-	-	-
S	-	-	-	0.999***	-	-	-	-
TSR	-	-	-	0.995***	-	0.997***	-	-
Tree cover	-	-	-	-	-	-	-	-
Tall herb cover	-	-	-	-	-	-	-	-
Herb cover	-	-	0.884*	-	-	-	-	-
Moss cover	-	-	-	-	-	-	-	-

b)

	Plant community	Landform	Elevation (m)	H'	H'max	J	S	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover
Soil depth	-	-	-	-	-	-	-	-	-	-	-	-
pH	-	-	-	-	-	-	-	-	-	-	-	-
SMC	-	-	-	-	-	-	-	-	-	-	-	-
OMC	-	-	-	-	-	-	-	-	-	-	-	-
Unvegetated gravel	-	-	-	-	-	-	-	-	-	-	-	-
Sand drape	-	-	-	-	-	-	-	-	-	-	-	-
Leaf litter	-	-	-	-	-	-	-	-	-	-	-	-
MEAN	-	-	-	-	-	-	-	-	-	-	-	-
MINDOM	-	-	-	-	-	-	-	-	-0.881*	-	-	-
MAXDOM	-	-	-	-	-	-	-	-	-	-	-	-
MEDOM	-	-	-	-	-	-	-	-	-	-	-	-
MODOM	-	-	-	-	-	-	-	-	-	-	-	-
Range	-	-	-	-0.935*	-	-	-0.948*	-0.964***	-	-	-	-
Heterogeneity	-	-	-	-0.935*	-	-	-0.948*	-0.964***	-	-	-	-
Soil/substrate class	-	-	-	-	-	-	-	-	-	-	-	-

Table 4.13: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the point bar landform. $n = 8$ (two-tail test); critical value = 0.6319; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

a)

	Plant community	Landform	Elevation (m)	H'	H' max	J	S	TSR
Landform	-	-	-	-	-	-	-	-
Elevation (m)	-	-	-	-	-	-	-	-
H'	-	-	-	-	-	-	-	-
H' max	-	-	-	0.727*	-	-	-	-
J	-	-	-	-	-	-	-	-
S	-	-	-	0.750*	0.982***	-	-	-
TSR	-	-	-	0.747*	0.980***	-	0.998***	-
Tree cover	-	-	-	-	-	-	-	-
Tall herb cover	-	-	-	-	-	-	-	-
Herb cover	-	-	-	-	-	-0.808**	-	-
Moss cover	-	-	-	-	-	-	-	-

b)

	Plant community	Landform	Elevation (m)	H'	H' max	J	S	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover
Soil depth	-	-	-	-	-	-	-	-	-	-	-	-
pH	-	-	-	-	-	-	-	-	-	-	-	-
SMC	-	-	-	-	-	-	-	-	-	-	-	-
OMC	-	-	-	-	-	-	-	-	-	-	-	-
Unvegetated gravel	-	-	-	-	-0.766*	0.635*	-0.739*	-0.751*	-	-	-0.884**	-0.729*
Sand drupe	-	-	-	0.690*	0.655*	-	0.693*	0.717*	-	-	-	-
Leaf litter	-	-	-	0.655*	-	-	0.714*	0.724*	-	-	-	-
MEAN	-	-	-	-	-	-0.779*	-	-	-	-	-	-
MINDOM	-	-	-	0.779*	-	-	0.785*	0.756*	-	-	-	0.753*
MAXDOM	-	-	-	-	-	-	-	-	-	-	-	-
MEDOM	-	-	-	-	-	-	-	-	-	-	-	-
MODOM	-	-	-	-	-	-	-	-	-	-	-	-
Range	-	-	-	-	-	-	-	-	-	-	-	-
Heterogeneity	-	-	-	-	-	-	-	-	-	-	-0.633*	-
Soil group	-	-	-	-	-	-	-	-	-	-	0.643*	-

species have colonised. The pioneer species to colonise these harsh environmental conditions tend to occupy more equal coverage, thus leading to an increase in the equitability index. The coarseness of the unvegetated gravel is indicated by the negative relationship between moss cover and unvegetated gravel. Bryophytes also typically colonise zones that have a degree of stability, as they tend to be intolerant of disturbance. Species diversity indices tend to increase with an increase in substrate fineness indicated by the positive correlation between the indices and MINDOM. Moss cover also increases with substrate fining suggested by the relationship with the mean particle size index. Herb cover tends to decrease with an increase in the range of particle size classes.

Several significant correlations are found within the floodplain, shown in Table 4.14. Plant community type is related to elevation and vegetation structure. Plant community type also influence species richness indicated by TSR, highlighting the importance of a mosaic of habitat types to promote species richness. The floodplain vegetation types range from grassland to mature woodland communities. The extent of tree cover is positively correlated with species richness showing that species diversity is greater within the more mature vegetation types with a more complex structure.

Table 4.14b reveals that soil properties are correlated with elevation, vegetation type, species diversity and community structure. Soil depth is shown to hold a negative relationship with elevation within the floodplain. This is a result of the of the newly developing floodplain zone being of higher

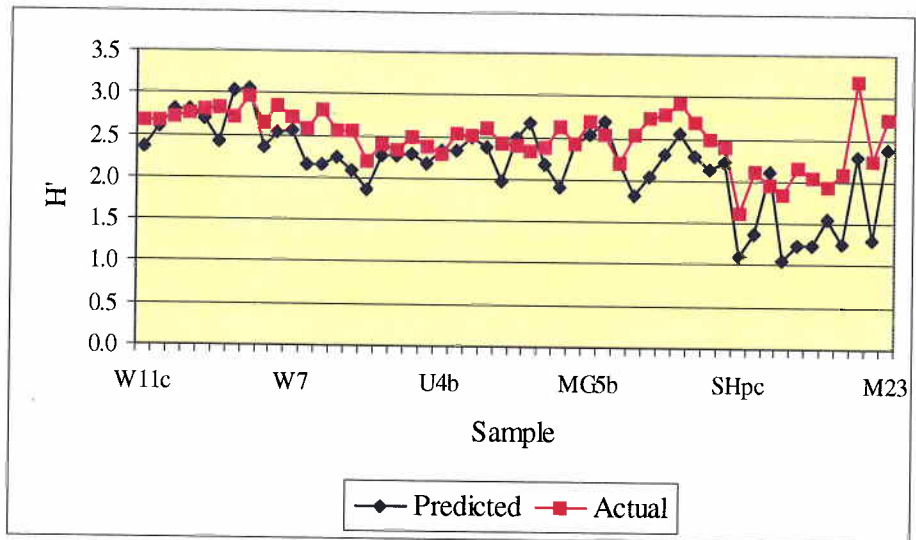
Table 4.14: Significant Pearson correlations ($p < 0.05$) between environmental variables and indices within the floodplain on Ballinluig Island SSSI. $n = 28$ (two-tail test); critical value = 0.3610; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; - = not significant.

a)												
	Plant community	Landform	Elevation (m)	H'	H' max	J	S	TSR				
Landform	-											
Elevation (m)	0.825***	-										
H'	-	-										
H' max	-	-	0.466**									
J	-	-	0.739***									
S	-	-	0.499***	0.993***								
TSR	0.846***	-	0.752***	-								
Tree cover	-0.429*	-	-0.440*	0.579**	0.645***	-	0.670***	-0.456*				
Tall herb cover	-	-	-	-	-	-	-	-0.414*				
Herb cover	-	-	-	-	-	-	-	-				
Moss cover	-0.508**	-	-0.445*	-	-	-	-	-				
b)												
	Plant community	Landform	Elevation (m)	H'	H' max	J	S	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover
Soil depth	-0.386*	-	-0.411*	-	0.548**	-	0.557**	-0.481**	0.659***	0.387*	-	-
pH	-	-	-	-	-	-	-	-	-	-	-	-
SMC	-0.443*	-	-	-	-	-	-	-	-	-	0.411*	-
OMC	-	-	-	-	-	-	-	-	-	-	0.372*	-
Unvegetated gravel	-	-	-	-	-	-	-	-	-	-	-	-
Sand drape	0.466**	-	0.501**	-	-	0.392*	-	0.446*	-	-	-	-0.369*
Leaf litter	-	-	-	-	-	-	-	0.373*	-	-	-	-
MEAN	-	-	-	-	0.520**	-	0.533**	-	0.647***	-	-	-
MINDOM	-0.507**	-	-0.657***	-	-	-	0.410*	-0.522**	0.497**	-	-	-
MAXDOM	-	-	-	-	-	-	-	-	0.459*	-	-	-
MEDOM	-	-	-	-	0.508**	-	0.529**	-	0.605**	-	-	-
MODOM	-	-	-	-	-	-	-	-	-	-	-	-
Range	-	-	-	-	-	-	-	-	-	-	-	-
Heterogeneity	-	-	-	-	-	-	-	-	-0.370*	-	-	-
Soil_group	-	-	-	-	-0.364*	-	-0.372*	-	-0.461*	-0.393*	-	-

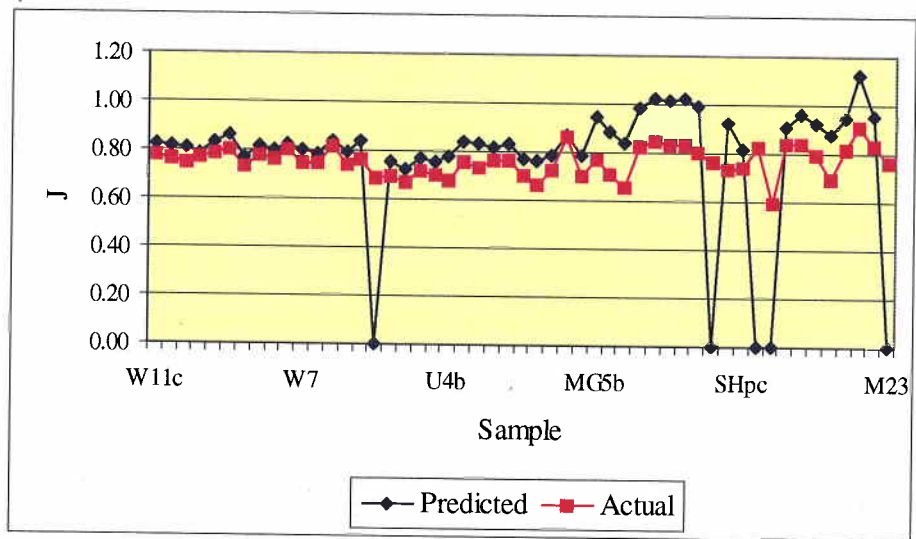
elevation than the mature zones of the floodplain. This area was a zone of unvegetated gravel during the 1940s. Possibly as a result of a relatively large scale flood with extensive gravel deposition occurring in this zone raising the height, it has now developed a bank face and is being incorporated into the floodplain and is no longer a point bar feature. Due to only approximately 50 years of isolation from annual inundation, only immature shallow soil profiles have developed. The negative relationship between soil depth, MINDOM and plant community type suggest that the more mature vegetation communities occur on the deeper soil profiles with a finer substrate mix. Species diversity and community structure complexity is also positively related to deeper soil profiles with finer substrate size.

4.3.8ii. Regression

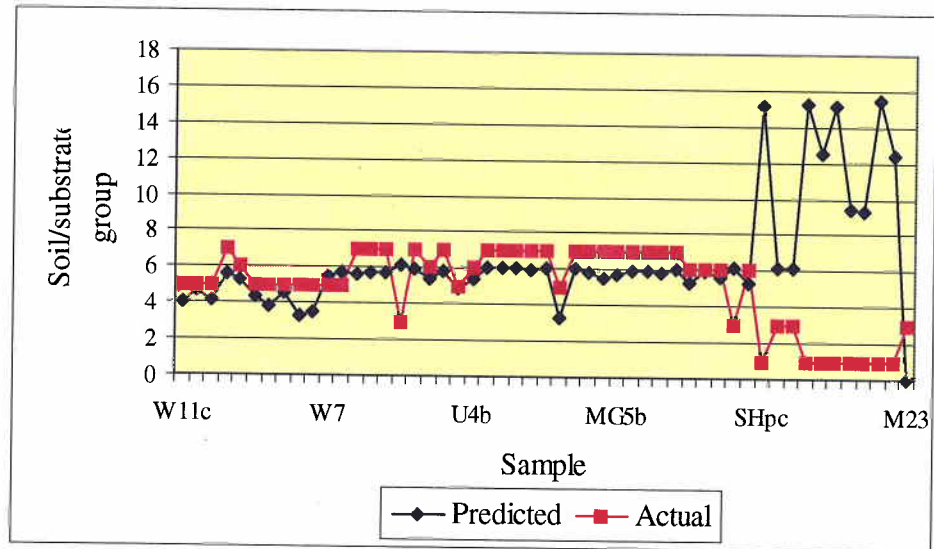
The regression equations derived in Chapter 3 for the whole data set failed to accurately predict the actual values recorded within the Ballinluig data set. All regression equations tested had a *t*-statistic greater than the critical value, therefore indicating that the null hypothesis that paired values are equal should be rejected. In all cases there was evidence to reject the null hypothesis at the 95% significance level as all returned *p*-values were 0.000. Actual-*v*-predicted values were plotted to examine where the models were failing. These graphs are illustrated in Figure 4.9. Figure 4.9 suggests that the regression model for predicting the Shannon index of diversity has the potential to accurately determine the value within the W11c, W7 and U4b communities on Ballinluig Island. These samples were tested separately for similarity using the paired



a)



b)



c)

Figure 4.9: Predicted values from regression models plotted against actual values for the dependent variables H' , J and soil/substrate group within the Ballinluig dataset, a) Shannon index (H'), b) equitability index (J) and c) soil substrate type.

t-test. The results revealed that the model can predict the Shannon index within the W11c community based on elevation, plant community type, species richness, herb cover and moss cover with a R^2 of 72.1%; the results of the analysis are presented in Table 4.15. The paired t-test returned a low t-statistic which lies between the upper and lower confidence interval and a high p-value indicating that the values are not significantly different. The graph in Figure 4.9b shows that the regression model for predicting equitability yields fairly accurate results within the W11c, W7 and U4b communities. The model fails in the MG5b and SHpc communities. This is due partly because the MG5b community is not present within the Tomdachoille dataset from which the models were derived, and secondly due to the heterogeneity within the gravel bars. The regression equation for predicting soil/substrate class failed but only marginally. The graph in Figure 4.9c shows that the regression equation failed to predict the substrate characteristics within the point bar landform. However, when testing a sub-set of this data to examine whether the regression equation has predictive capacity within some of the samples the results indicated that the null hypothesis that predicted and actual values are equal should be rejected.

Table 4.15: Paired t-test for the predictive capacity of the regression model for determining the Shannon index of diversity within the W11c sub-set of data from the Ballinluig Island database. Critical value = 2.26, 95% significance level.

	Paired differences	St dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
Predicted - Actual	-9.1546E-02	0.2329	7.365E-02	-0.2581	7.505E-02	-1.243	9	0.245

Regression models derived for environmental variables within the landform types were tested. The results show nine regression models with R^2 values between 65.4-97.7% proved successful at predicting the value of the dependent variable. The regression model for predicting plant community type within the backwater failed. Within the abandoned channel on Ballinluig Island, four regression models proved to have predictive ability. The results of the paired t-test between predicted and actual values are given in Table 4.16. The results show that not only species diversity indices of species count and the Shannon index for richness have been successfully modeled, but also species assemblage in terms of tree cover and tall herb cover can also be predicted with confidence within abandoned channels. The regression models for these dependent variables are very strong with R^2 values of 97.7% for species richness, 80.1% for H' , 81.9% for tree cover and 88.1% for tall herb cover. Species richness and the Shannon index are predicted based on the amount of shrub cover within this landform. Tree cover and tall herb cover are dependent on soil depth.

Within the point bar landform opposite Tomdachoille, two regression models accurately predicted values of H' and soil/substrate type. The results of the comparison of the predicted-v-actual results using the paired t-test are given in Table 4.17. The model for predicting the Shannon index is the strongest with a R^2 of 82.7% and shows that species diversity can be predicted from the independent variables TSR, herb cover and particle size range with confidence. Despite the poor predictive capacity of the regression models for the whole dataset in determining values within the point bar, the regression

models derived specifically for this landform type have proven to have some success. The regression models for predicting across the whole dataset failed as they are predicting across a steep environmental gradient with high heterogeneity across very short distances. The regression models derived

Table 4.16: Paired t-test for the predictive capacity of the regression model for determining a) species richness, b) Shannon index, c) tree cover and d) tall herb cover within the abandoned channel on Ballinluig Island. Critical value = 2.78, 95% significance level.

a)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
	Mean							
Predicted - Actual	2.8700	3.4205	1.5297	-1.3771	7.1171	1.876	4	0.134

b)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
	Mean							
Predicted - Actual	3.828E-03	0.1155	5.164E-02	-0.1396	0.1472	0.074	4	0.944

c)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
	Mean							
Predicted - Actual	-2.9200E-02	1.0678	0.4775	-1.3551	1.2967	-0.061	4	0.954

d)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
	Mean							
Predicted - Actual	-9.5204	8.6868	3.8849	-20.3065	1.2657	-2.451	4	0.070

Table 4.17: Paired t-test for the predictive capacity of the regression model for determining a) Shannon index and b) soil/substrate type within the point bar opposite Tomdachoille Island. Critical value = 2.26, 95% significance level.

a)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
	Mean			Lower	Upper			
Predicted - Actual	3.000E-02	9.487E-02	3.000E-02	-3.786E-02	9.786E-02	1.000	9	0.343

b)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
	Mean			Lower	Upper			
Predicted - Actual	1.0732	1.6075	0.5084	-7.6735E-02	2.2232	2.111	9	0.064

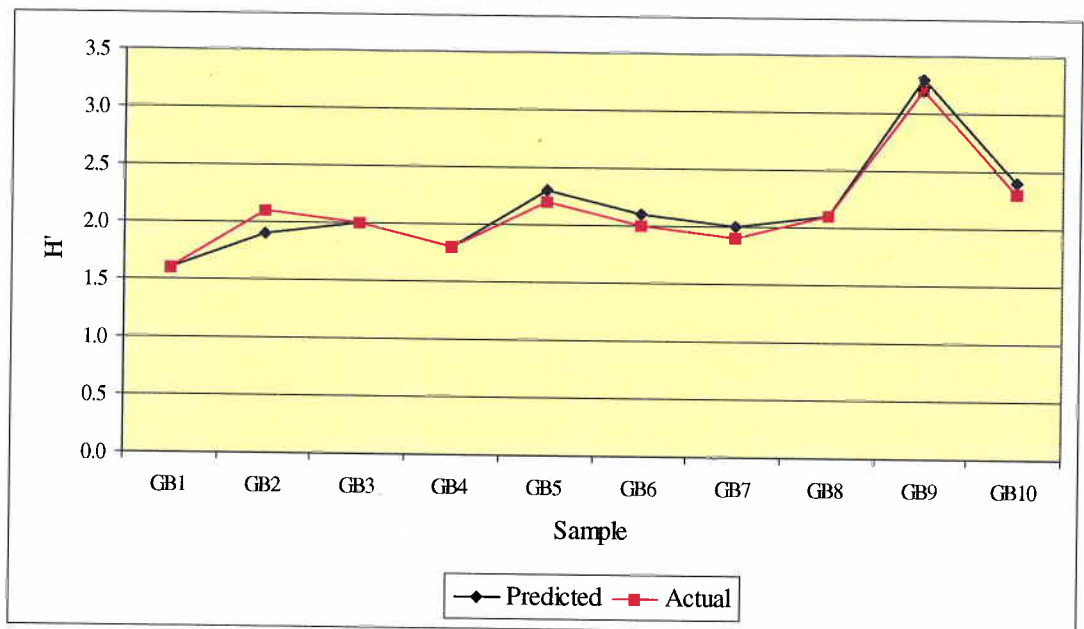


Figure 4.10: Predicted values plotted against actual values for the dependent variable H' within the point bar landform opposite Tomdachoille Island SSSI.

within the discrete landscape units therefore have a greater probability of success due to the elimination of a great source of variation induced by amalgamating the mosaic of landscape units. The graph in Figure 4.10 shows that the predicted values of H' within the point bar closely match the actual values calculated from the dataset. Thus species diversity expressed by the Shannon index can be predicted with confidence based upon three independent variables with an R^2 of 82.7%. Substrate type is predicted using independent variables of substrate characteristics MEDOM, mean and particle size range with a R^2 of 81.9%.

The results of the paired t-test to examine the ability of the regression models to predict environmental variables within the floodplain landform on Ballinluig Island are presented in Table 4.18. The analysis has proven that plant community type, species richness and soil type can be predicted with accuracy using the regression models produced from the Tomdachoille dataset with R^2 values of 82.5%, 65.4% and 82.3% respectively. The graph in Figure 4.11 shows that species richness can be predicted with great accuracy despite the relatively low R^2 value. The graph shows that the predicted values closely mirror actual values within each sample. The regression model has successfully predicted species richness using information on shrub cover, OMC and the proportion of fine gravel within the soil matrix. The model has probably succeeded in accurate prediction due to similar processes operating along this river in the creation of landform and species assemblages. Although it has been reported that the spatial organisation and heterogeneity of plant communities is similar within fluvial environments (Malanson, 1993) this

regression model may not be able to predict with such accuracy at other locations due to different local factors coming into play. Plant community type within the floodplain is predicted by diversity indices species richness, H' and J along with tree cover, shrub cover and soil depth. Tree cover, MODOM and the proportion of small cobbles in the soil matrix predict soil type using this regression model. Where the soil type is composed of a coarser substrate mix, the plant community is typically grassland and woodland communities have developed on the soil profiles with a finer substrate texture.

4.3.9. ANOVA

One-way ANOVA was carried out on the data to examine whether there was significant variation between environmental variables between the landform types. The results of the analysis are presented in Table 4.19 for elevation and species diversity variables and Table 4.20 for pedological variables. Bonferroni post hoc tests were carried out on significant results to reveal where the main source of variation between the landform types lie. The results of the post hoc tests are presented in Appendix 14. Table 4.19 shows that there is significant variation between the environmental variables between the landform types with the exception of the equitability index. This reveals that there is significant difference in elevation and species diversity properties within the study area and that these properties vary between the different geomorphic units. However the consistency between J and the null hypothesis

Table 4.18: Paired t-test for the predictive capacity of the regression model for determining a) plant community type, b) species richness and c) soil/substrate type within the floodplain landform zones on Ballinluig Island. Critical value = 2.05, 95% significance level.

a)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
Predicted - Actual	0.2500	0.6387	0.1428	-4.8905E-02	1.8489	1.751	29	0.096

b)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
Predicted - Actual	-.2969	1.2187	0.2225	-1.7519	0.1582	-1.334	29	0.193

c)

	Paired differences	St. dev	St. error mean	95% Confidence Interval of the difference		t	df	Sig. (two-tailed)
				Lower	Upper			
Predicted - Actual	-5.7621E-02	1.2475	0.2317	-0.5321	0.4169	-0.249	29	0.805

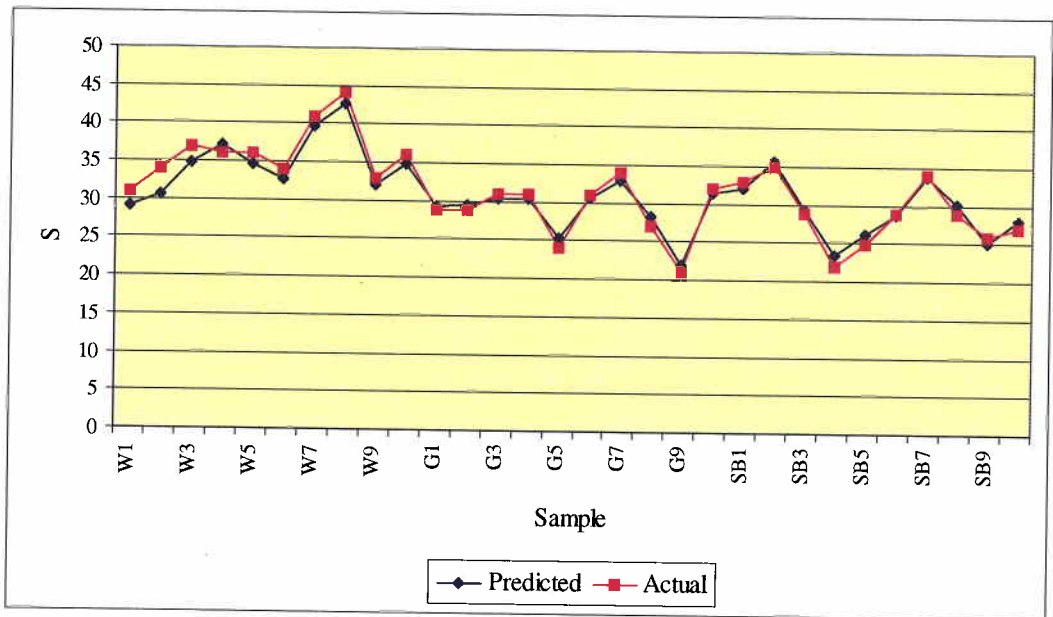


Figure 4.11: Predicted values from the regression model plotted against actual values for the dependent variables species richness (S) within the Ballinluig dataset.

that there is no variation between landform types suggests that although species diversity does differ significantly in terms of richness between landforms, the evenness of species distribution is similar within and between landform types. This is indicated by the negligible difference in the mean square values in Table 4.19c and the low F-statistic which show that there is little difference between the within group variability and between group variability. The low F-statistic therefore implies that the data is consistent with the null hypothesis in the case of species equitability; this is also reinforced by the high p-value. Table 4.19d shows that the greatest difference between the landforms are species richness. This is indicated by the large difference between the between groups and within groups mean square values and the high F-statistic.

The post hoc tests in Appendix 14a-c show where the main source of variation lies between the landform types. In terms of elevation, the results show that the variation lies predominantly between the point bar and the abandoned channel, and the floodplain with the backwater and abandoned channel. This is due to the large contrast in elevation between the floodplain zones and the low-lying backwater and abandoned channel. In addition, despite being a bank feature, the point bar has zones of relatively high elevation as a result of extensive gravel deposition during a large scale flooding event in 1993 which has been estimated to be the largest flood on the Tay catchment since 1814 (Gilvear and Winterbottom, 1998). The predominant source of variation between the Shannon index scores of diversity lie between the point bar

Table 4.19: Results of analysis of variance (ANOVA) of elevation and species diversity indices between the landform types within the Ballinluig dataset.

a) Elevation (m)

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	13.70	3	4.57	11.85	0.000
Within Groups	18.12	47	0.39		
Total	31.82	50			

b) H'

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	1.92	3	0.64	10.62	0.000
Within Groups	2.83	47	0.06		
Total	4.75	50			

c) J

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	0.03	3	0.01	2.62	0.062
Within Groups	0.16	47	0.00		
Total	0.19	50			

d) S

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	1889.15	3	629.72	20.59	0.000
Within Groups	1437.20	47	30.58		
Total	3326.35	50			

landform with the abandoned channel and floodplain zones. The strongest test result for species richness is reinforced with the post hoc test where Appendix 14c shows that the point bar landform is significantly different in terms of species richness with the other landform types present.

Table 4.20 shows the results of analysis of variance between pedological properties. All variables proved to be significantly different between the landform classes with the exception of particle size heterogeneity. This is not a surprising result however as it is merely a count of the number of particle size

classes present and gives no indication of variation in the actual substrate sizes. Very large differences are observed in the mean square values for between groups and within groups for soil depth, particle size range and MAXDOM, with the latter having the most pronounced difference and exceptionally large F-statistic in comparison to the other results. The significant result for soil/substrate type also indicates that soil profile development shows marked differences between the landform types within the study area. This further supports the hypothesis that pedological variation does occur in relation to the geomorphic structure of the landscape.

Table 4.20: Results of analysis of variance (ANOVA) of pedological properties between the landform types within the Ballinluig dataset.

a) Soil depth (cm)

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	18337.88	3	6112.63	6.99	0.001
Within Groups	41074.10	47	873.92		
Total	59411.98	50			

b) MEAN

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	21.97	3	7.32	6.39	0.001
Within Groups	48.14	42	1.15		
Total	70.11	45			

c) MINDOM

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	39.10	3	13.03	4.02	0.013
Within Groups	136.13	42	3.24		
Total	175.23	45			

d) MAXDOM

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	257643.09	3	85881.03	96.45	0.000
Within Groups	37395.86	42	890.38		
Total	295038.96	45			

e) MEDOM

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	18.76	3	6.25	5.04	0.005
Within Groups	52.11	42	1.24		
Total	70.87	45			

f) MODOM

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	256.59	3	85.53	44.69	0.000
Within Groups	80.39	42	1.91		
Total	336.98	45			

g) Range

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	168179.31	3	56059.77	27.12	0.000
Within Groups	95099.73	46	2067.39		
Total	263279.05	49			

h) Heterogeneity

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	43.02	3	14.34	1.44	0.243
Within Groups	457.30	46	9.94		
Total	500.32	49			

g) Soil/substrate group

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	170.92	3	56.97	44.70	0.000
Within Groups	59.90	47	1.27		
Total	230.82	50			

The results of the post hoc tests to analyse where the main source of variation lies between the pedological properties and landform type are presented in Appendix 14d-k. Variation in soil profile depth lies predominantly between the point bar landform with limited soil profile development with the abandoned channel and the floodplain zones. The variation between the point bar and backwater proved to be insignificant due to both landforms being composed predominantly of gravel substrate with little or no soil development. Pedological particle size properties MEAN, MINDOM and MEDOM vary

significantly between the point bar and the floodplain landforms indicating a contrast between substrate dominated by coarse particle sizes to soil profiles composed of a relatively fine particle size matrix. Significant variation is indicated for the properties MAXDOM, MODOM, range and soil/substrate group between the point bar landform with the backwater, abandoned channel and floodplain zones.

4.4. Discussion

4.4.1. Spatial patterns of succession within the Ballinluig dataset

The geomorphic and pedological patterning within the study area have given rise to the development of six distinct plant communities. There is a less complex mosaic of vegetation types within the Ballinluig dataset as a result of less dynamic geomorphic activity within these areas in recent years in comparison to Tomdachoille. The greater stability of the channel results in fewer landforms being present within the study area and consequently fewer pedological units and plant communities. Channel change is occurring within the vicinity of Ballinluig due to lateral erosion of the floodplain and active deposition on the inside of meander bends. This has led to accretion of an area of active deposition during the 1940s and bank profile development thus leading to the incorporation of the more elevated areas of this feature into the floodplain. This feature is now fully colonised and only inundated during large-scale floods where the river exceeds bankfull discharge. More dynamic geomorphic activity has occurred along this reach in the past identified in

historical records. These past channel dynamics have created the suite of landform types present today and there is considerable evidence in the field of former river channels which are now fully infilled with sediment with mature plant communities.

As a result of the Ballinluig dataset being composed of fewer vegetation types, landforms and pedological units, this indicates a lower landscape diversity due to the landscape components having a lower richness score. However, the landscape units, in contrast to Tomdachoille, form larger landscape patches and are therefore arguably more stable. The larger patch size can also be linked to greater connectivity within the system as opposed to Tomdachoille where the local landscape is predominantly composed of numerous patches with small interiors indicative of fragmentation. However the landscape richness scores high in such scenarios and a landscape composed of small patches with a relatively large perimeter in contrast to area means that there is a high proportion of ecotone area which are ecologically rich habitats (Forman and Godron, 1986). The Ballinluig dataset is composed of ecologically important habitats with extensive broad-leaved woodland communities which have high species richness and diversity scores. In addition, different woodland communities are present relative to elevation. There is a distinct lack of scrub communities within the Ballinluig dataset thereby reducing the landscape richness score but increasing the ecological importance of the landscape. Analysis of the data from both datasets revealed that scrub communities are associated with a general decline in species richness. It is the scrub communities at Tomdachoille which also seem to be

the prime cause of habitat fragmentation, thus they are not ecologically favourable for the preservation of landscape diversity along the river valley floor.

4.4.2. Spatial patterns and relationships between the landscape components

The analysis of species-environmental relationships using CANOCO revealed that very similar patterns occur between the Ballinluig and Tomdachoille dataset. The Ballinluig dataset has commonalities with the Tomdachoille results in that the patterns of species distribution tend to hold strong correlations with tree cover, the presence of open water within the landforms, the proportion of unvegetated gravel, elevation and substrate particle size. The correlations between species and environmental variables are very strong indicated by the high coefficient thus giving confidence in the patterns of species arrangement in relation to environment suggested by the model. In addition, the strength of the relationships are reinforced by the fact that 60.9% of the variation in species distribution patterns are explained by the environmental variables included in the model for the first two axes. The eigenvalues for the first two axes are notably higher than in the Tomdachoille analysis indicating that the relationships and patterns observed in the model are stronger within the Ballinluig dataset. This may be a result of there being less spatial heterogeneity within this study area in contrast to Tomdachoille.

In comparing the ordination diagrams, although the diagram in Figure 4.3 is rotated at 90° to the diagram in Figure 3.3, very similar patterns of species

distribution along environmental gradients are observed. Species associated with grassland communities in both datasets are strongly correlated with areas of relatively high elevation within the valley floor. Tree cover in contrast declines along a gradient of increasing elevation. The wet woodland communities are correlated with dense tree cover located within the low lying zones within abandoned channels, backwaters and within the depressions on point bars. These communities are also associated with open water within these landforms either forming ponds, small streams or backwaters. Species associated with the gravel habitats are related to unvegetated gravel and coarse substrate texture in relation to the distribution of other species typical of other communities. Canonical correspondence analysis has therefore shown that the spatial organisation of species is related to similar environmental gradients within both datasets. The key variables explaining the variation are elevation and pedological properties, notably particle size characteristics. This supports the hypothesis that the spatial organisation of species and plant communities along rivers is related to geomorphic heterogeneity and pedological characteristics.

Canonical correspondence analysis also revealed congruence between the two datasets in sample heterogeneity measures. The results indicate that the gravel bar communities have the lowest diversity in terms of heterogeneity due to low species richness in comparison to the other samples taken from different landform types. Species rich samples within both datasets are found within the floodplain zones, most notably within the *Betula* woodland communities. No similarities were found between species having a low tolerance to

environmental heterogeneity between Tomdachoille and Ballinluig datasets. This suggests that localised factors are influencing the spatial distribution of sensitive species. However, grassland species *A. odoratum* and *A. elatius* show high species tolerance within both study areas. Other species common within the different landform and community types within both the Tomdachoille and Ballinluig datasets are *V. chamaedrys*, *V. riviniana* and *R. squarrosus*. These species are insensitive to environmental heterogeneity and are common to most habitat types within the datasets.

4.4.3. Spatial patterns of landscape diversity within the Ballinluig dataset

The spatial patterns of diversity within the landscape range from alluvial deposits with coarse substrate texture and relatively low species richness with early colonisers through to landforms infrequently inundated with relatively deep soil profile development, fine substrate texture and species rich communities. Despite the gravel bars having low species richness relative to the other landforms, they do host species unique to that landform only and provide a suitable habitat for locally rare species. The point bar features do however score highest on the diversity measure of equitability indicating that colonisation progresses in relatively uniform patches which are more stable ecologically than patches composed of many species with relatively low abundance. This is an important strategy for succession development within the gravel communities.

Plant community development appears to be related to geomorphic landforms within the Ballinluig dataset as there is no geodiversity within most of the vegetation types sampled. This is in agreement with the observations made at Tomdachoille for the same or similar plant community assemblages. This supports the hypothesis that the geomorphic structure of the landscape is the underlying template for botanical diversity within fluvial environments. Furthermore the analysis suggests that the spatial organisation of plant communities are related to the pattern of pedological heterogeneity, which in turn is linked to geomorphic patterning. The low number of vegetation types present within each of the soil/substrate classes indicates this.

Although the results show that the plant communities are unique to one landform type within the Ballinluig dataset, the landforms do host more than one vegetation type. The patterns of plant community richness within the landforms ranges from low diversity within the lower elevation land units through to relatively high richness within the more elevated landforms within the valley floor which are less frequently inundated and only impacted during large-scale flooding events.

Pedological diversity within the landform units show no distinct pattern with the results from the Tomdachoille data. This may be a consequence of other influencing factors related to flow patterns which are important in determining localised erosion and deposition and sediment sorting. In addition differences in connectivity and plant community structure between the two datasets will also effect the patterns of sediment deposition and sorting. Congruence does

exist between the floodplain landforms at Tomdachoille and Ballinluig however, where similar levels of soil development and substrate properties are observed.

Within both the Tomdachoille and Ballinluig datasets, similarity in the patterns of diversity in the parallel and perpendicular orientations to the channel are observed. Biodiversity increases along the perpendicular axis along an aquatic-terrestrial environmental gradient. Pedodiversity shows distinct variations in both orientations to the main channel. The patterns of pedodiversity are possibly related to the processes of deposition and gradual isolation from frequent inundation. Consequently as a result of channel avulsion, uneven patterns of pedodiversity are observed if this hypothesis is true.

The high number of species unique to either one or two landform units further emphasized the importance of a suite of landforms for maintaining species richness and diversity. The high number occurring in just one landform class shows that the preservation of these geomorphic units is vital for the continued presence of these species locally. In addition the maintenance of a flooding regime and or a shifting mosaic of landforms is also essential in order to reset successional stages so that a mosaic of plant communities at all successional stages are present within the valley floor. The occurrence of locally rare species within each of the landforms also reinforces their ecological importance in contributing to landscape diversity. The number of unique species declines dramatically with an increase in the number of landforms

indicating considerable floristic differences between the community types present. This pattern is further supported by the high number of species unique to one or two land units and decreasing to relatively few species being common to an increasing number of vegetation types. The backwater and abandoned channel have relatively few species unique to them in contrast to the other landforms present. However, the analysis has shown that the carr woodland within these two land units has the highest number of species unique to that community type in contrast to the other vegetation assemblages. Locally rare species are present in all community types further emphasizing their ecological importance.

The findings of the correlation analysis show agreement with the results at Tomdachoille where species diversity and vegetation structure are related to geomorphic and pedological variables. These results thus further support the hypothesis that plant communities and diversity are arranged according to the geomorphic units within the landscape and the pedological variation within them. Species diversity is also significantly correlated with plant community type providing further statistical evidence that a suite of landforms, soil types and plant communities play a crucial role in determining the landscape diversity value of alluvial valley floors. The correlations suggest that species diversity increases along a gradient of reduced frequency of inundation and substrate fining, which supports the findings of canonical correspondence analysis. Despite species diversity tending to be greater in the more elevated areas of the valley floor, tree cover is also important in increasing species richness and dense tree cover is typical of the low lying land units. This

supports the ecological importance of carr woodland communities as they increase species richness locally within the frequently inundated zones. Species richness is possibly higher within the carr woodland communities due to firstly the addition of tree species to the species count, and dense tree cover will slow the velocity of flood waters thus encouraging sediment deposition. Finer substrate sizes are typical within the carr communities which provide a more suitable niche for species colonisation in contrast to the coarse substrate on the gravel bars. The finer matrix will also increase moisture retention capacity and tree cover will provide shelter from the harsh environmental conditions on the exposed gravel. The canopy will have the effect of reducing diurnal temperature fluctuations whereas extreme temperature variation can be experienced on the exposed gravel. The canopy will also increase organic matter content locally as a result of greater leaf litter input into the ecological functioning of the habitat.

Correlation analysis within the landform types revealed that particle size characteristics were the predominant environmental variable to which species diversity and plant community type and structure are related to. Substrate size is possibly very influential due to finer substrates having a greater moisture retention capacity and provides stronger anchorage for rooting systems than the coarser substrate classes.

Although correlation analysis revealed species richness to increase with tree cover within landforms such as the floodplain zones, the mosaic of plant community types is important for maintaining the overall landscape diversity

rather than having woodland dominate the landscape. A mosaic of different habitat patches within the floodplain increases overall species richness as the species composition of the communities varies greatly. This is illustrated in the analysis of the species unique to different landform and community types in Table 4.8 and 4.9 and Appendix 13. Although the woodland communities have a higher species richness than the other plant communities present within the study areas, the grassland communities have a very rich herb layer with rare species and are of floristic and aesthetic value. The woodland field layers in contrast are dominated by graminiae species with a less diverse range of dicotyledons.

The testing of the regression models derived from the baseline survey proved to be ineffective for predicting environmental variables across the landscape. However, regression models produced within the discrete land units proved to have the capability of prediction with a high level of accuracy. The models produced from the whole baseline dataset were incapable of prediction due to the high degree of spatial heterogeneity within the valley floor. Examination of where the models failed revealed that the models were incapable of incorporating the spatial heterogeneity introduced by the point bar landforms. This suggests great environmental heterogeneity within these landform features which are controlled by factors which were not measured during this study. Channel dynamics and flow patterns during high flows will be a major influence of the spatial patterns of heterogeneity within point bars. These factors will influence the substrate sorting which consequently influence patterns of colonisation due to substrate size and heterogeneity being

important factors in determining the spatial patterns of colonisation within fluvial environments (Nilsson *et al.*, 1991; Ward and Stanford, 1983). The regression models produced to predicted species diversity, plant community assemblage and substrate type within the distinct landforms provided very accurate predicted values which were proven to not differ significantly from the actual values measured in the field.

The analysis of variance further added support for the hypothesis that landscape diversity is organised in accordance with the geomorphic patterning in the landscape due to the significant differences in species diversity indices and pedological variables between the land units and with little internal variation of a given property. Species richness varies most notably between the land units. This can be tied in with the analysis showing that a high number of species are unique to a single geomorphic unit. In terms of pedodiversity, the spatial pattern of soil/substrate characteristics varies predominantly according to soil profile depth and particle size characteristics.

4.5. Summary

This validation study revealed that similar patterns of spatial organisation of the landscape components observed within the baseline survey were repeated. The analysis has suggested that geomorphic heterogeneity is the prime control in determining the richness of pedological and botanical variables. Various statistical analyses have provided strong evidence to support the hypotheses proposed. The results have revealed that a considerable degree of congruence

exists between the spatial organisation of landforms, soil types and plant communities between Tomdachoille and Ballinluig datasets.

Regression analysis within the discrete land units proved to be highly successful. This demonstrates that despite the complexity of the processes operating within this dynamic river system, environmental heterogeneity can be modeled provided the baseline survey is of adequate intensity incorporating a large range of local variation. In addition validation studies can also be carried out on other river systems to test the robustness of the models. By developing and improving predictive models will lead to a better understanding of fluvial processes and enable more sustainable ecological management of riverine ecosystems. The development of widely applicable strong predictive models will also lead to the need for less intensive and time consuming field studies thus enabling rapid appraisal of landscape diversity within fluvial environments.

Chapter 5: Temporal analysis of landscape patterns.

5.1. Introduction

To date the data presented in this thesis has covered spatial patterns of diversity within specific study areas of the River Tummel. The analysis has shown that complex patterns of spatial heterogeneity occur as a result of channel change. Therefore with resource material available, temporal change in the patterns of diversity can be assessed and, using indices for describing landscape diversity, it should be possible to show how the number and spatial arrangement of patches and land cover types vary through time. The chapter presents an integrated landscape ecology approach to assessing temporal landscape diversity change via the combination of a variety of diversity measures. The results can be presented in conjunction with knowledge of species richness and distribution within the different land cover types in order to derive a more informed review of the significance of landscape pattern change. From this analysis it will be possible to decipher the potential loss or gain of species as a result of landscape pattern change.

5.2. Methodology

5.2.1. Digitising aerial photographs

Analysis was carried out over a 131.4 ha area of the River Tummel. The floodplain was defined as land either side of the river channel with no active

flood protection embankments up to the railway embankment and the valley walls. In addition the study area was determined by having comparable records for the study years. Patch boundaries were defined and mapped by aerial photograph interpretation and field verification. Vegetation and geomorphic landform patch boundaries identified on the aerial photographs were digitised in ArcInfo for the years 1946, 1968, 1971, 1988 and 1994. Ordnance survey 1:10 000 map sheets NN95SE and NN95NE were digitised into ArcInfo. The features digitised included all landscape patches of the river and floodplain zones, buildings, field boundaries and road intersections. The OS vector maps were registered to 'real world' co-ordinates derived from the OS maps and the two maps were appended. Ten tic marks were plotted on the aerial photograph vector maps at the corner of static features for geocorrection. The tic points were allocated widely across the vector map to ensure greater accuracy of the geocorrection. Tic marks were plotted in the same positions on the digitised OS maps. The tics were edited in order for tic identity to correspond on the OS and aerial photograph maps using the UPDATE command in the TRANSFORM routine. Aerial photograph vector maps were geocorrected to the OS vector maps. The geocorrected maps of the aerial photographs were appended to produce one map of the study area for each year of analysis. 'Dangling node' errors were corrected in order to convert the arcs into polygon features. The arcs were 'cleaned' to produce a polygon coverage.

5.2.2. Classification and analysis of polygon coverages

The coverages were exported into ArcView for classification and analysis. The coverages were classified according to land cover type. The attribute tables for each classified image containing information on land use type, area and perimeter of each patch were exported as dBASE files into Excel for analysis.

Aerial photography for 1971 was only available for the Tomdachoille reach of the River Tummel. Hence equivalent areas on the coverages from the other years were isolated for analysis by splitting the polygons giving a study area of 54.5ha. This was done as visual comparison of the photographs from 1968 and 1971 showed considerable variation in the floodplain landscape patterns. The indices were calculated for all years within this reach and compared. The split polygons from 1946, 1968, 1988 and 1994 were re-merged using the union feature routine in ArcView and the analysis was repeated over the full study area. The following indices of diversity were calculated for the classified coverages.

1. S = richness (number of land cover types)
2. N = number of patches in each land cover type
3. Total N = total number of landscape patches in the study area
4. A = mean area of patches
5. p_i = proportion of each land cover type
6. H' = Shannon index

7. J = evenness
8. D = dominance
9. Reciprocal of Simpson's index ($1/S$)
10. $S1$ and $S2$ = mean shape index
11. C = change

The first ten indices relate to pattern and the latter measures change in the area of each land cover class with time. The Shannon index is calculated using the following equation:

$$H' = - \sum_{i=1}^s p_i * \ln p_i$$

where:

p_i = the proportion of the landscape unit i (ha) contributing to the total area

S = number of landscape units present

\ln = natural logarithm

Large values of H' indicate a diverse landscape with high patch richness. The Shannon index accounts for the evenness of the distribution of patches by the equitability index (J) which is calculated by:

$$\text{Equitability (evenness) } J = \frac{H'}{H'_{\max}} = \frac{- \sum_{i=1}^s p_i * \ln p_i}{\ln s}$$

where:

p_i = the proportion of the landscape unit i (ha) contributing to the total area

S = number of landscape units present

\ln = natural logarithm

Values of J close to one indicate that landscape patches occupy an even area, indicating a higher diversity based upon evenness. The dominance index describes the composition of the landscape patches. A low value indicates that the landscape is composed of patches which occupy equal areas, and a high value suggests that the landscape is dominated by a few land cover classes within a complex matrix of smaller patches. It is calculated from the formula:

$$D = \ln(S) - H'$$

(Marston *et al.*, 1995).

The reciprocal of Simpson's index is a measure of the likelihood of selecting two patches of the same land cover type within the study area when undertaking random sampling. The index shows a decrease in landscape diversity with an increase in the index value. It is calculated using the equation:

$$1/S = 1/\sum p_i^2$$

(Marston *et al.*, 1995).

Two shape indices were calculated for the analysis. The first shape index is a measure of the mean perimeter-to-area ratio of each land cover type. A low value for SI indicates that the landscape is composed of few patches with

large interiors. The $S2$ shape index measures the deviation of a patch from an isodiametric shape (circle or square). The closer the value is to 1.00 the more isodiametric the shape is. The indices are calculated using the following equations:

$$S1 = 1/N_{il} * \sum (l_i/a_i)$$

and

$$S2 = 1/N_{il} * \sum (l_i/(2\sqrt{a_i\pi}))$$

where:

N_{il} = number of patches of land cover i in map l

l_i = perimeter of each patch in land cover i

a_i = area of each patch in land cover i .

The rate of change in the total area of each land cover type through time was measured using the following index:

$$C = ((p_{k2} - p_{k1})/(t2 - t1))/n$$

where:

$(p_{k2} - p_{k1})$ = the difference in area (ha) of land cover k

$(t2 - t1)$ = the difference in years between the maps being compared

n = total surface area of the study reach (km^2)

(Hulshoff, 1995)

Patterns of species diversity were also mapped on the 1994 image using quantitative data collected on species richness along the reach. The temporal

variation in channel planform was examined with the use of maps and aerial photographs. In addition earlier work on channel change on the River Tummel by Winterbottom (1995) was available for consultation. Maps from 1867, 1900, and 1989 were compared for changes in physical diversity. The following information was derived from the maps and aerial photography:

1. Planform
2. Number of unvegetated mid-channel bars
3. Number of vegetated mid-channel bars
4. Number of mature islands
5. Number of point bars
6. Number of lateral bars
7. Number of backwaters
8. Number of cut-off channels

The data derived was compared to illustrate the patterns of change in the physical characteristics of the river and bank features. Finally an overall measure of landscape diversity was calculated by taking the average diversity results for number of land cover types, total number of patches, H' , J' , D and reciprocal of Simpson's index.

5.3. Results

5.3.1. Temporal change in landscape patterns within the Tomdachoille reach

The classified images of the Tomdachoille reach of the River Tummel are presented in Figure 5.1. Figure 5.2a shows the temporal variation in the number of the land cover types and total number of patches present within the reach.

5.3.1a. 1946 coverage

Figure 5.1a shows that the river occupied one main channel in 1946. Figure 5.2a shows that this coverage has the lowest number of land cover classes present for the years analysed. Figure 5.1a shows that semi-natural herb-rich grassland and pasture with areas of unvegetated gravel along the whole reach dominate the landscape. Overall the reach is characterised by ecologically important habitat types with cut-off channels, patches of carr woodland and a relatively large area of *Betula* woodland. Species poor habitats such as scrub and pasture are present, however scrub covers only a small fraction of the area. The results for the mean area of each land cover type are given in Figure 5.2b and Appendix 15.1. Pasture covers the largest area, however herb-rich grassland and *Betula* woodland cover a considerable area of the floodplain.

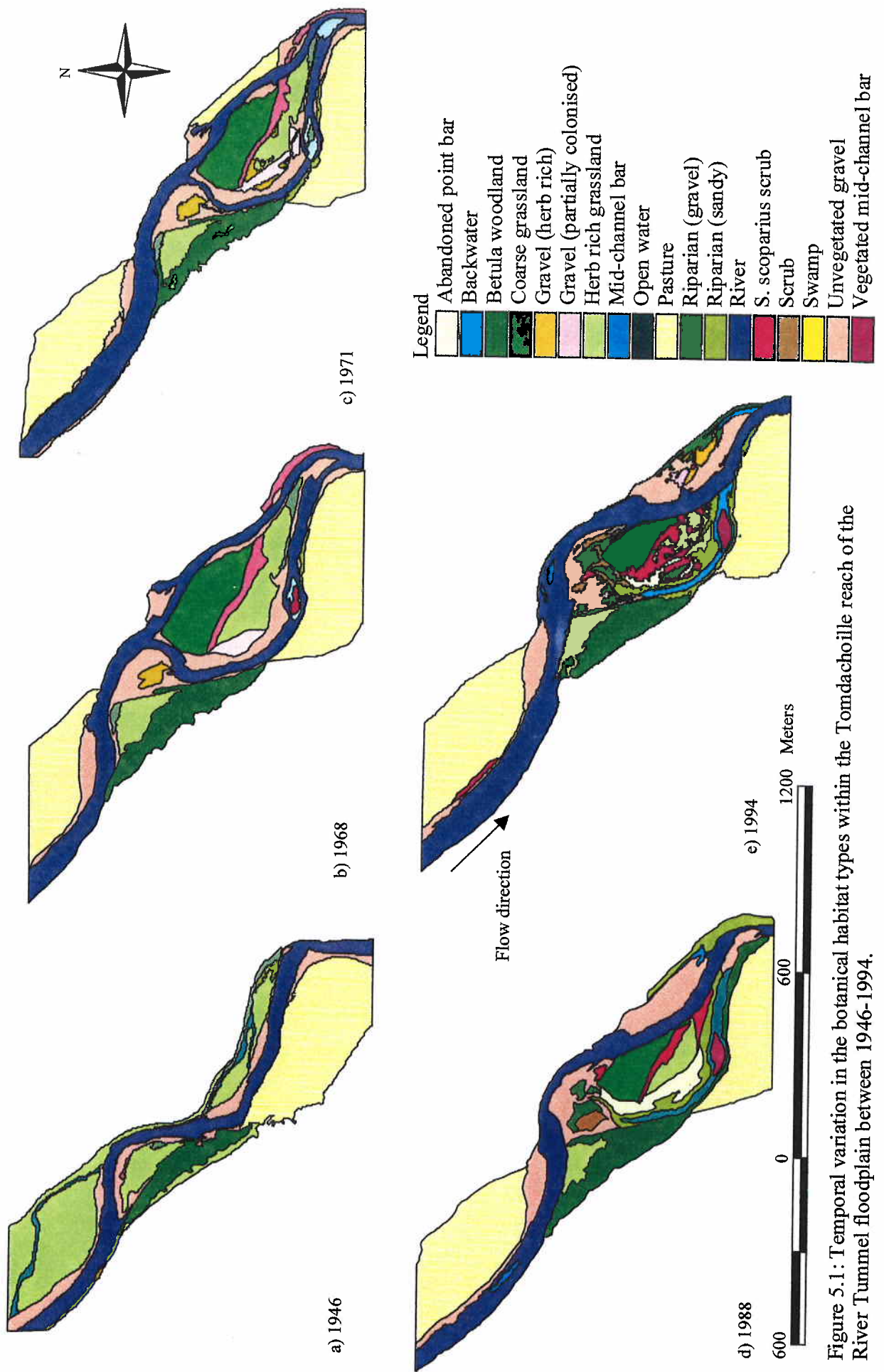
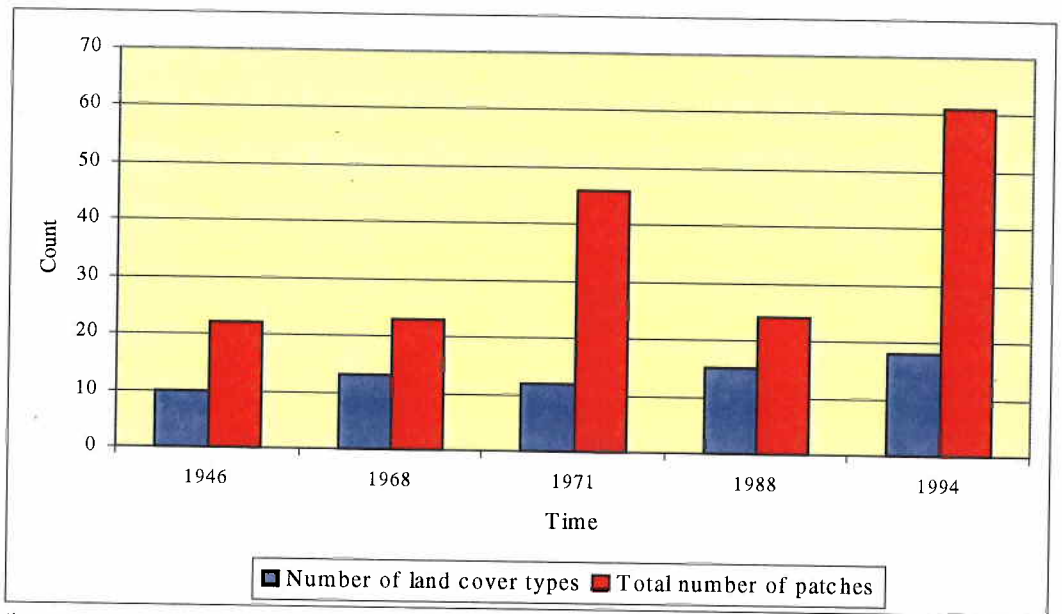
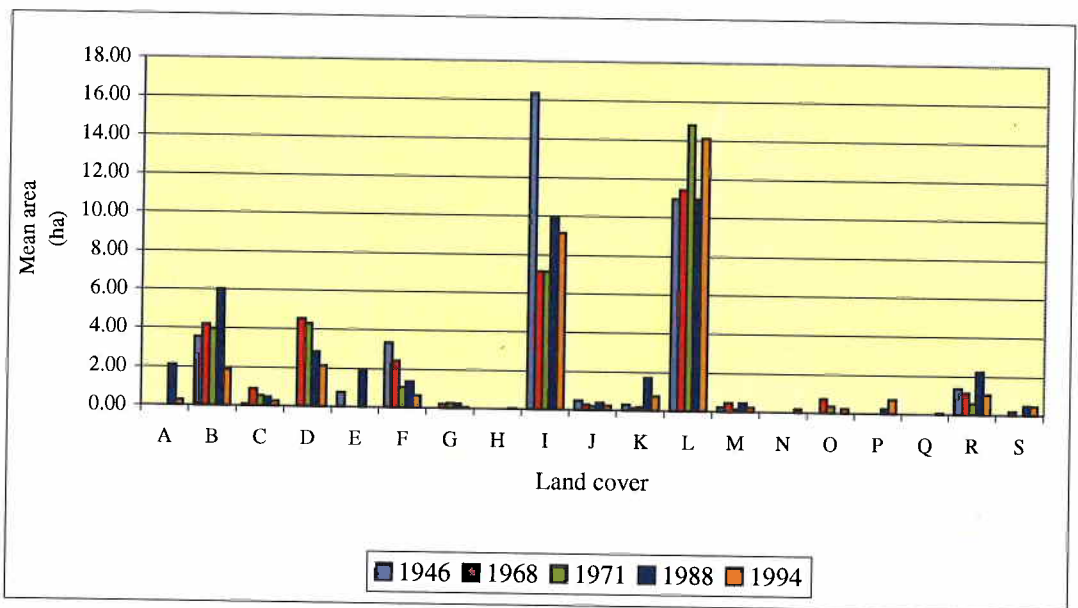


Figure 5.1: Temporal variation in the botanical habitat types within the Tomdachoille reach of the River Tummel floodplain between 1946-1994.



a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	K	Riparian (sandy)
B	<i>Betula</i> woodland	L	River
C	<i>S. scoparius</i> scrub	M	Scrub
D	Coarse grassland	N	Gravel (herb rich)
E	Cut-off channel	O	Gravel (partially colonised)
F	Herb rich grassland	P	Backwater
G	Mid-channel bar	Q	Swamp <i>G. fluitans</i>
H	Open water	R	Unvegetated gravel
I	Pasture	S	Vegetated mid-channel bar
J	Riparian (gravel)		

Figure 5.2: Temporal variation in the number of land cover types and total number of patches (a) and change in the mean area of the land cover types (b) within the Tomdachoille reach of the River Tummel between 1946-1994.

5.3.1b. 1968 coverage

Figure 5.1b shows the classified coverage for 1968. Figure 5.2a shows that there is an increase in both the number of land cover types and the total number of landscape patches within the study reach. The river now occupies two main channels. It can be seen from aerial photograph examination (given in Plate 1.1) that the new channel has been cut along the course of an ancient abandoned channel within the floodplain. This has caused the creation of a mature island within the channel adding to the complexity of the landscape pattern. Areas of unvegetated gravel are extensive within the reach. The area of herb-rich grassland has decreased illustrated in Figure 5.2b. This is due to the conversion of herb-rich grassland to pasture. Scrub cover has almost doubled since 1946 and *S. scoparius* scrub has increased ten-fold. The extent of *Betula* woodland has increased and vegetated mid-channel bars are present.

5.3.1c. 1971 coverage

Figure 5.1c shows the classified coverage for 1971. Figure 5.2a shows that there is a slight decline in the number of land cover types but the total number landscape patches present has doubled. The river still occupies two main channels. Unvegetated gravel remains extensive and mid-channel bars are present. Figure 5.2b shows that there has been a decline in the mean area of several land cover types within the three-year period. There has been a loss of ecologically valuable habitats, *Betula* woodland, herb-rich grassland and

unvegetated- and partially colonised-gravel. The extent of scrub and *S. scoparius* scrub has also declined within this period.

5.3.1d. 1988 coverage

Figure 5.1d shows the classified coverage for 1988. Figure 5.2a shows a slight increase in the number of land cover types but the total number of landscape patches present is reduced by almost a half. The increase in the number of land cover classes sees the introduction of backwaters and a new habitat developing on the abandoned point bar. The river occupies one main channel; the main channel in the 1946 coverage is now a large cut-off channel blocked by an alluvial plug at both the upstream and downstream ends. Extensive carr woodland has colonised along the former channel. Figure 5.2b and 15.1 shows the dramatic increase in the mean area for riparian woodland communities in comparison to the coverage in other years. The extent of riparian woodland is at its maximum for the study period. Unvegetated gravel is extensive in coverage and the mean area has increased considerably since 1971. *Betula* woodland, herb-rich grassland and pasture have also increased in extent, whilst the area of scrub cover has doubled. The area of coarse grassland has declined.

5.3.1e. 1994 coverage

Figure 5.1e shows the classified coverage for 1994. This year has the maximum number of land cover classes and total number of patches, shown in

Figure 5.2a. There has been a dramatic increase in the total number of landscape patches during this six-year period. Figure 5.1e shows that the landscape is now composed of a highly complex mosaic of small landscape patches within the zone of channel abandonment. This has created high diversity in terms of richness. The river still occupies one main channel, however connectivity with the former channel is now restored due to erosion of the downstream alluvial plug, opening up the former channel as a backwater. The extent of *S. scoparius* scrub is greater despite the reduced mean area shown in Figure 5.2b and Appendix 15.1. This is due to the presence of smaller, more fragmented patches of this community type within the landscape. The spread of this vegetation type within the area of the abandoned point bar has led to a loss of herb-rich grassland. The mean area of herb-rich grassland is now less than 1 ha. There has also been a considerable decline in the mean area of *Betula* woodland, now having the lowest average area for the study period. Figure 5.1e shows that riparian woodland has extended within the zones of previously unvegetated gravel. However, these habitats are more fragmented leading to a lower mean area for these land cover classes. The abandonment of the former channel has enabled the development of *Glyceria fluitans* swamp community within the backwater.

5.3.2. Temporal change in diversity indices within the Tomdacheuille reach

Figure 5.3 shows the results of the diversity indices for the study reach. An inverse relationship exists between the results for the Shannon index and the reciprocal of Simpson's index. The Shannon index shows diversity to be

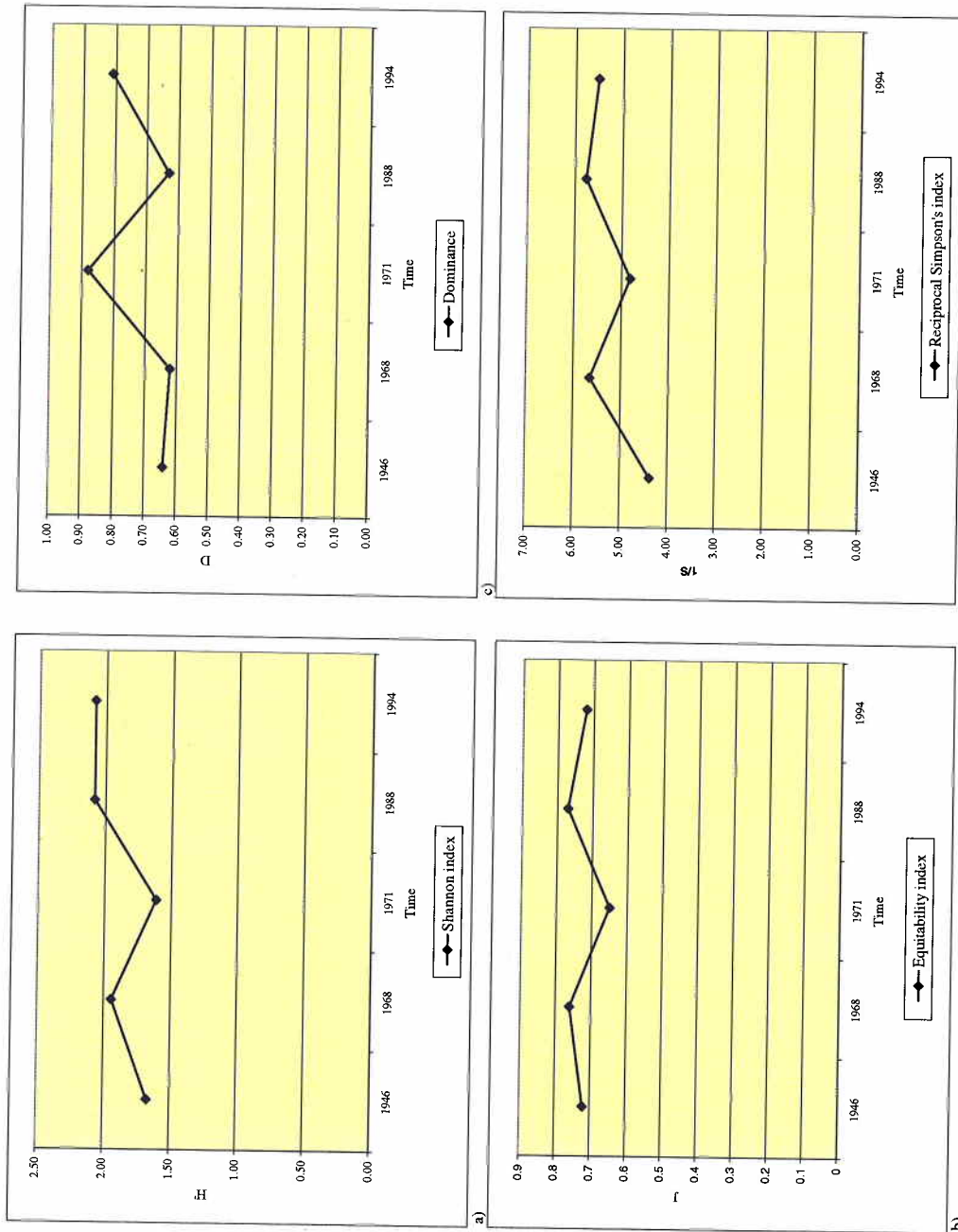


Figure 5.3: Temporal variation in diversity indices for plant community types within the Tomdachoille reach of the River Tummel between 1946-1994. a) Shannon index; b) Equitability index; c) Dominance index; d) Reciprocal of Simpson's index.

lowest in 1946 and 1971 with values of H' at 1.67 and 1.61 respectively. The coverages for 1988 and 1994 have the highest diversity when measured on the Shannon index with a value of 2.08. The reciprocal of Simpson's index shows landscape diversity is highest in 1946 with a value of 4.37 and lowest in 1988 with a score of 5.76. The coverages for 1968 and 1994 also score relatively high on the reciprocal of Simpson's index with values of 5.65 and 5.51 respectively. The equitability index and the dominance index measure the evenness of the distribution of landscape patches. An inverse pattern exists between these two indices, however both reveal the same results. Both show that the landscape is composed of small uneven patches within a heterogeneous matrix in the 1971 coverage. This implies low diversity. The two indices show that the landscape patches are more even in their distribution in the 1968 and 1988 coverages. This suggests that the land units cover more equal areas.

Figure 5.4 shows the patterns of species richness for the Tomdachoille and Ballinluig reaches of the river. Tomdachoille Island shows a complex pattern of species richness due to recent disturbance. The most species rich habitats are the *Betula* woodland and carr woodland patches. The high species richness in the riparian communities indicates that only relatively short time-scales are required for species richness recovery following disturbance or channel abandonment. Riparian woodland rapidly colonises the low elevation areas of gravel habitats. Where conditions prevent carr woodland development, such as coarse very well drained substrate with low moisture retention capacity at higher elevations on the point bars, species richness is typically low. However

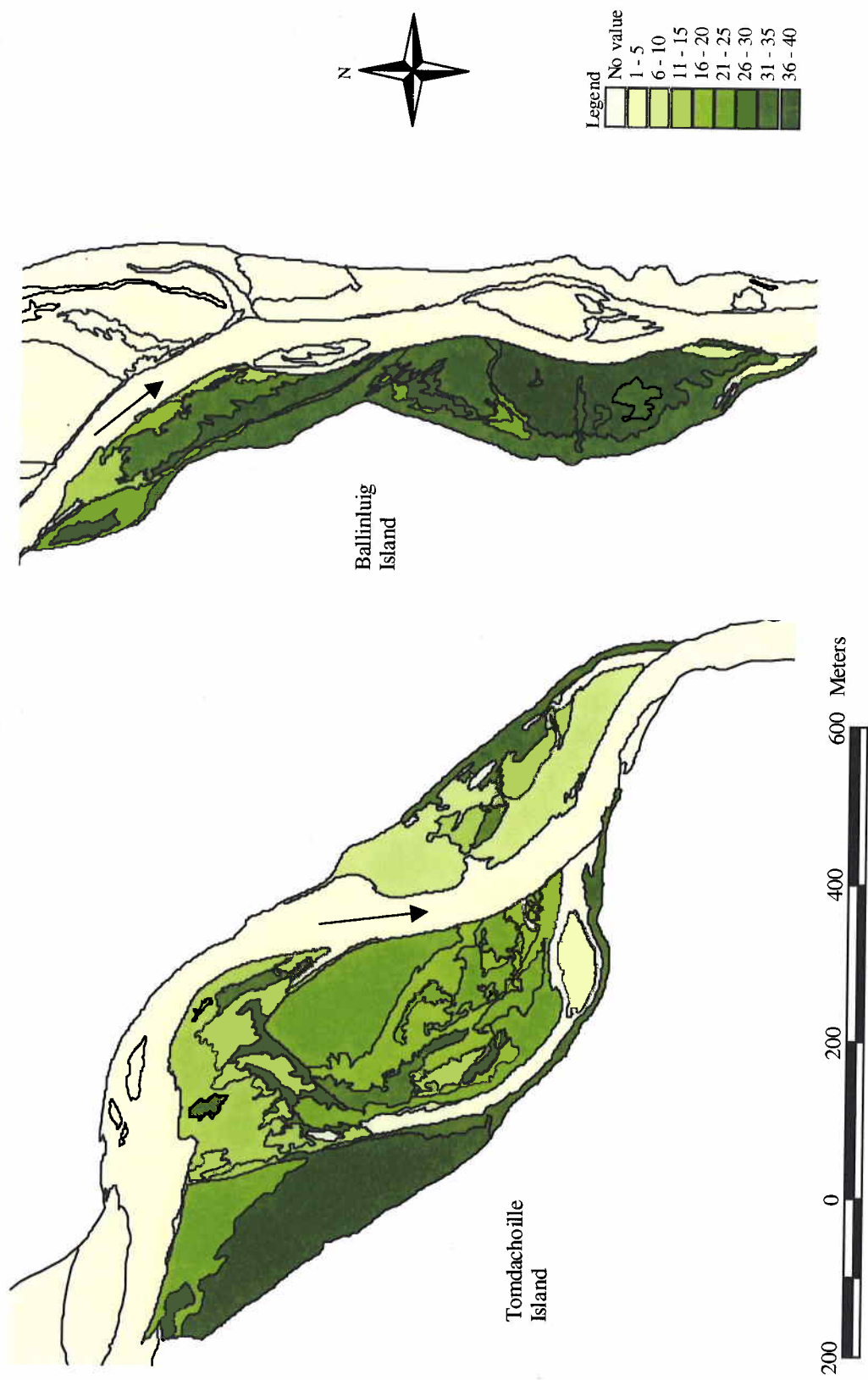


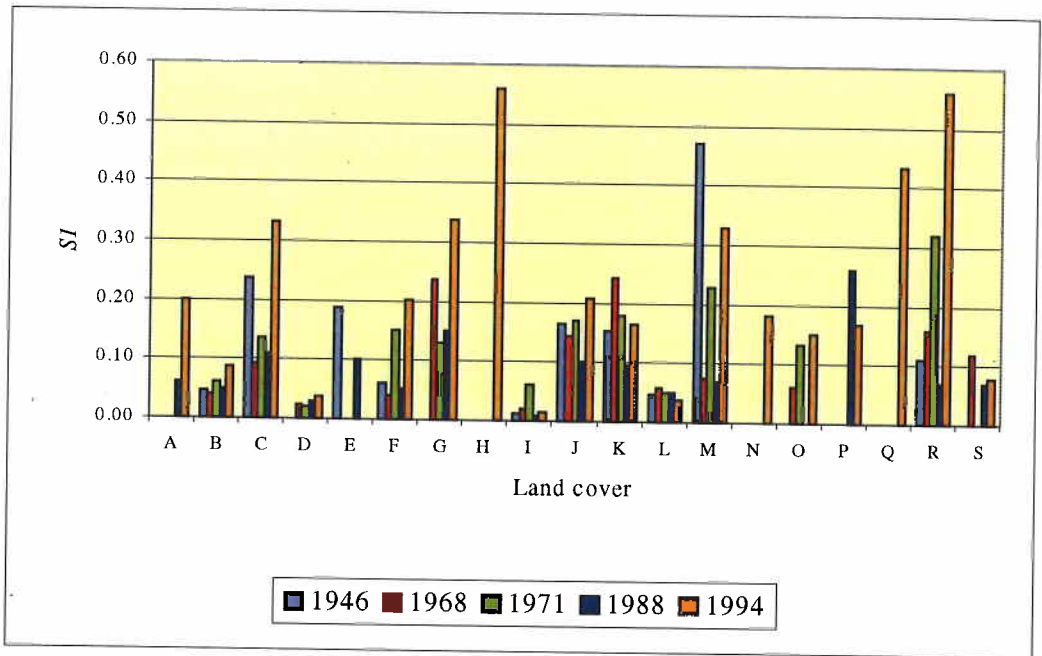
Figure 5.4: Patterns of species richness within the plant communities on Tomdachoille Island and Ballinluig Island on the River Tummel.

the vegetation survey revealed that several locally and nationally rare species colonise the exposed gravel, thus they are important habitats for enhancing total species richness within the floodplain environments despite only supporting a low species richness.

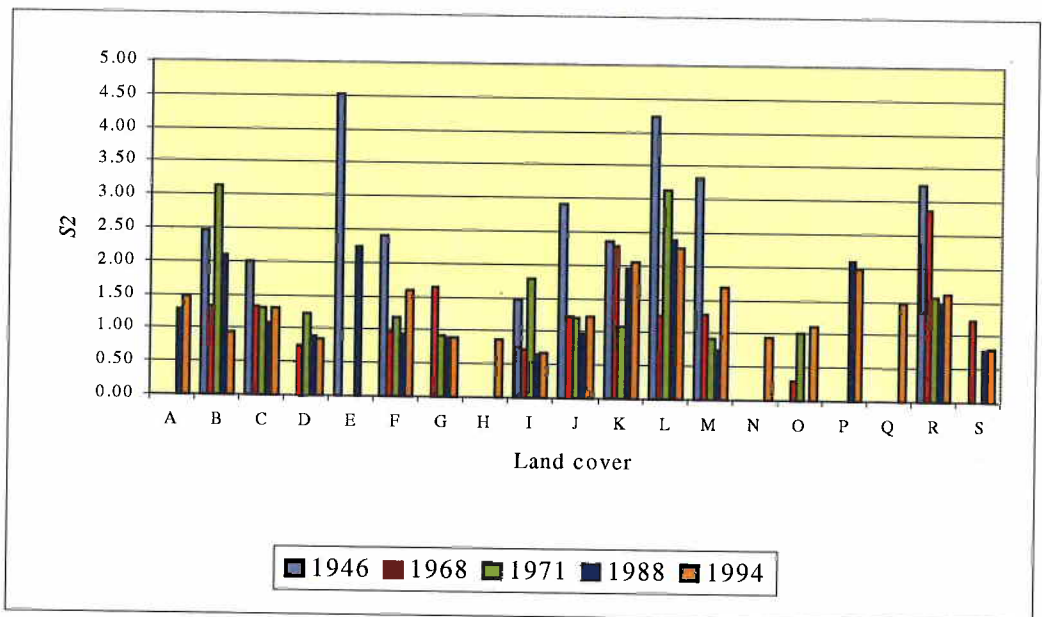
The species richness distribution at Ballinluig Island is more even and dominated by relatively high species richness. This area has not had a major disturbance in recent years. The rate of plant community development can be inferred by comparing the present species richness to the areas of previously unvegetated gravel. The extensive area of unvegetated gravel in the Ballinluig reach in 1946 now supports a species richness of between 26-35 species across most of the area. The cut-off channels and backwaters at Ballinluig in 1946 are also poorly colonised. These areas are now covered in dense riparian woodland supporting up to 35 species.

Figure 5.5 shows the temporal variation in shape indices $S1$ and $S2$. Figure 5.5a shows that the $S1$ index scores low (<0.20) for most of the land cover classes over time. This indicates that relatively few patches with large interiors in respect to landscape area dominate the study area over time. There is a trend for $S1$ to increase within the land cover types over time. This suggests that the landscape patches are decreasing in area and are becoming more fragmented.

The results of the second shape index, illustrated in Figure 5.5b, show that six land cover types have relatively isodiametric shapes (index value is close to 1.00). The most isodiametric land cover classes are coarse grassland,



a)



b)

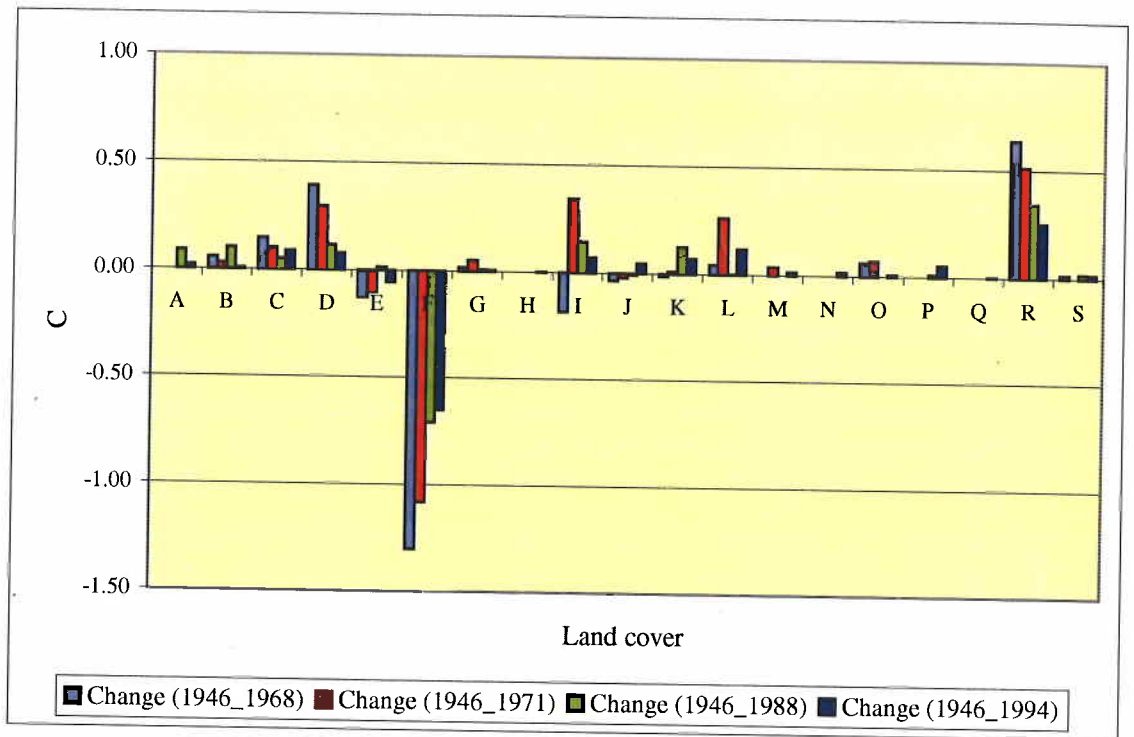
Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	K	Riparian (sandy)
B	<i>Betula</i> woodland	L	River
C	<i>S. scoparius</i> scrub	M	Scrub
D	Coarse grassland	N	Gravel (herb rich)
E	Cut-off channel	O	Gravel (partially colonised)
F	Herb rich grassland	P	Backwater
G	Mid-channel bar	Q	Swamp <i>G. fluitans</i>
H	Open water	R	Unvegetated gravel
I	Pasture	S	Vegetated mid-channel bar
J	Riparian (gravel)		

Figure 5.5: Temporal variation in the shape indices $S1$ (a) and $S2$ (b) within the plant community types in the Tomdachoille reach of the River Tummel between 1946-1994.

mid-channel bars, open water, gravel (herb-rich and partially colonised) and vegetated mid-channel bars. The other land unit classes have more complex shapes deviating from a circle or square pattern. Some patches, e.g. coarse grassland and vegetated mid-channel bar, show little variation in shape over time. This supports the hypothesis that isodiametric patches are more stable (Forman and Godron, 1986). *Betula* woodland, the channel, scrub and unvegetated gravel patches show considerable variation in shape over time and show strong deviations from isodiametric shapes.

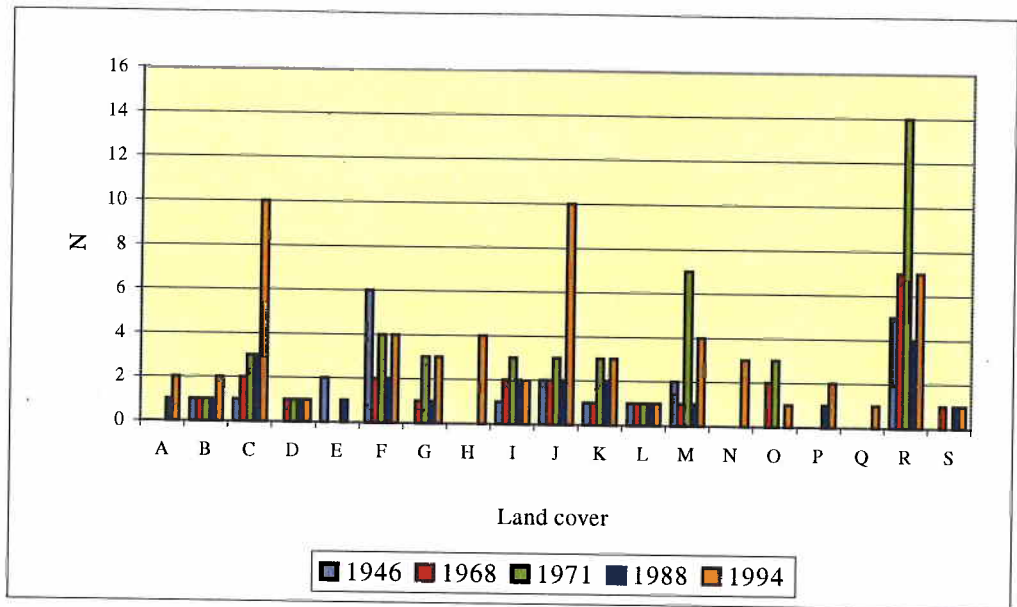
5.3.3. Temporal change in total area of each land cover class within the Tomdachoille reach

Temporal change in the total area occupied by each land cover type is presented in Figure 5.6. The results are presented in conjunction with the number of patches and the proportion of the study area occupied by each land cover type over time (Figure 5.7). Figure 5.6 shows that considerable change has occurred in the total area of each land unit category over the time period. The overall trend shows that there has been an increase in area of fourteen land cover types in comparison to the 1946 coverage, and a net loss in total area of two land unit classes. Of the land unit classes to show an increase in comparison to 1946, nine of them are ecologically valuable floodplain habitats. The other four classes to increase in area are scrub communities, coarse grassland and pasture. The land units to show a decline in spatial coverage are both ecologically valuable riverine habitats.

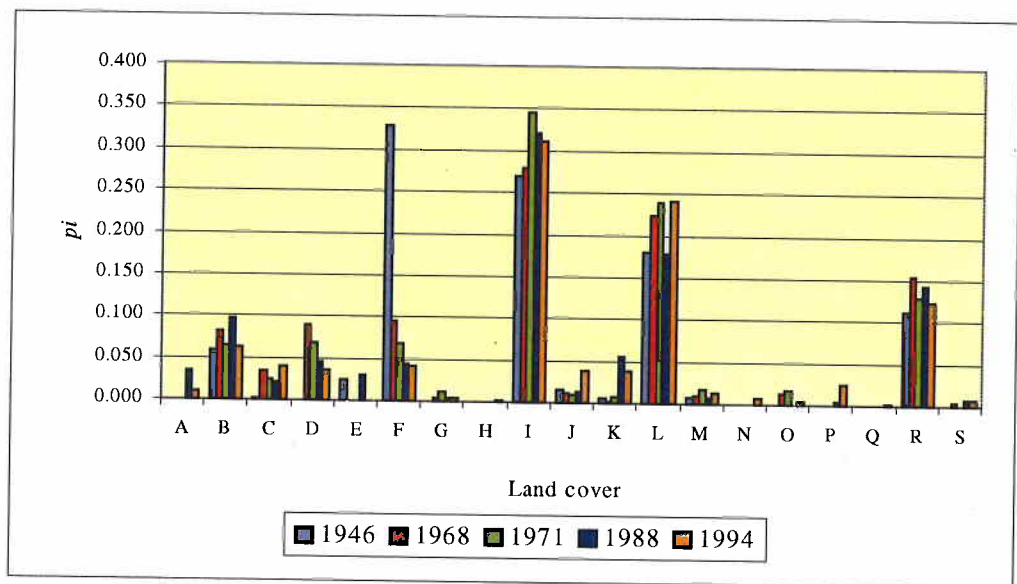


Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	K	Riparian (sandy)
B	<i>Betula</i> woodland	L	River
C	<i>S. scoparius</i> scrub	M	Scrub
D	Coarse grassland	N	Gravel (herb rich)
E	Cut-off channel	O	Gravel (partially colonised)
F	Herb rich grassland	P	Backwater
G	Mid-channel bar	Q	Swamp <i>G. fluitans</i>
H	Open water	R	Unvegetated gravel
I	Pasture	S	Vegetated mid-channel bar
J	Riparian (gravel)		

Figure 5.6: Temporal variations in the total area of each land cover type measured by the change index (C) within the Tomdachoille reach of the River Tummel between 1946-1994.



a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	K	Riparian (sandy)
B	<i>Betula</i> woodland	L	River
C	<i>S. scoparius</i> scrub	M	Scrub
D	Coarse grassland	N	Gravel (herb rich)
E	Cut-off channel	O	Gravel (partially colonised)
F	Herb rich grassland	P	Backwater
G	Mid-channel bar	Q	Swamp <i>G. fluitans</i>
H	Open water	R	Unvegetated gravel
I	Pasture	S	Vegetated mid-channel bar
J	Riparian (gravel)		

Figure 5.7: Temporal variations in the number (a) and proportion (b) of each land cover type within the Tomdachoille reach of the River Tummel between 1946-1994.

In most cases the greatest contrast in the total area of each land cover type is between the 1968 coverage and 1946. The trend for the difference in total area of each land unit type in comparison to 1946 has been one of decline. The total area of *Betula* woodland has declined markedly in the 1994 coverage in comparison to 1988, however, the total area is still slightly greater than in 1946. The greatest loss of habitat is herb-rich grassland within the study area. The total area of unvegetated gravel shows a marked decline over time despite covering a greater area than in 1946. This is likely to be the result of scrub encroachment and the expansion of riparian woodland.

Figure 5.7a shows that within half of the land cover types, very little variation has occurred in the number of patches present over time. The land unit classes to show greatest variability are *S. scoparius* scrub, herb-rich grassland, mid-channel bars, riparian woodland communities, scrub and unvegetated gravel. Figure 5.7b shows temporal change in the proportion of the floodplain occupied by each land unit. Little temporal variation is seen for twelve of the land cover types over time. The figure shows that the study area is dominated by pasture, the channel, unvegetated gravel, with *Betula* woodland, coarse grassland and herb-rich grassland as co-dominants. The proportion of the floodplain occupied by pasture has increased over time and occupies between a quarter and a third of the study area. The proportion of the study area under unvegetated gravel has also tended to increase. There has been a decline in the proportion of coarse grassland and herb-rich grassland.

The number of riparian woodland patches has increased since 1971 with a dramatic increase in the number of riparian woodland patches on gravel

substrate in 1994. The proportion of the study area occupied by this community has also increased over time. However, the mean area of this community has declined from 0.48 ha in 1946 to 0.22 ha in 1994. The proportion of the study area occupied by riparian woodland on sandy substrate has increased over time. Figure 5.7b shows the proportion of the area occupied by this community to be considerably higher in 1988 and 1994 in comparison to the other study years. Patches of *S. scopraius* scrub have increased considerably over the study period. The most notable loss in the number of landscape patches is for herb-rich grassland. This community has shown the greatest loss in the proportion of the floodplain it occupies over time. This community occupied approximately one third of the study area in 1946. Herb-rich grassland occupied less than 5% of the total area in 1994 due to habitat loss.

5.3.4. Temporal change in landscape patterns within the River Tummel study area

The full GIS coverages were analysed to assess temporal change in landscape diversity. This analysis was carried out for years 1946, 1968, 1988 and 1994. Figure 5.8a-d shows the classified images of the reach upstream of Tomdachoille to downstream of Ballinluig. Figure 5.9 shows the results of the number of land cover types and total number of landscape patches within the study reach.

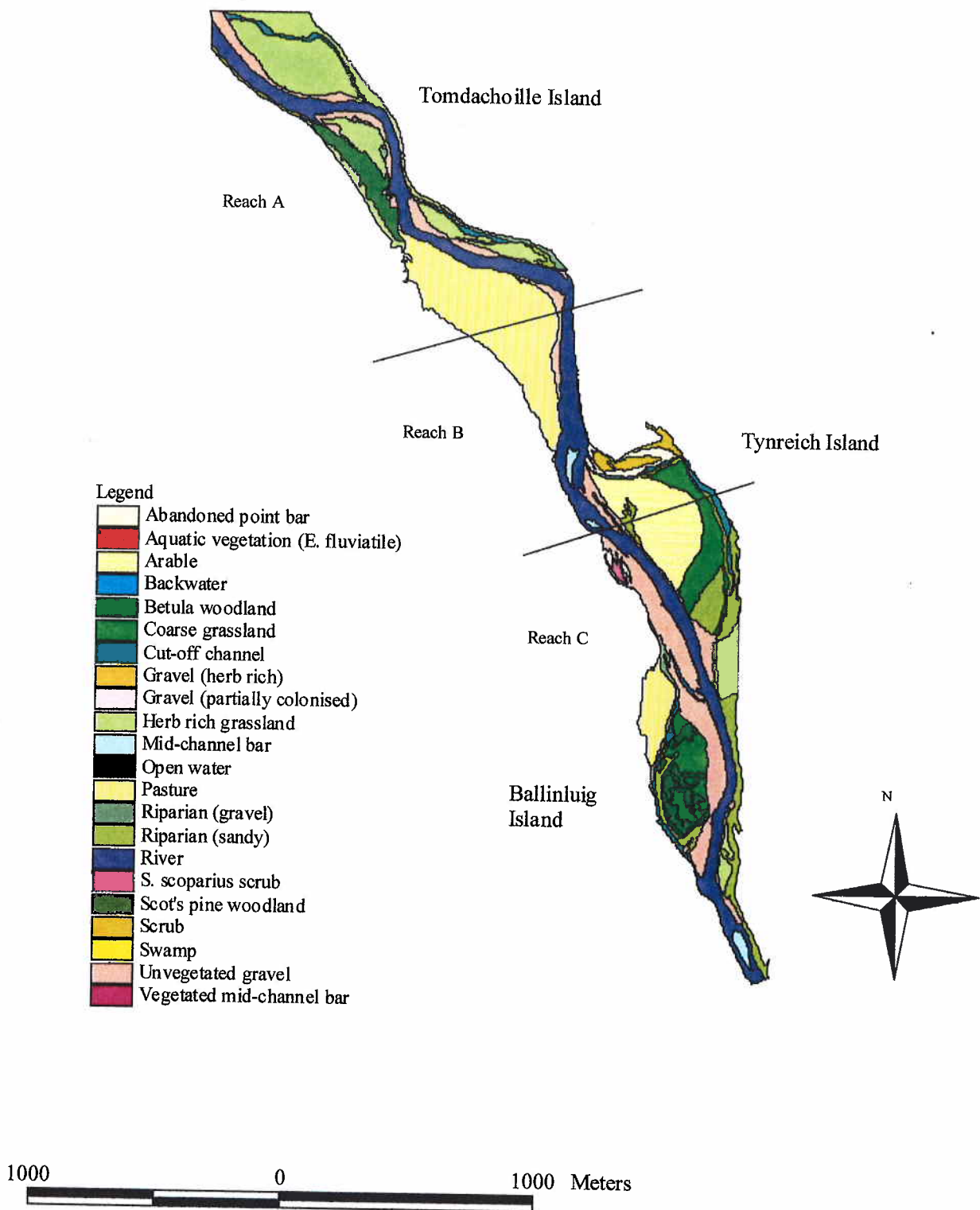


Figure 5.8a: Classified image of the botanical habitat types within the River Tummel study area, May 1946.

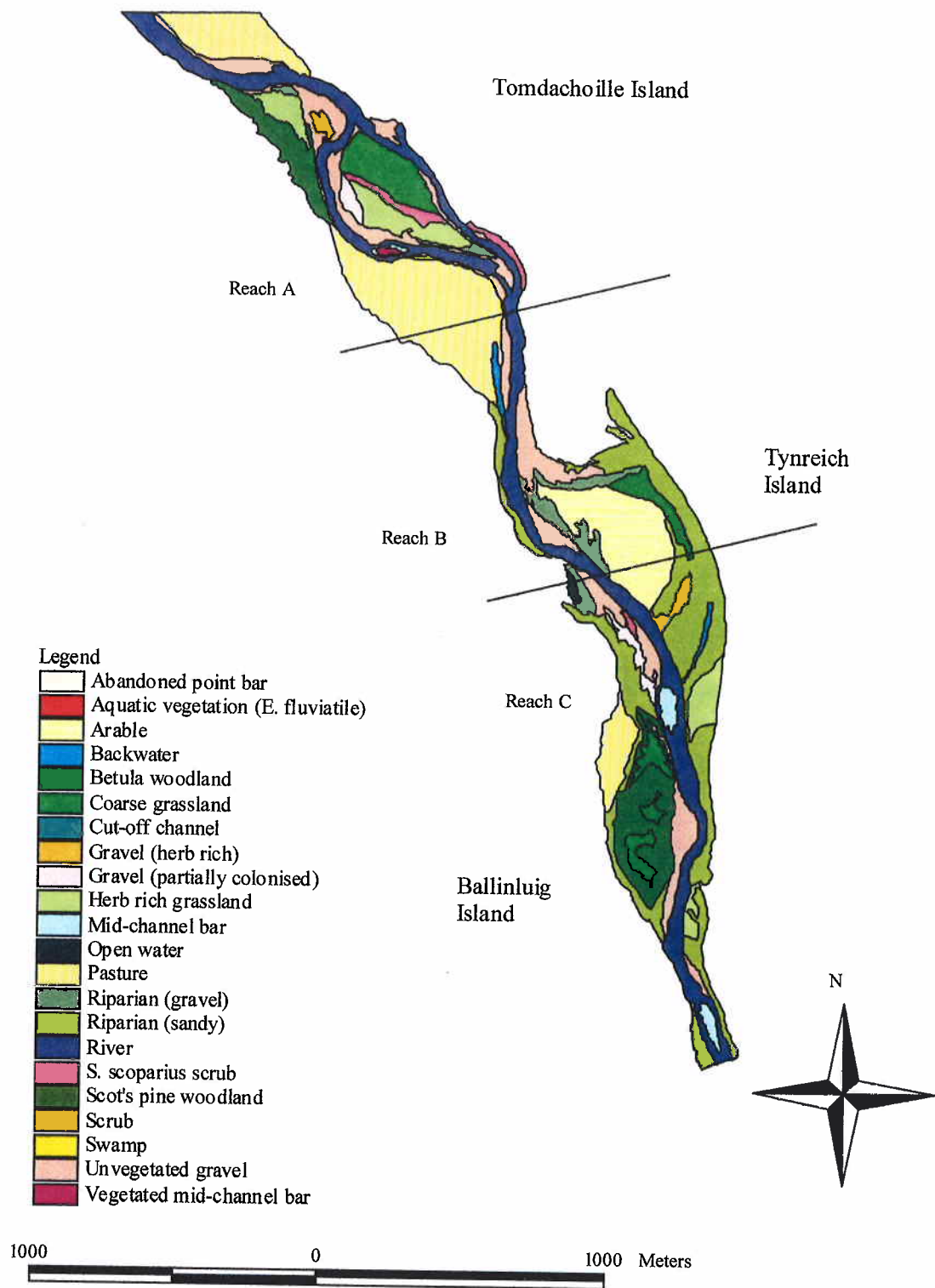


Figure 5.8b: Classified image of the botanical habitat types within the River Tummel study area, August 1968.

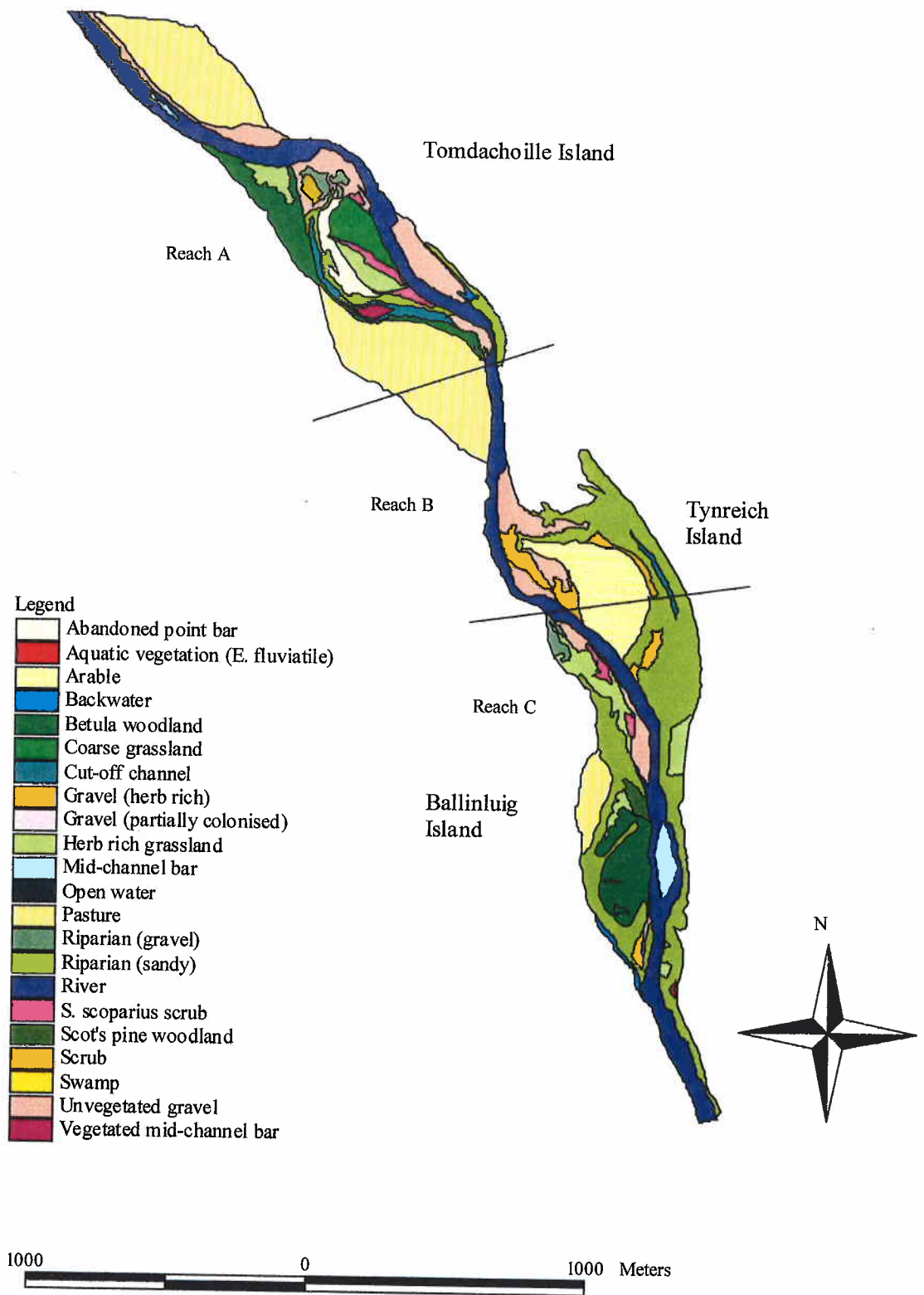


Figure 5.8c: Classified image of the botanical habitat types within the River Tummel study area, 1988.

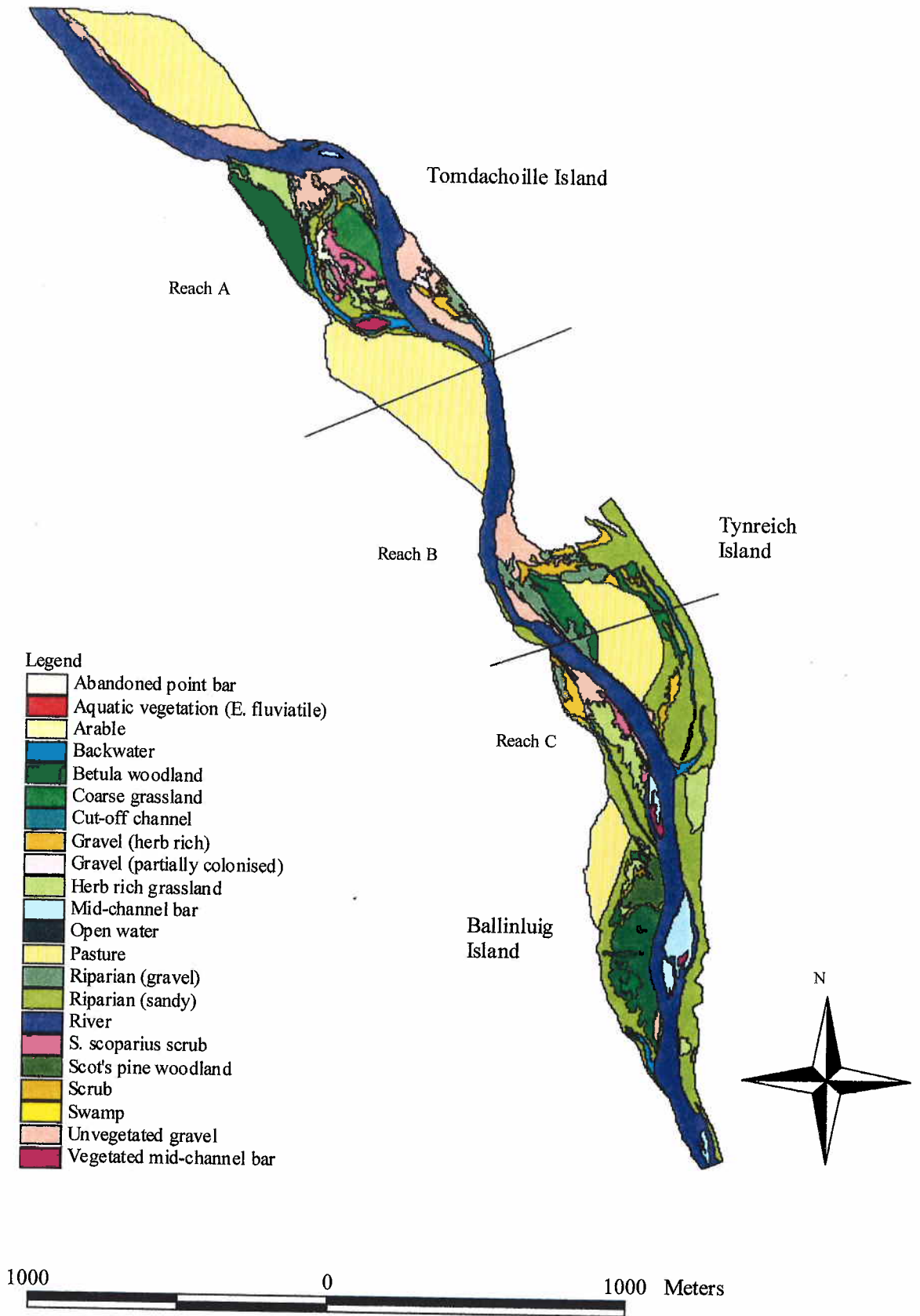
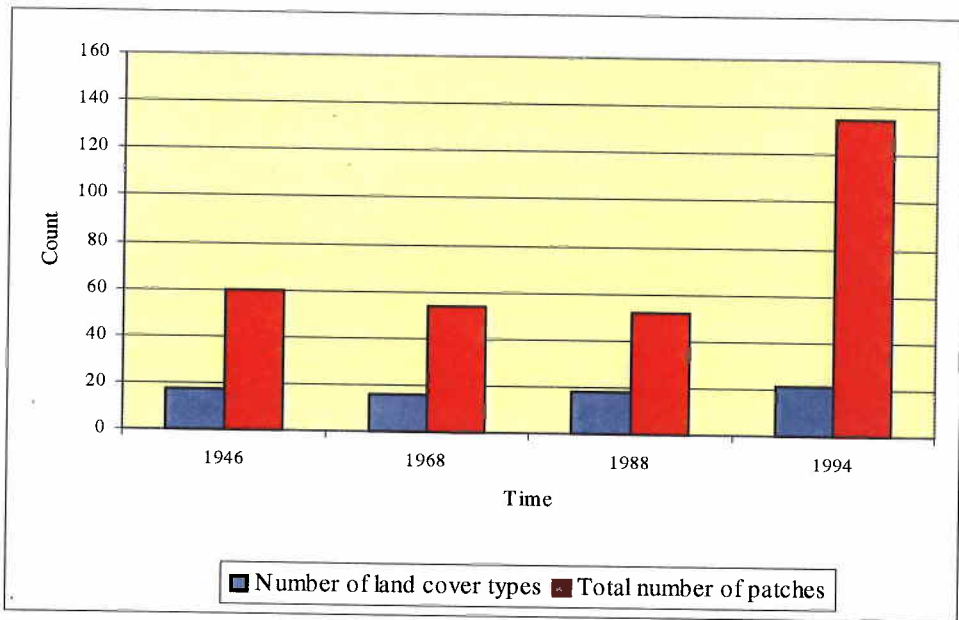
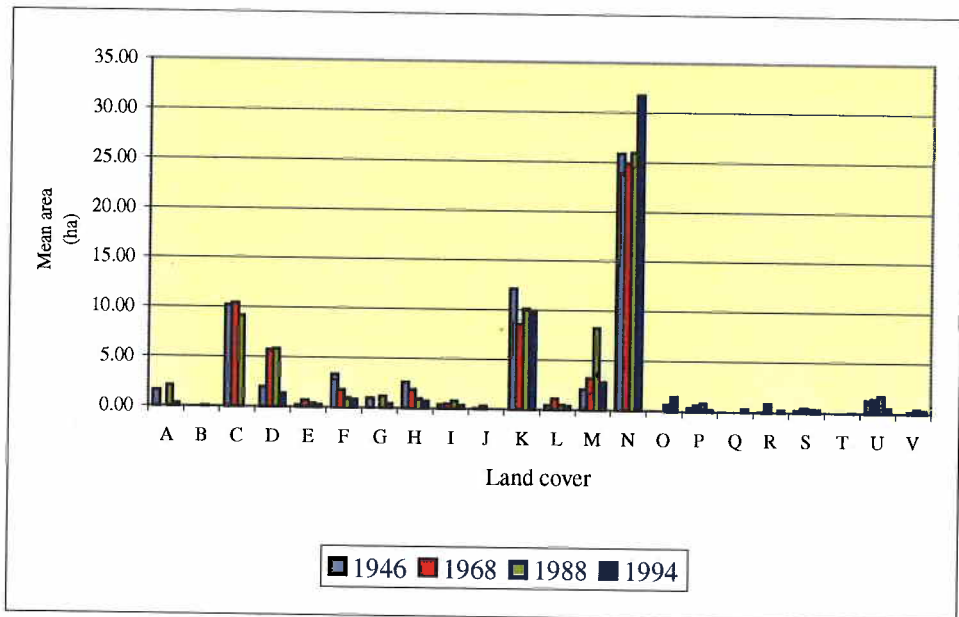


Figure 5.8d: Classified image of the botanical habitat types within the River Tummel study area, May 1994.



a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	L	Riparian woodland(gravel)
B	Aquatic vegetation <i>E. fluviatile</i>	M	Riparian woodland(sandy)
C	Arable	N	River
D	<i>Betula</i> woodland	O	Scot's pine wood
E	<i>S. scoparius</i> scrub	P	Scrub
F	Coarse grassland	Q	Gravel (herb rich)
G	Cut-off channel	R	Gravel (partially colonised)
H	Herb rich grassland	S	Backwater
I	Mid-channel bar	T	Swamp <i>G. fluitans</i>
J	Open water	U	Unvegetated gravel
K	Pasture	V	Vegetated mid-channel bar

Figure 5.9: Temporal variation in the number of land cover types and total number of patches (a) and the mean area of each land cover type (b) within the botanical habitat types on the River Tummel floodplain between 1946-1994 (excluding 1971).

5.3.4a. 1946 coverage

Figure 5.8a shows that the river occupies one main channel along the study reach. The channel is split with 3 mid-channel bars. Several cut-off channels are present within the floodplain. The upper reach of the study area is dominated by herb-rich grassland and the lower reach has extensive areas of unvegetated gravel. Fragments of riparian woodland are present along the reach. Figure 5.9a shows 17 land cover types are present within the area and a total of 60 landscape patches. Figure 5.9b shows that the river occupies the largest mean area of the study area, followed by high values for pasture and arable land. The mean area for all semi-natural floodplain habitats is very low throughout the reach. The high standard deviations, given in Appendix 15.3, show that there is considerable variation in the size of the patches within this landscape.

5.3.4b. 1968 coverage

Figure 5.9a shows that the 1968 coverage has the lowest number of land cover types present out of the four years studied. The most notable change between 1946 and 1968 coverage, shown in Figure 5.8a and b, is the increase in sinuosity of the channel. The second main channel in the Tomdachoille reach is an indication of this. There has been a notable decline in the number of patches of herb rich grassland, along with a loss of area occupied by this land unit, shown in Figure 5.9b. The extent of riparian woodland within the reach has increased between 1946-1968. Pasture and arable land still occupy a large

area of the study area. All semi-natural floodplain habitats have a low mean area with high standard deviations.

5.3.4c. 1988 coverage

Figure 5.9a shows 18 land cover types are present within the study area in 1988, and that the landscape is composed of the lowest number of patches for the years compared. Figure 5.8c shows that the river has reverted back to one main channel, abandoning the main channel the river occupied in the Tomdachoille reach in 1946. A large cut-off channel is now present. There are three mid-channel bars, which have almost doubled in extent since 1946 (see Appendix 15.3). New habitats are developing within the zone of channel abandonment. Riparian woodland has generally increased in coverage especially the community developing on sandy substrate, shown in Figure 5.9b and Appendix 15.3. *Equisetum fluviatile* community has also developed within the Ballinluig area of the floodplain, this is inferred from its current presence in this location.

5.3.4d. 1994 coverage

Figure 5.8d shows that there is complex spatial patterning of land cover types along the study reach in the 1994 coverage. This is clearly demonstrated in Figure 5.9a showing that there has been a dramatic increase in the total number of patches increasing from the minimum number of landscape patches in 1988 to 139 patches in 1994. The increase in the total number of land cover

types is not proportional to the increase in number of patches. This stresses that the landscape has become considerably more fragmented and is now dominated by many patches with small interiors. The river channel occupies a larger mean area of the study area, however this may be a result of higher water levels at the time of the aerial survey rather than due to changes in channel geometry or flow regime. With the exception of the channel, the mean area of the landscape patches in 1994 is lower than for the previous study years. This supports the notion that the habitats are becoming increasingly fragmented. The high standard deviations for patch mean area show that there is considerable variability in patch size along the reach.

5.3.5. Temporal change in diversity indices within the River Tummel study area

The results of the diversity indices are presented in Figure 5.10. The results show that there is very little change in landscape diversity through time when assessed using the Shannon index as the results merely fluctuate between 2.21 and 2.29 (Figure 5.10a). The maximum diversity is in 1994, and the minimum in 1988. This is a direct reflection of the richness of landscape patches for these years. In contrast, the reciprocal of Simpson's index suggests that landscape diversity is highest in the 1988 coverage, shown in Figure 5.10d. The pattern of results for the equitability index and dominance shows an opposite trend, but both reveal the same results (Figure 5.10b and c). These indices show that the landscape is composed of fewer land cover types occupying more equal areas in 1968. The graphs show that one or a few land

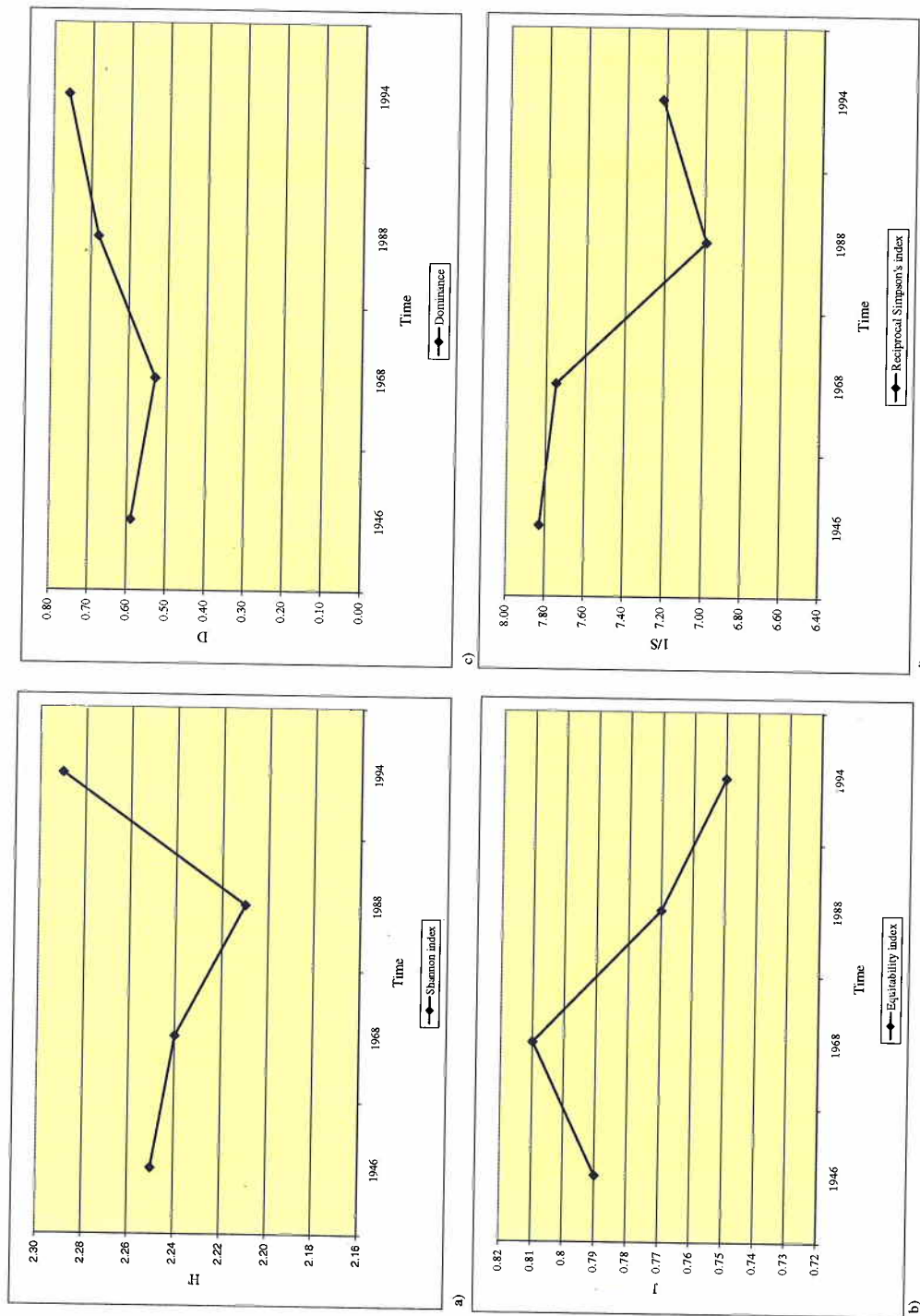


Figure 5.10: Temporal variability in botanical diversity indices within the River Tummel study area between 1946-1994 (excluding 1971).
a) Shannon index (H), b) Equitability index (J), c) Dominance index (D), d) Reciprocal of Simpson's index (1/S)

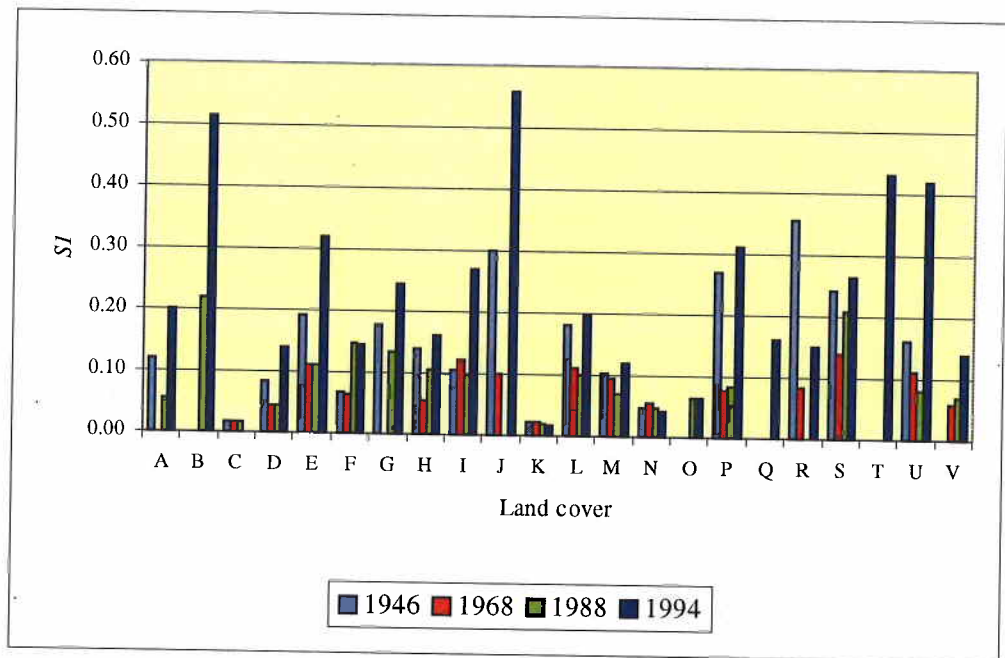
cover types within a complex matrix of small patches dominate the landscape in the 1994 coverage.

The results of temporal change in the shape of the landscape patches are summarised in Figure 5.11. Figure 5.11a shows that the *S1* index increases considerably over the study period for several land cover types. This suggests that the landscape has changed over time from being composed of relatively few patches with large interiors, to a landscape composed of relatively numerous patches with small areas. The most stable patches are arable land, pasture, the main channel and Scot's pine woodland.

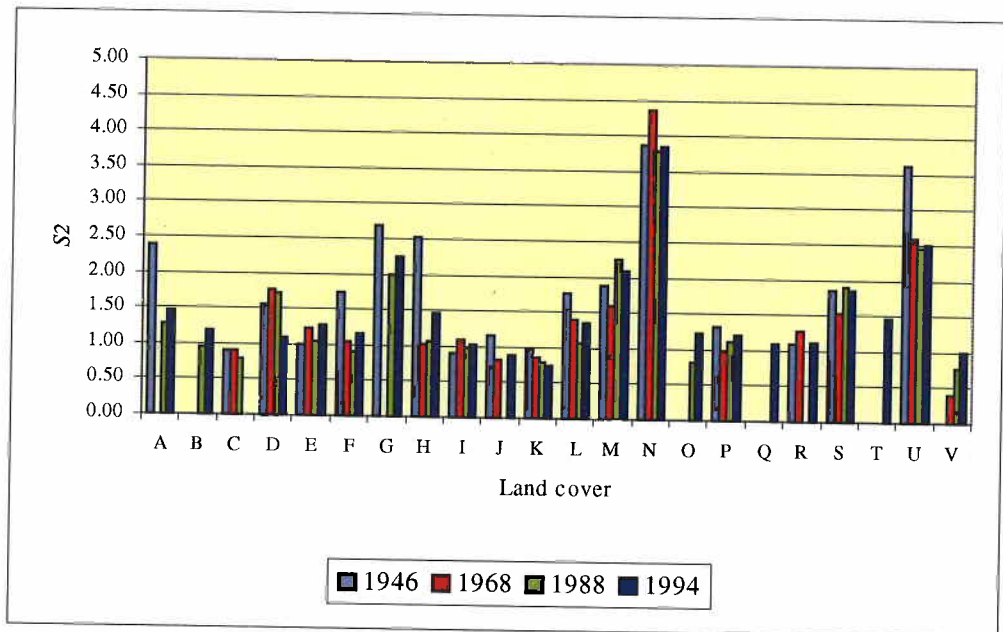
The *S2* index, given in Figure 5.11b, shows that the majority of the landscape patches score approximately 1.00. This suggests that the patches are approximately isodiametric in shape. The land units deviating most from isodiametric shapes are cut-off channels, riparian woodland, main channel, backwaters, and unvegetated gravel. Within class variance is minimal over the study period for this index shown in Appendix 15.4.

5.3.6. Temporal change in the area of each land unit within the River Tummel study area

The patterns of temporal change in the total area of the study reach occupied by each land cover type are presented in Figure 5.12. The figure shows that more land cover classes have increased in area in comparison to the 1946 coverage. The most notable increase is in the riparian woodland (sandy) land



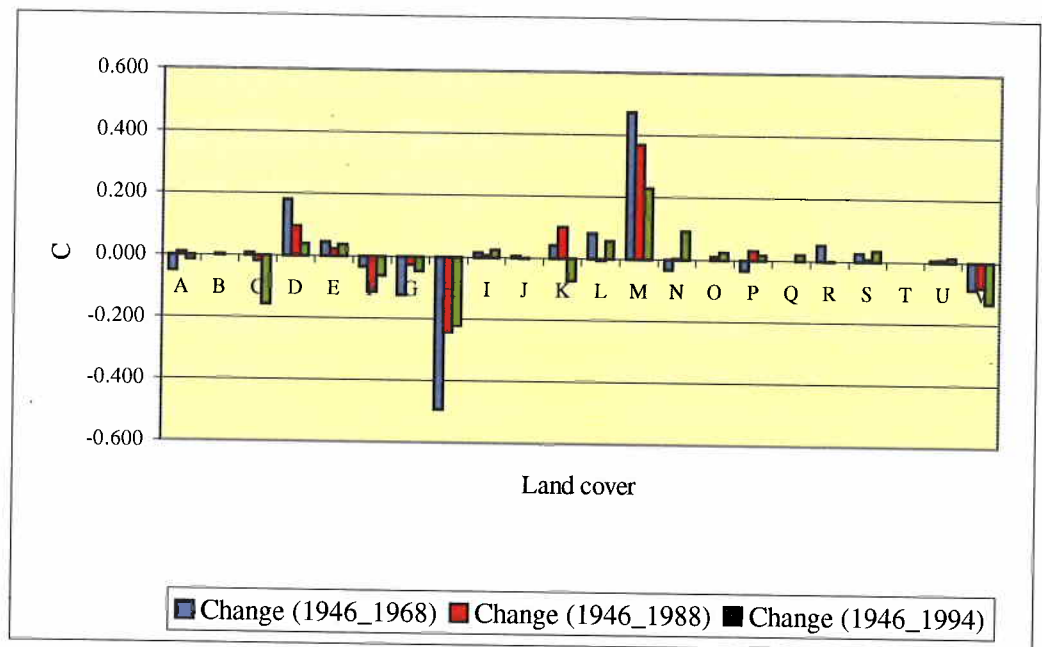
a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	L	Riparian woodland (gravel)
B	Aquatic vegetation <i>E. fluviatile</i>	M	Riparian woodland (sandy)
C	Arable	N	River
D	<i>Betula</i> woodland	O	Scot's pine wood
E	<i>S. scoparius</i> scrub	P	Scrub
F	Coarse grassland	Q	Gravel (herb rich)
G	Cut-off channel	R	Gravel (partially colonised)
H	Herb rich grassland	S	Backwater
I	Mid-channel bar	T	Swamp <i>G. fluitans</i>
J	Open water	U	Unvegetated gravel
K	Pasture	V	Vegetated mid-channel bar

Figure 5.11: Temporal variation in shape indices SI (a) and $S2$ (b) within the River Tummel study area between 1946-1994 (excluding 1971).



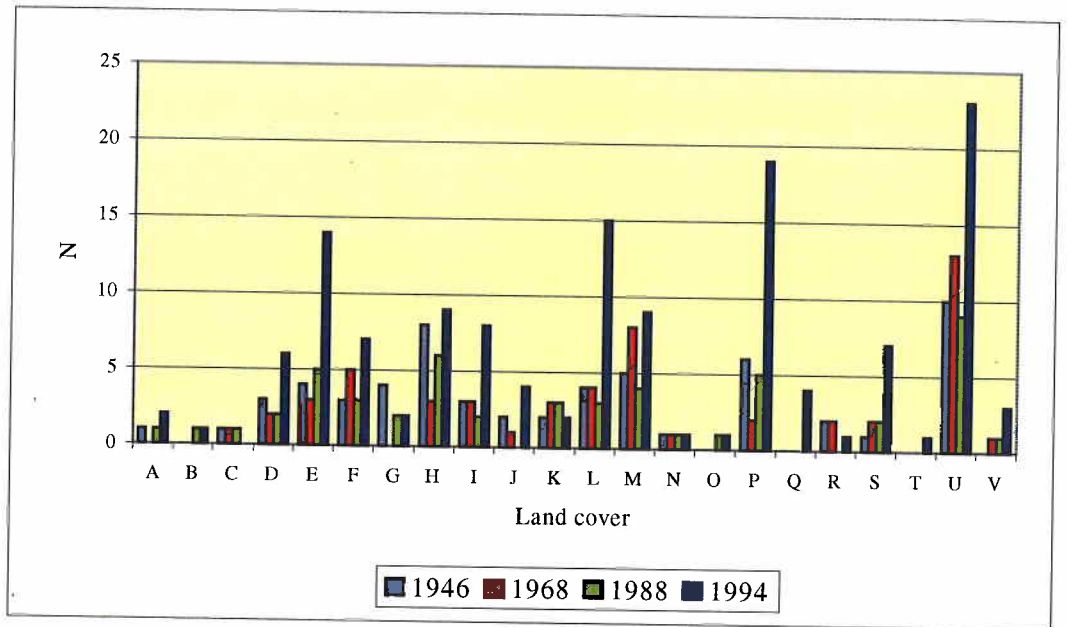
Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	L	Riparian woodland (gravel)
B	Aquatic vegetation	M	Riparian woodland(sandy)
C	Arable	N	River
D	<i>Betula</i> woodland	O	Scot's pine wood
E	Broom scrub	P	Scrub
F	Coarse grassland	Q	Gravel (herb rich)
G	Cut-off channel	R	Gravel (partially colonised)
H	Herb rich grassland	S	Backwater
I	Mid-channel bar	T	Swamp <i>G. fluitans</i>
J	Open water	U	Unvegetated gravel
K	Pasture	V	Vegetated mid-channel bar

Figure 5.12: Temporal variation in total area of each land cover measured by the change index (C) within the River Tummel study area between 1946-1994 (excluding 1971).

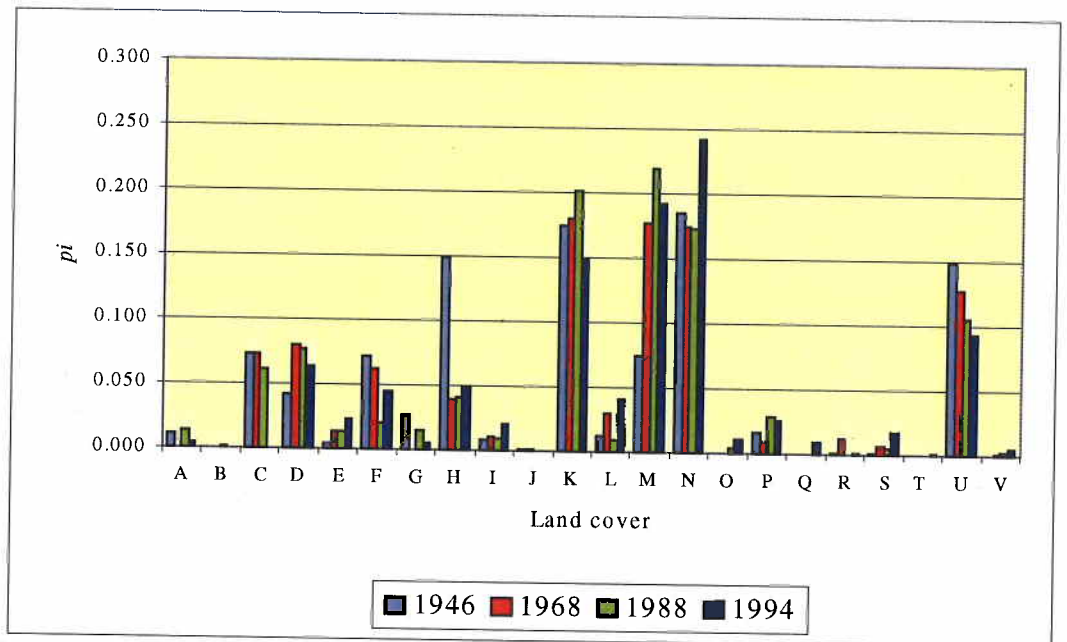
unit. There has been an increase in total area of eight ecologically important habitats within the study area in comparison to 1946. The habitats increasing in area are *Betula* woodland, mid-channel bars, carr woodland and vegetated mid-channel bars. There has also been an increase in the species-poor *S. scoparius* scrub community. Despite the overall increase in total area of land units in comparison to the 1946 cover, the trend within each of these classes is for a gradual decline in extent post 1968. The coverages showing the greatest contrast are between 1968 and 1946.

Of the land cover types to show an overall decline in total area over time two classes are of little ecological value, and four are important floodplain habitats. The most notable loss of habitat is the herb-rich grassland. Other ecologically important habitats to have decreased in area are abandoned point bar, cut-off channels and vegetated mid-channel bars. Arable land and coarse grassland has declined since 1946, and there is less land under pasture in 1994 compared to 1946.

Figure 5.13a shows the temporal change in the number of patches within each land unit. The results show that there has been a considerable increase in the number of patches of *Betula* woodland, mid-channel bars, riparian woodland communities and unvegetated gravel. The number of patches of herb-rich grassland has fluctuated over time and has a higher number of patches in the 1994 cover. However the mean area of the patches is considerably lower, illustrated in Appendix 15.3. The number of landscape patches under scrub vegetation has increased considerably over the study period.



a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned point bar	L	Riparian woodland (gravel)
B	Aquatic vegetation <i>E. fluviatile</i>	M	Riparian woodland (sandy)
C	Arable	N	River
D	<i>Betula</i> woodland	O	Scot's pine wood
E	<i>S. scoparius</i> scrub	P	Scrub
F	Coarse grassland	Q	Gravel (herb rich)
G	Cut-off channel	R	Gravel (partially colonised)
H	Herb rich grassland	S	Backwater
I	Mid-channel bar	T	Swamp <i>G. fluitans</i>
J	Open water	U	Unvegetated gravel
K	Pasture	V	Vegetated mid-channel bar

Figure 5.13: Temporal variation in the number, N (a) and proportion, pi (b) of each land cover type within the River Tummel study area between 1946-1994 (excluding 1971).

Figure 5.13b shows the results of the proportion of the study area occupied by each land cover type in relation to total area for each year analysed. The results reveal pasture, riparian woodland (sandy) and the main channel land units dominate the landscape. Herb-rich grassland occupied approximately 15% of the study area in the 1946 coverage. This figure has declined to 5% in 1994. The extent of *Betula*- and carr-woodland is greater than in 1946 when the landscape seems to have been more frequently inundated due to the large areas of unvegetated gravel and little woodland development. Ecologically important habitats to have declined in proportion are cut-off channels, herb-rich grassland and unvegetated gravel. The proportion of the study area to be occupied by coarse grassland has also declined considerably.

5.3.7. Temporal change in geomorphic landform patterns within the River Tummel study area

The distribution of geomorphic landforms within the study area between 1946-1994 are illustrated in Figure 5.14a-d. The number of land cover types present and the total number of landscape patches within each coverage are given in Figure 5.15.

5.3.7a. 1946 coverage

Figure 5.14a shows that a few landform types with each patch having a relatively large interior dominate the landscape. Semi-natural and agricultural floodplain dominates the reach. The upper section of the reach is more

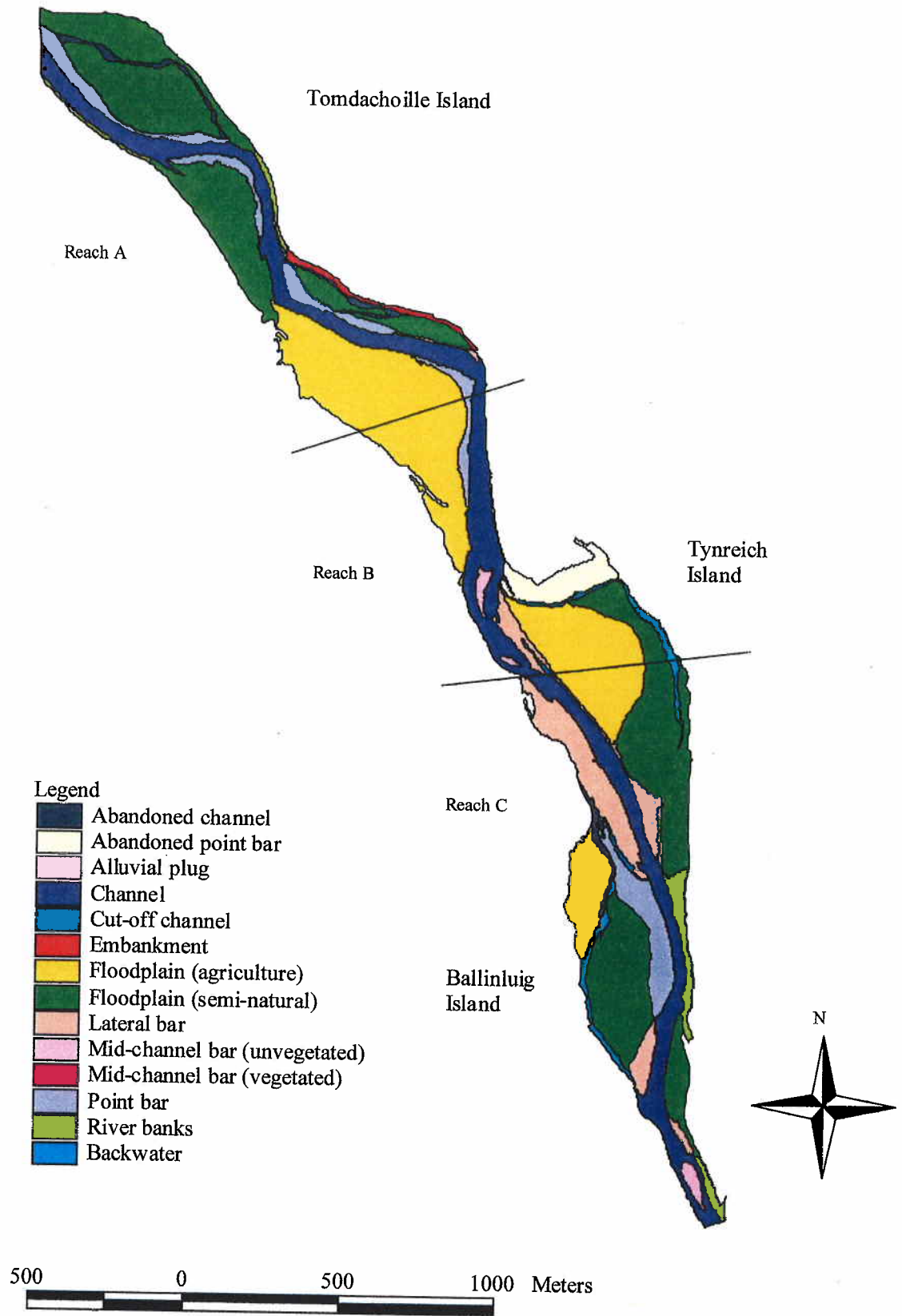


Figure 5.14a: Classified image of the geomorphic landforms within the River Tummel study area, May 1946.

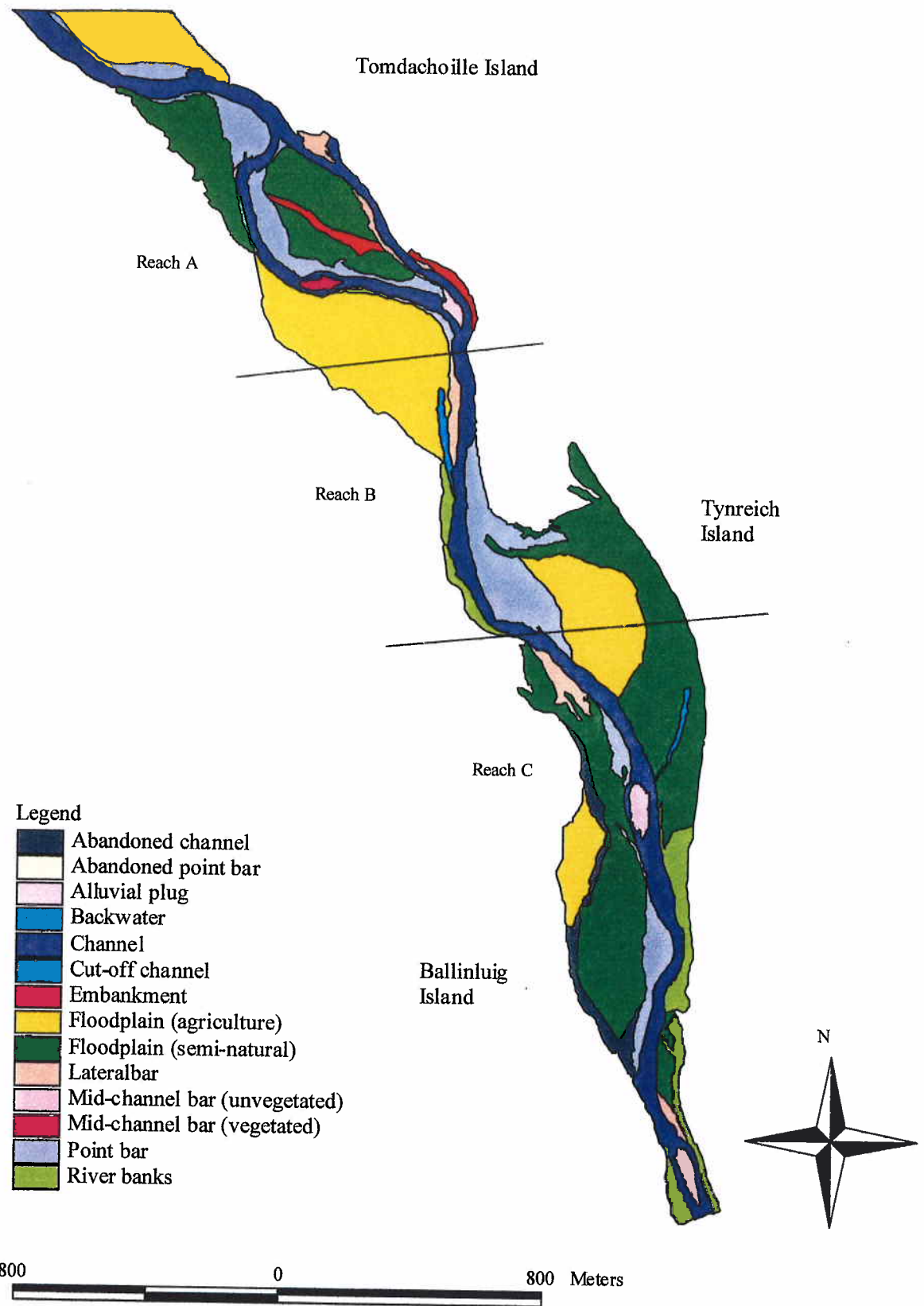


Figure 5.14b: Classified image of the geomorphic landforms within the River Tummel study area, August 1968.

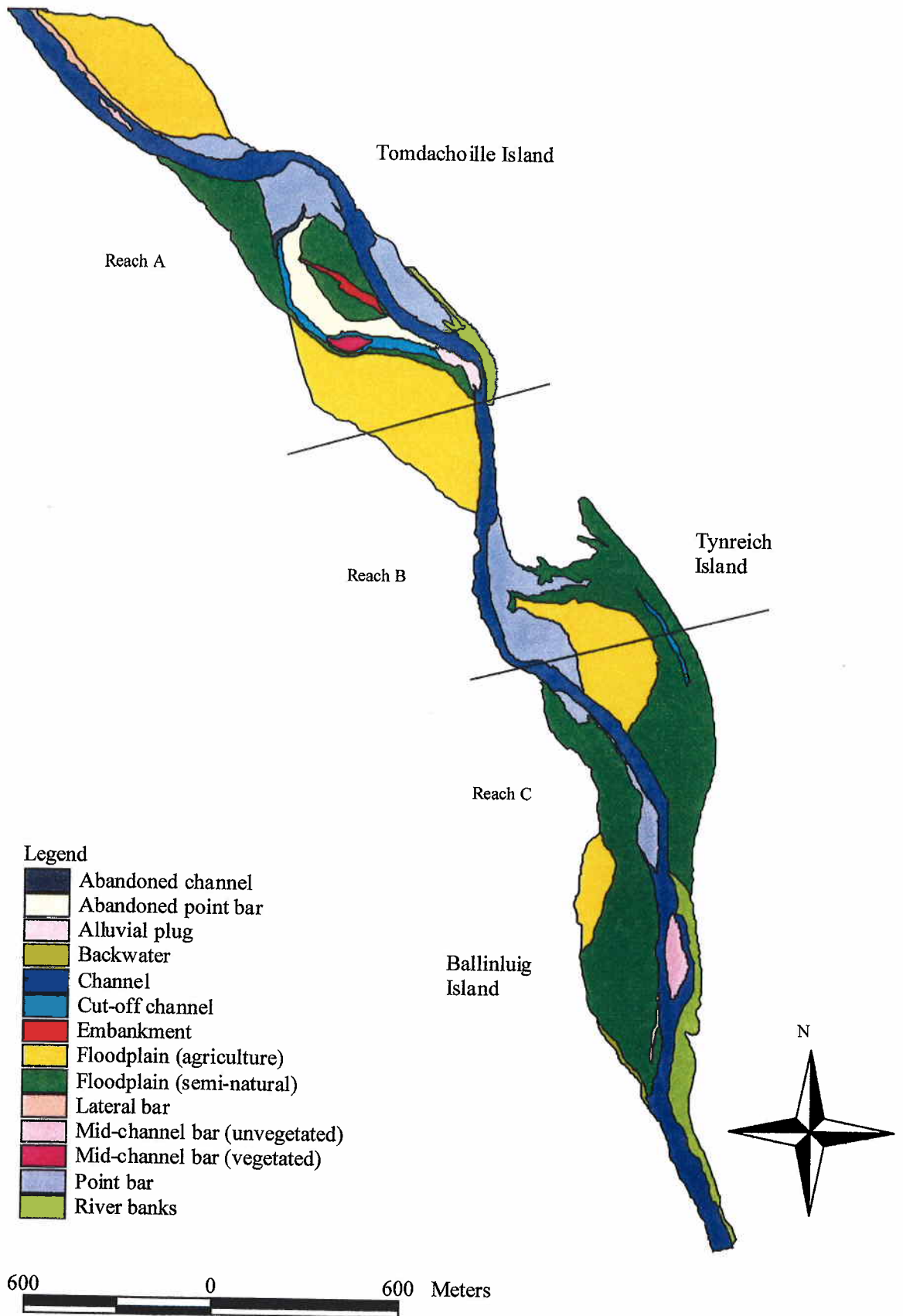


Figure 5.14c: Classified image of the geomorphic landforms within the River Tummel study area, 1988.

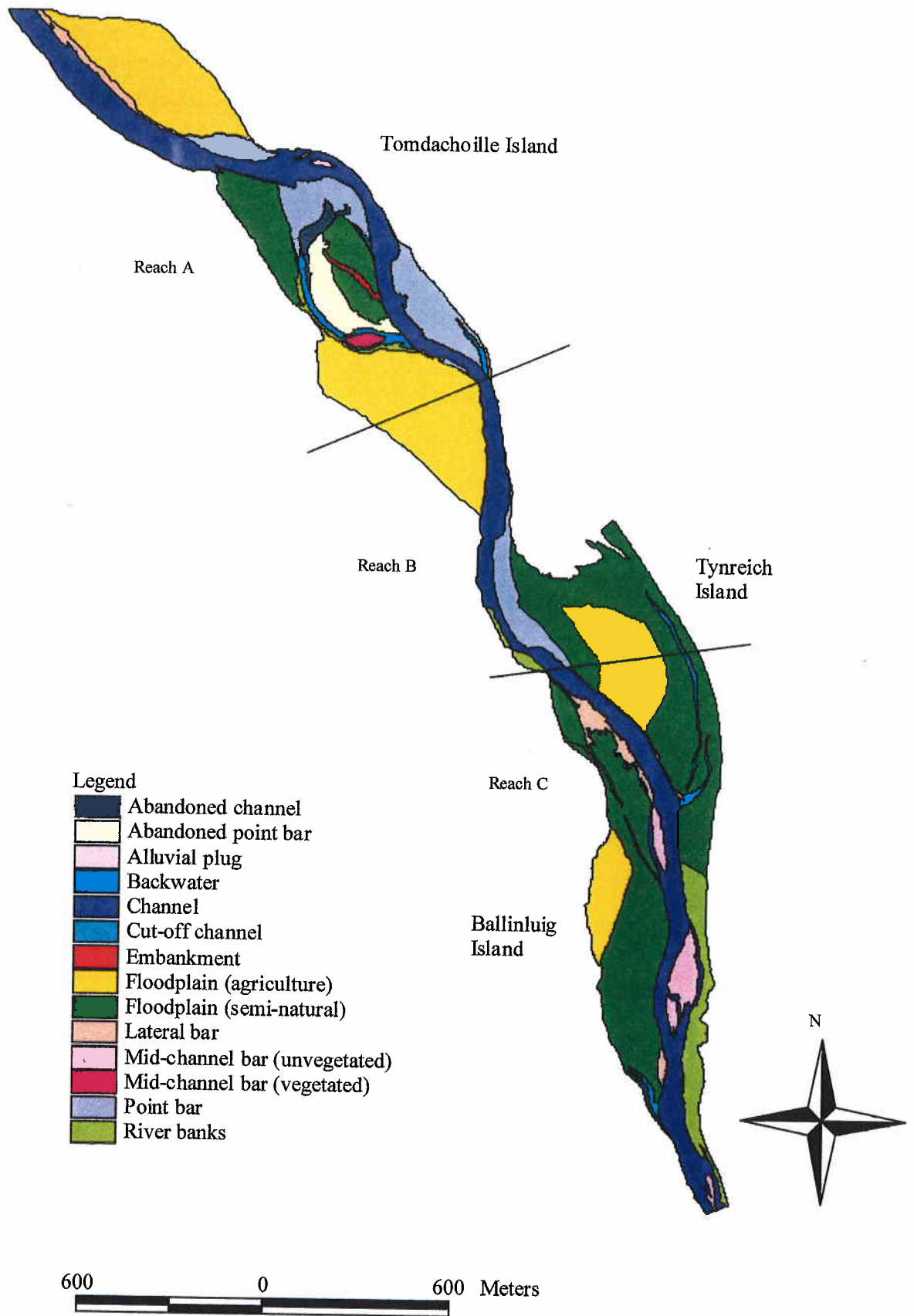
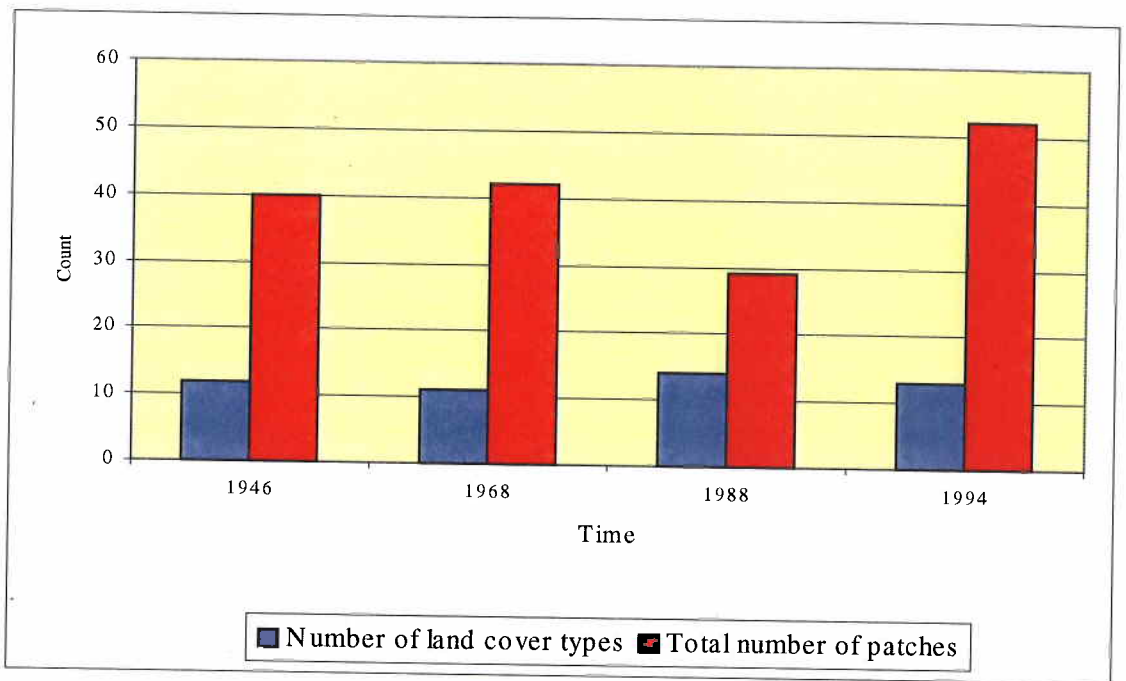
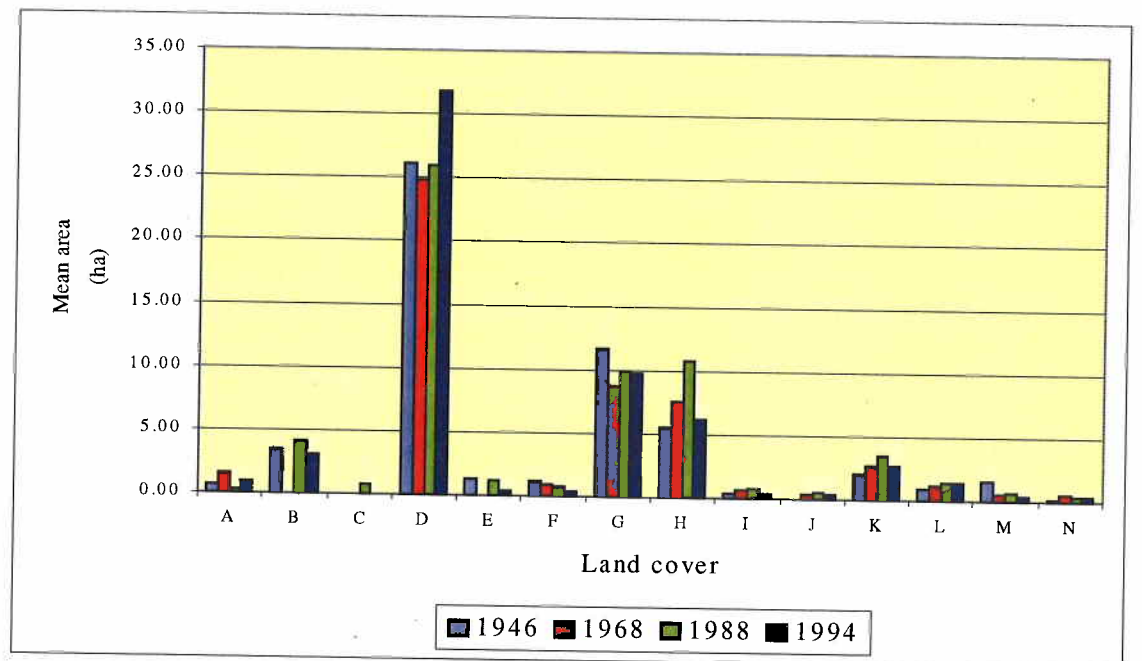


Figure 5.14d: Classified image of the geomorphic landforms within the River Tummel study area, May 1994.



a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned channel	H	Floodplain (semi-natural)
B	Abandoned point bar	I	Mid-channel bar (unvegetated)
C	Alluvial plug	J	Mid-channel bar (vegetated)
D	Channel	K	Point bar
E	Cut-off channel	L	River banks
F	Embankment	M	Lateral bar
G	Floodplain (agriculture)	N	Backwater

Figure 5.15: Temporal variation in the number of land cover types and total number of patches (a) and the mean area (b) of the geomorphic landforms within the River Tummel study area between 1946-1994.

sinuous, indicated by the extent of point bars. The lower reach is straighter with extensive areas of lateral bars. There are twelve landform classes present and forty landscape patches, shown in Figure 5.15a. The channel occupies the largest area of the reach. The landforms to occupy considerable areas aside from the channel are the floodplain landform (semi-natural and agricultural). The area of the landscape patches within each land unit varies considerably indicated by the large standard deviation values, given in Appendix 15.5.

5.3.7b. 1968 coverage

The most notable change in 1968 is an increase in sinuosity of the channel and increase in the size and number of point bars within the study reach, illustrated in Figure 5.14b and Figure 5.15b. With an increase in point bars there has been a loss in the number and extent of lateral bars due to the more sinuous nature of the river. This coverage has the lowest number of land units present, shown in Figure 5.15a. Figure 5.15b shows that there has been a decrease in the mean area of floodplain under agriculture and an increase in semi-natural floodplain.

5.3.7c. 1988 coverage

Figure 5.14c shows that the river remains fairly sinuous with extensive point bars along the reach. Figure 5.15b shows a further increase in the mean area of point bars in 1988. The landscape is composed of fourteen land units and now has the lowest number of landscape patches present, illustrated in Figure

5.15a. The mean area of semi-natural floodplain has increased considerably since 1968. This is a result of a decline in the number of landscape patches, thus raising the mean area.

5.3.7d. 1994 coverage

The 1994 coverage in Figure 5.14d shows that there is complex geomorphic patterning within the zone of recent channel change in the Tomdachoille reach. The river remains fairly sinuous with several point bars and lateral bars present. The mean area of point bars has declined since 1988, shown in Figure 5.15b. There has also been a loss in mean area of semi-natural floodplain, illustrated in Figure 5.14d and Figure 5.15b as a result of an increase in the number of patches present. The highest number of landscape patches is present in the 1994 coverage showing that the geomorphic patterning is more complex than in the past (Figure 5.15a). The geomorphic landforms appear to have been relatively stable in terms of the number of land units present and the total number of patches between 1946 and 1968. Active channel change during the 1970's and 1980's has resulted in altering the number of landform types present and an increase in patch number in 1994.

5.3.8. Temporal change in diversity indices within the River Tummel study area

The results of the temporal change in the diversity of landforms are presented in Figure 5.16. The results show that there has been an overall decline in the

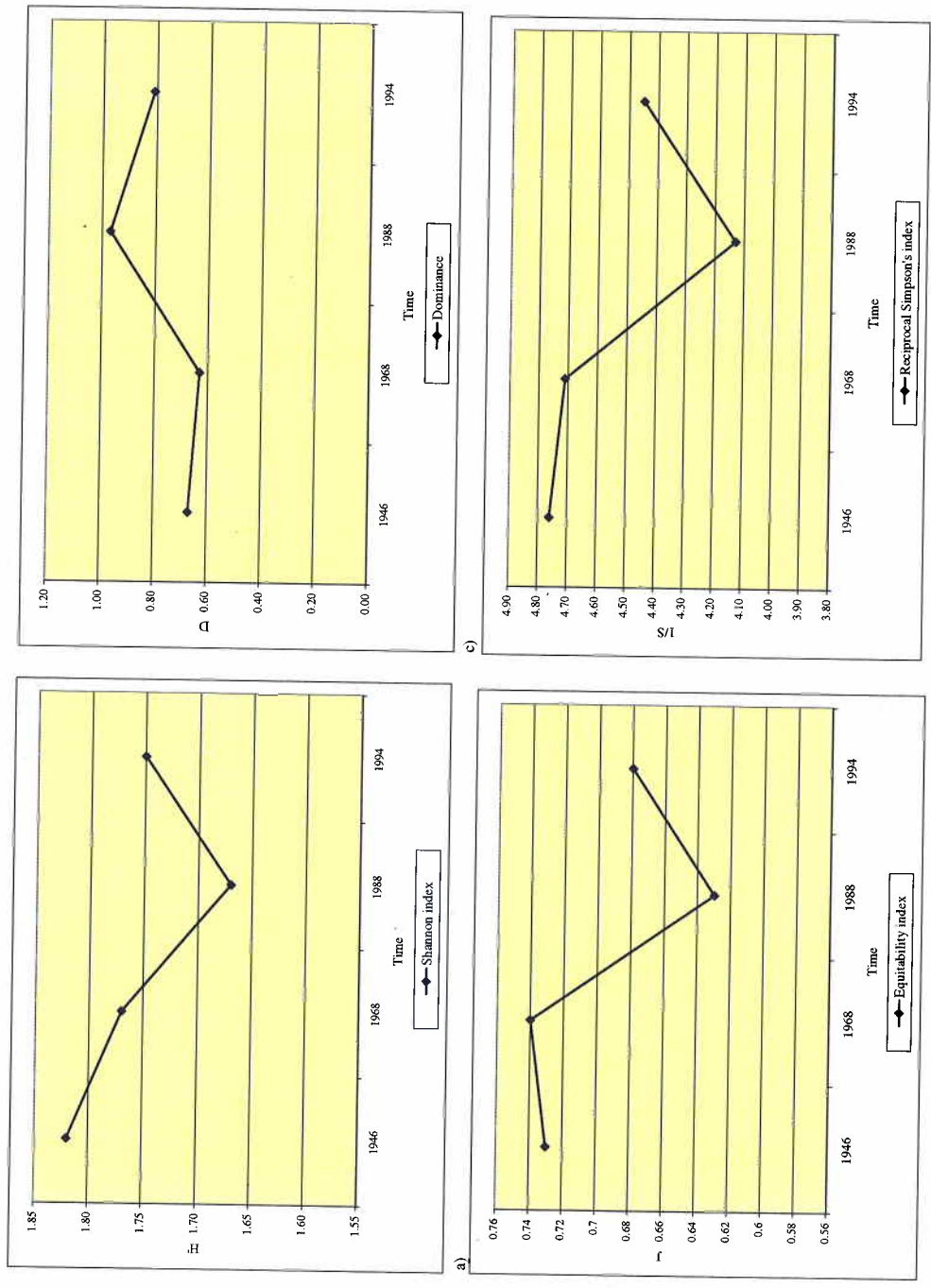
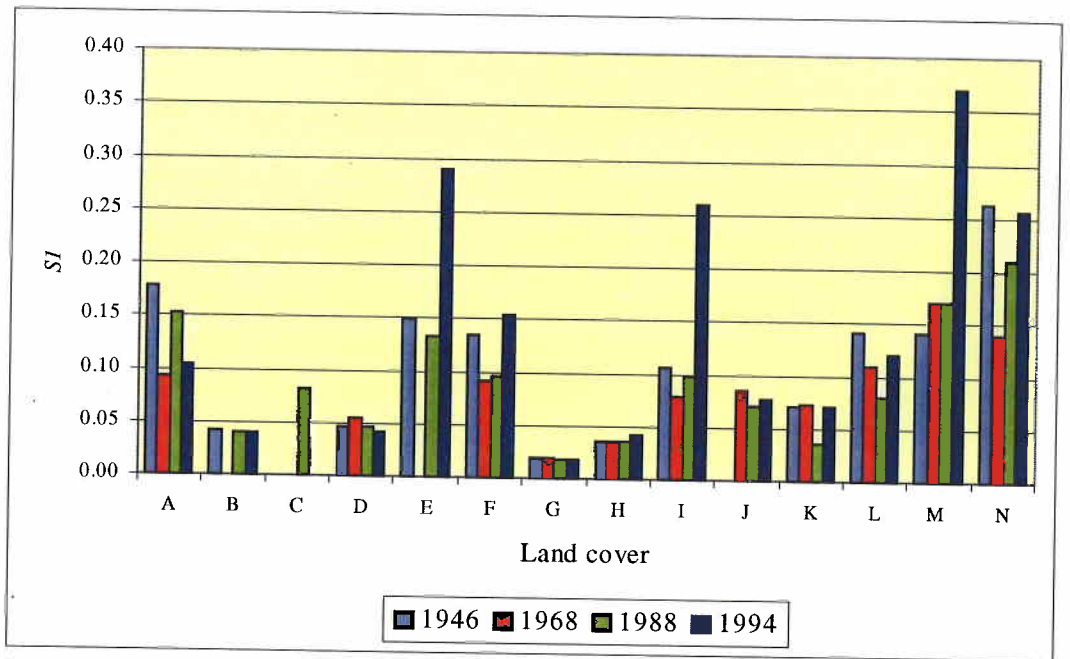


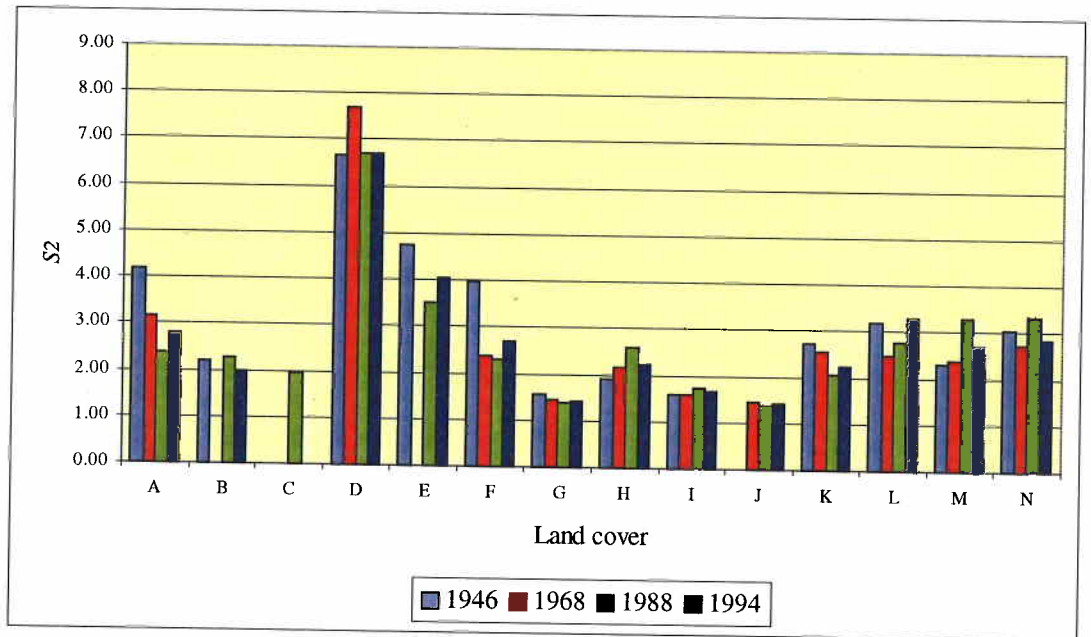
Figure 5.16: Temporal variation in the diversity of geomorphic landforms within the River Tummel floodplain between 1946-1994.
 a) Shannon index; b) Equitability index; c) Dominance index; d) Reciprocal of Simpson's index.

diversity values over time with the exception of the dominance index. The Shannon index indicates that there has been a decline in the diversity of landforms in terms of richness (H') between 1946-1988. The lowest H' score also coincides with the lowest Shannon index score for equitability (J) showing that not only is landform richness low, but the landform distribution is very uneven. Landscape diversity is highest measured on the Shannon index in 1946 and lowest in 1988. An inverse relationship again exists between the Shannon index and the reciprocal of Simpson's index whereby this index indicates the landscape to be most diverse in 1988 and least diverse in 1946. Congruence occurs between the equitability and dominance indices which indicate that the highest geomorphic diversity exists in 1968 and 1946, and the lowest landform diversity is in 1988.

The results of the analysis of landscape patch shape are given in Figure 5.17. Figure 5.17a shows that approximately half of the landform classes show marginal temporal variation in the mean perimeter-to-area ratio of the patches. This indicates that these patches are few in number with relatively large interiors. The remainder of the landforms show notable variation in the SI index, especially the cut-off channels, mid-channel bar (unvegetated) and lateral bars. The standard deviation for the shape indices are given in Appendix 15.6. The standard deviation for lateral bars in 1994 is relatively high indicating considerable variability in the patch area of this landform feature along the study reach. The standard deviation for all other landforms over time is relatively low, indicating that all patches within each landform class are of similar shape.



a)



b)

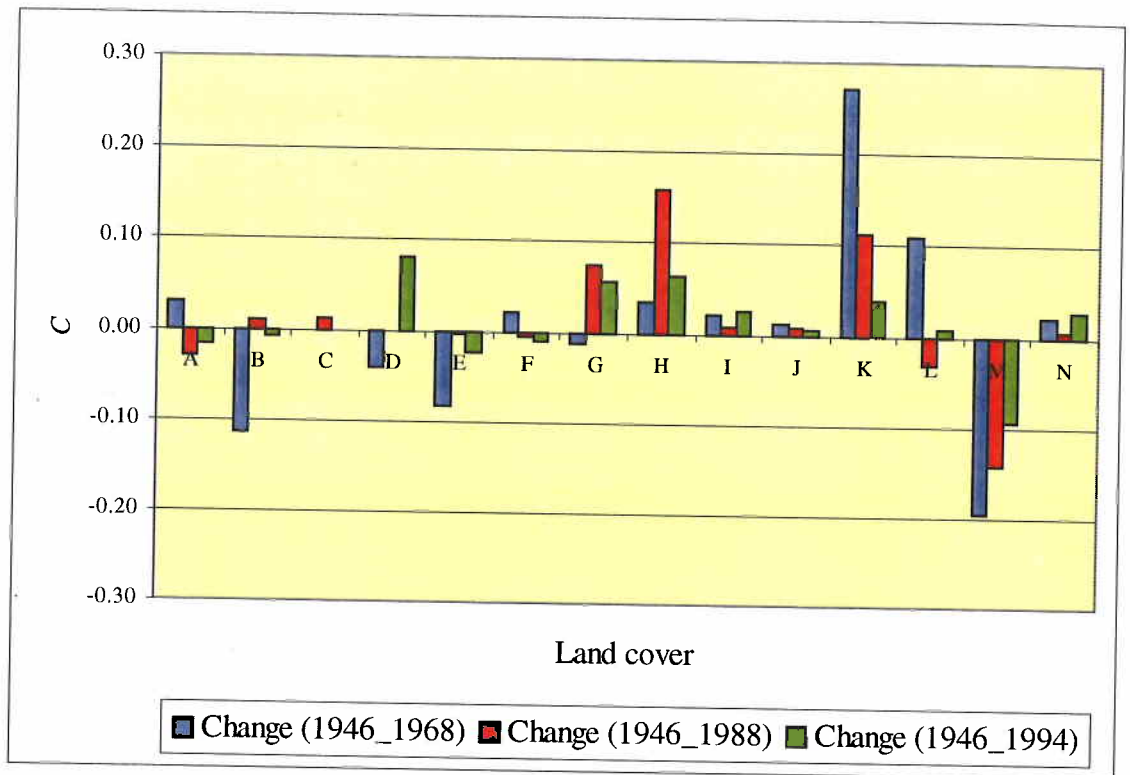
Axis label	Land cover	Axis label	Land cover
A	Abandoned channel	H	Floodplain (semi-natural)
B	Abandoned point bar	I	Mid-channel bar (unvegetated)
C	Alluvial plug	J	Mid-channel bar (vegetated)
D	Channel	K	Point bar
E	Cut-off channel	L	River banks
F	Embankment	M	Lateral bar
G	Floodplain (agriculture)	N	Backwater

Figure 5.17: Temporal variations in shape indices $S1$ and $S2$ within the geomorphic landforms within the River Tummel study area between 1946-1994.

Considerable variation occurs between the shape of the landform patches between classes, illustrated in Figure 5.17b. Overall little variation in $S2$ occurs within the land units over time, with the exception of abandoned channels, cut-off channels, embankment, mid-channel bar (unvegetated) and lateral bars. The landforms with the most isodiametric shapes are floodplain (agriculture) and mid-channel bars (vegetated and unvegetated). The greater the $S2$ index deviates from 1.00, the more the shape deviates from being isodiametric. The landforms with the highest scores are those which are linear in nature due to the processes of formation. These are the channel landform categories, river banks and lateral bars. $S2$ standard deviations for each landform class over time is given in Appendix 15.6. The results show little variation in the shape of each landscape patch within a given land unit for each year studied.

5.3.9. Temporal change in the area of each land unit within the River Tummel study area

Figure 5.18 shows the rate of change in total area of each landform class over time. The figure shows a net increase of eight and a net decrease of four land units. The most notable difference is the total area of point bars and lateral bars over time. The total area of point bars is greater for all years in comparison to the 1946 coverage. However, the change in total area of point bars has shown a downward trend since 1968. The increase in the total area of point bars is balanced by a considerable loss of lateral bars. The greatest contrast in area being between the 1946 and 1968 coverage. The total area of



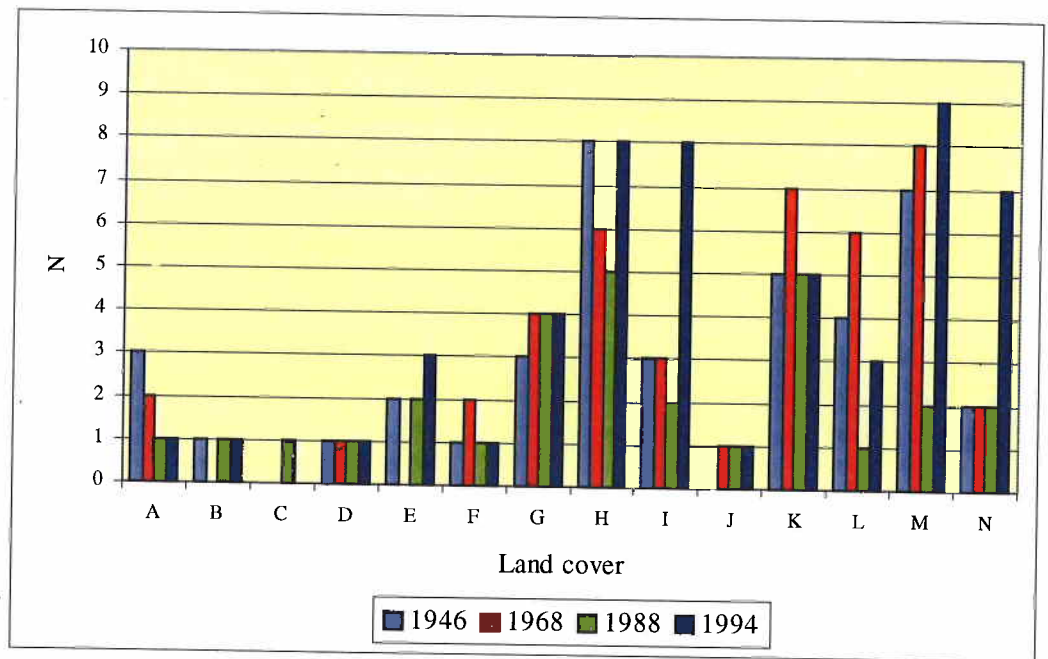
Axis label	Land cover	Axis label	Land cover
A	Abandoned channel	H	Floodplain (semi-natural)
B	Abandoned point bar	I	Mid-channel bar (unvegetated)
C	Alluvial plug	J	Mid-channel bar (vegetated)
D	Channel	K	Point bar
E	Cut-off channel	L	River banks
F	Embankment	M	Lateral bar
G	Floodplain (agriculture)	N	Backwater

Figure 5.18: Temporal variation in the total area of each landform land cover types measured by the change index (C) within the River Tummel study area between 1946-1994.

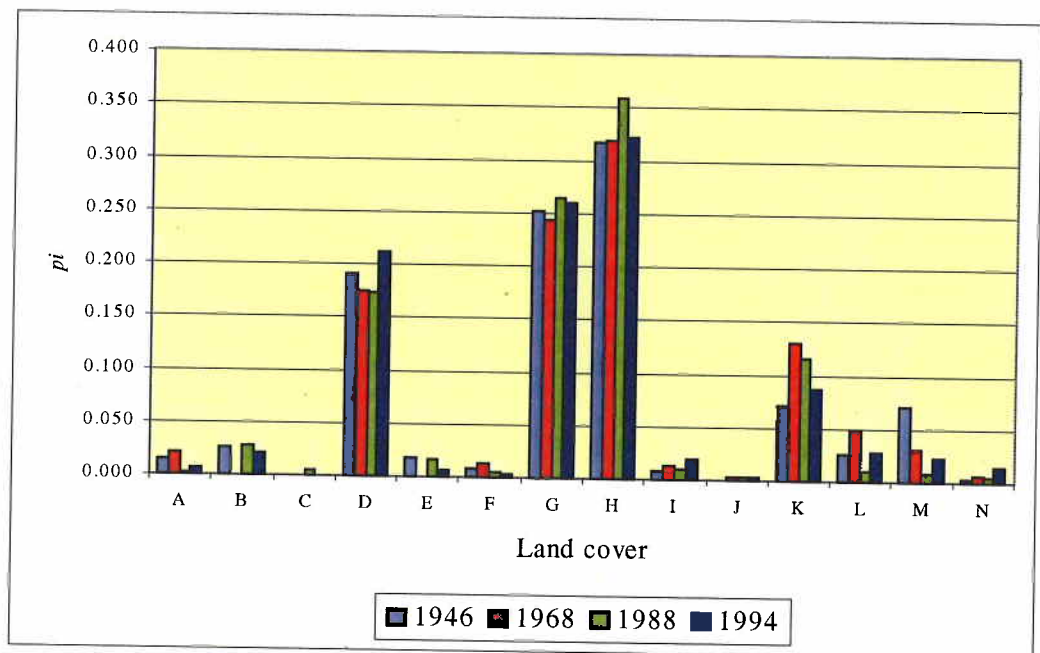
floodplain (agricultural and semi-natural) has increased in extent in comparison to the 1946 cover. The increase in these landform patches has resulted in the loss of landform types which were more extensive in 1946 due to landform features gradually becoming incorporated into the floodplain. A net loss of abandoned point bars and cut-off channels has occurred within the study area in contrast to 1946.

Figure 5.19 shows the temporal variability in the number of landscape patches within each landform class and the change in the proportion of the study area occupied by each landform over time. Figure 5.19a illustrates that semi-natural floodplain, mid-channel bar (unvegetated), point bars, river banks and lateral bars exhibit the most variability in the number of landscape patches. The number of backwaters also increases in 1994. Semi-natural floodplain, mid-channel bars (unvegetated) in 1994, and lateral bars are the most numerous landform types within the study area. The remaining of the landforms shows relative stability in number over time. There are also fewer patches of these landforms within the reach.

Figure 5.19b shows that there is little change in the proportion of the study area occupied by each land unit over time. The channel, floodplain (agriculture) and floodplain (semi-natural) dominate the study area. The landforms to show the greatest variation in the proportion of the study reach occupied are point bars, riverbanks and lateral bars.



a)



b)

Axis label	Land cover	Axis label	Land cover
A	Abandoned channel	H	Floodplain (semi-natural)
B	Abandoned point bar	I	Mid-channel bar (unvegetated)
C	Alluvial plug	J	Mid-channel bar (vegetated)
D	Channel	K	Point bar
E	Cut-off channel	L	River banks
F	Embankment	M	Lateral bar
G	Floodplain (agriculture)	N	Backwater

Figure 5.19: Temporal variation in the number (a) and the proportion (b) of the geomorphic land cover types within the River Tummel study area between 1946-1994.

The implications of the temporal patterns of landscape change observed will be discussed in relation to the effect upon floristic diversity along the reach using results from chapters 3 and 4.

5.3.10. Temporal change in landscape diversity within the River Tummel study area

The results of the assessment of landscape diversity are presented in Table 5.1. Landscape diversity was calculated by averaging the results of the diversity measures for each study year. Landscape diversity in terms of the number of land cover types shows relative stability over the study period. In terms of richness, the 1994 cover is the most diverse due to the high number of landscape patches resulting from the complex landscape patterning in the zone of recent channel change and channel abandonment. However the evenness of the distribution of the landscape patches is low. This infers high landscape diversity resulting from a rich mosaic of habitat types. Overall the results show landscape diversity is greatest in the 1968 cover. This is due to a relatively even distribution of the landscape patches.

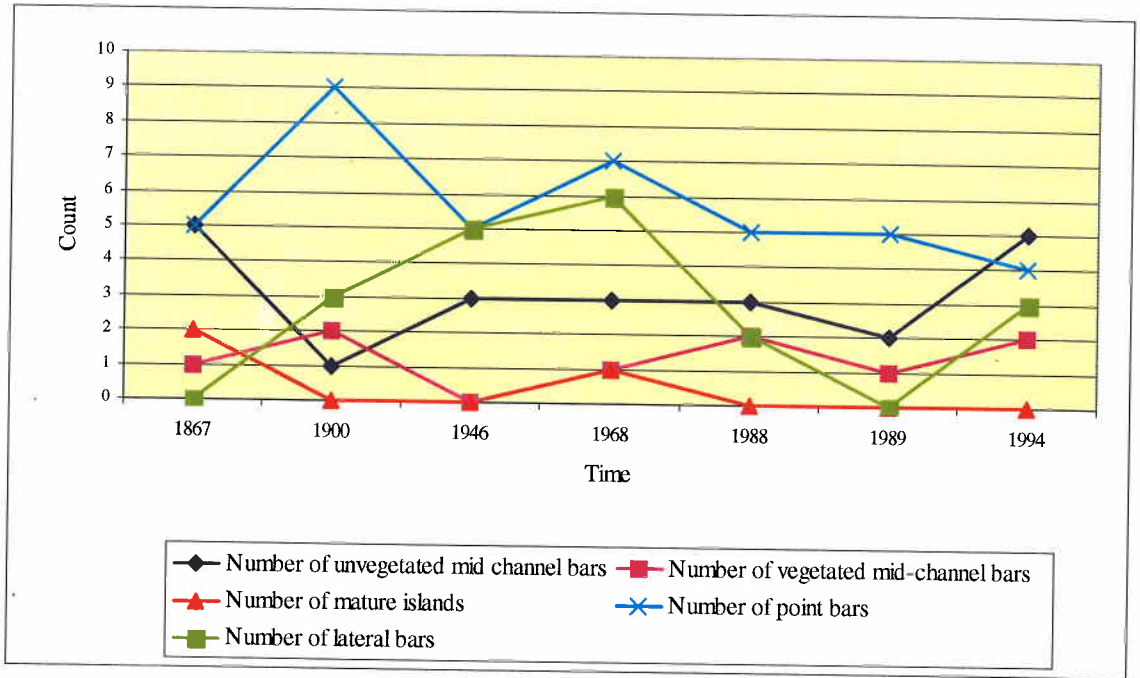
Table 5.1: Landscape diversity calculated as the average of the biodiversity and geodiversity results for the study area.

	1946	1968	1988	1994
Number of land cover types	15	14	16	17
Total number of patches	50	48	41	94
Shannon index	2.04	2.01	1.94	2.02
Equitability index	0.76	0.78	0.70	0.72
Dominance	0.63	0.58	0.83	0.79
Reciprocal Simpson's index	6.30	6.23	5.56	5.84

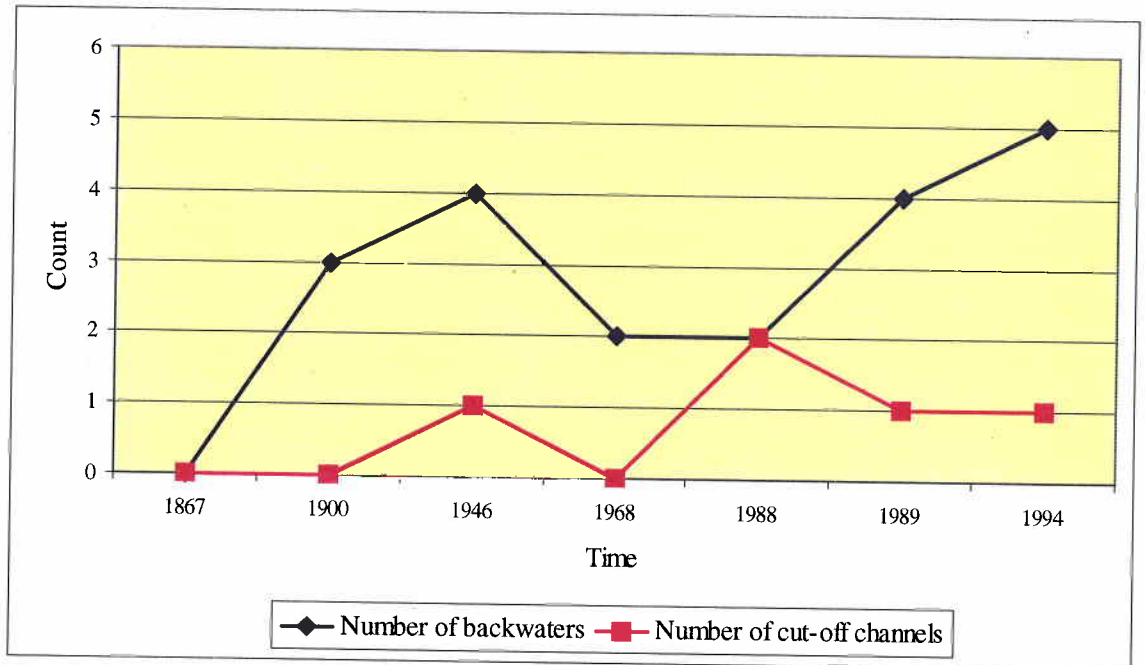
5.3.11. Long-term variation in habitat features on the River Tummel

Long-term variation in the physical channel and bank features was examined with the use of historical maps and aerial photographs. The results of the temporal variability in the physical features of the river and banks are presented in Figure 5.20. The natural planform of this river is a multi-thread braided channel with numerous mid-channel bars and islands. Historical data from 1747-1753 shows that the river is highly braided from Tomdachoille Island down to the confluence with the River Tay (Winterbottom,1995). The river was subsequently embanked causing changes to the planform. The river maintained its sinuosity and retained mid-channel bars and island features, although considerably less than when it was unconstrained. In 1867 the main channel was flowing through the present cut-off channels and backwaters found within Tynreich Island and Ballinluig Island. In 1867 the river is still multi-thread in nature, although fewer branches of the channel are present along with fewer in-channel depositional features. Since 1867, historical records show that the river predominantly occupies one main channel throughout this reach.

Temporal variability in the number of in-channel and bank features is given in Figure 5.20a. The graph shows that mature islands are a natural feature of this river, however they are now rare and intermittent features due to past management practices to constrain the channel. Unvegetated mid-channel bars are present in every year examined. The number of unvegetated mid-channel bars was at a maximum in 1867 and 1994. The lowest count was in 1900 at the



a)



b)

Figure 5.20: Temporal variation in physical features of the River Tummel between 1867-1994.

time when extensive embankments were maintained along the river. There has been little variation in the number of vegetated mid-channel bars through time. Although the number of point bars is shown to fluctuate over time, the general trend is for a considerable decline. Figure 5.20a shows the number of point bars to be at a maximum in 1900, and lowest with just 4 counts in 1994. The number of lateral bars increased rapidly from 0 in 1867 to 6 in 1968. The number of lateral bars has generally declined since 1968 with some recovery since 1989.

Figure 5.20b illustrates how channel change has led to a general increase in the number of backwaters and cut-off channels along the reach. Channel change and channel abandonment has left a legacy of cut-off channels and backwaters across the study area. Both of these features show a general increase in number over time. The highest number of backwaters present is in 1994. The count of cut-off channels is at a maximum in 1988, since then the cut-off channel at Tomdachoille has been reconnected to the main channel at the downstream end.

5.4. Discussion

The analysis has mapped the pattern of channel change that has occurred within the study period along this reach of the River Tummel and explored the linkages between channel change and landscape diversity. The pattern of channel change has resulted in a shifting mosaic of landform and vegetation types within the study area. Each of these landscape patches provides an

important habitat for the overall diversity value of the landscape. The history of channel change and its impacts upon landscape pattern are clearly identified in Figures 5.8 and 5.14. Complex landscape patterns are found in both figures in the zones of past active channel change. The most notable changes in recent history are the complex biodiversity and geodiversity patterns occurring within the Tomdachoille reach as a result of channel shifting. Simple landscape patterns in terms of both vegetation and landforms existed within this reach prior to the new channel being created between 1946 and 1968. Figure 5.8 shows that rapid colonisation does occur within the zones of unvegetated gravel. The extensive area of unvegetated gravel in the Ballinluig reach in 1946 has rapidly declined in area over time due to stabilisation and colonisation. The figures show that riparian woodland and scrub species are the first colonisers of the gravel habitats. Herbaceous species are also early colonisers, such as *T. drucei* and bryophytes. This pioneer community develops into herb-rich grassland. This is illustrated in Figures 5.8b and 5.8c in the Ballinluig reach. From the vegetation maps produced it can be inferred that these pioneer communities can establish over a 5-year period. This is consistent with the findings of Gilvear *et al.* (2000) that revealed that grassland development on bare gravel on the River Feshie in north-east Scotland takes approximately 5 years.

Figure 5.14 illustrates the degree of lateral erosion occurring within the floodplain. The most active areas of erosion are within the Tomdachoille, Tynreich and Ballinluig areas. Gilvear and Winterbottom (1998) report that 10 m of land has been eroded along a 200 m reach downstream of Moulinearn

within a 10 year period. A considerable loss of floodplain has occurred at Tomdachoille on the former mature island (reported by Winterbottom, 1995). This erosion is causing a loss of coarse grassland habitat, which has low species diversity and has been considerably impacted by past land management. The erosion on this bank has led to the deposition of an extensive point bar on the opposite bank. This has provided an important habitat for early colonisers and nesting gulls. However, this point bar is rapidly being colonised by *I. glandulifera* which is out-competing many of the native species that colonise gravel bars. In addition the erosion of the floodplain and loss of coarse grassland (MG1e) habitat is also threatening the extent of *P. veris* along the reach as it is abundant within this habitat patch. This species is rare nationally and endangered due to loss of suitable habitat and land management practices.

The active erosion occurring at Tynreich is causing a loss of floodplain habitat under pasture. This has led to an increase in deposition on the opposite bank. This depositional feature has partially stabilised since the 1940's and large areas are now forming a new floodplain zone and are fully vegetated with herb-rich grassland. Recent channel change has occurred in the Ballinluig reach causing a shift in the patterns of erosion and deposition. In the 1946 and 1968 coverages, Ballinluig Island was on the inside of a meander bend with a point bar accumulating. Channel change caused a shift of the point bar to form a mid-channel bar and now erosion is focused on the area of former deposition. In comparing Figure 5.14c and 5.14d, it is clear that a substantial proportion of the floodplain has been lost as a result of erosion at this location.

In comparing the results of the diversity indices in Figures 5.10 and 5.16, similar patterns are clearly evident. This suggests that there is a degree of congruence between the patterns of geodiversity and biodiversity within the study area. Biodiversity in terms of richness (H') is greatest in the 1994 cover as a result of the complex spatial mosaic of land cover types due to the geomorphic patterns and processes of channel change which have occurred along the reach. Although the levels of bio- and geo-diversity do not match, the general trends in the fluctuation of diversity levels measured on the different scales follow a similar trend. When diversity is assessed in terms of evenness, the 1968 coverage is the most diverse cover in terms of both plant communities and landforms. This is also supported in the overall assessment of landscape diversity. Thus the instability and channel change induced post 1946 has led to greater landscape diversity. This is due to more active erosion and deposition creating new zones for semi-natural vegetation development. The 1968 landscape also tends to be dominated by few patches with relatively large interiors. This will promote full community development by minimising the edge-effect influence upon the community as a whole. The 1968 cover is also dominated by ecologically valuable habitats with minimal scrub community development along the entire study reach. Subsequent to channel abandonment during the 1970's, increased stability of the landforms has led to scrub invasion and rapid expansion during the period 1988-1994 lowering the ecological value of the habitats. However, the channel abandonment has enabled the establishment of carr woodland communities which were sparse in extent in the 1968 cover.

In the 1968 cover, the dominant land cover types are pasture and riparian woodland (sandy) indicated in Figure 5.13b. Unvegetated gravel also contributes to a large proportion of the study area. In terms of geodiversity, the floodplain (agricultural and semi-natural) dominate the landscape with point bars also covering a considerable proportion of the area. The loss of unvegetated gravel is mirrored by a loss of point- and lateral bars. This is clearly evident in Figures 5.8 and 5.14. The loss of these habitats is due to channel shifting, stabilisation of the deposits, accretion and colonisation. In comparing Figures 5.13 and 5.19 the land cover types which dominate the landscape remain fairly static over time, with the main change being the loss of pasture/floodplain (agricultural) which are replaced by an increase in riparian woodland (sandy)/floodplain (semi-natural)

Figures 5.10d and 5.16d show that the likelihood of encountering two identical patches when random sampling is greatest in the 1988 cover. Thus suggesting repeatability of the land cover types inferring a degree of stability of the landscape matrix. Therefore it can be argued that the 1988 cover is the most diverse as it is composed of a mosaic of repeated land cover types and a suite of communities at various stages of development.

The diversity results for the Tomdachoille reach to include the 1971 image in the analysis are not directly comparable to the whole reach due to scale. When analysing in isolation, the results show that the 1971 cover generally scores lowest on the diversity scales. This cover has low diversity scores in terms of

evenness and richness. However, the low score for the reciprocal of Simpson's index indicates a degree of repeated pattern in the landscape. When comparing the dominance score with Figure 5.7b it can be seen that the landscape is dominated by pasture, covering almost 35% of the study area. Unvegetated gravel is also an extensive land cover type within this reach covering approximately 12.5% of the area.

The general trend when there is an increase in the number of landscape patches is for a reduction in the mean area of *Betula* woodland, mid-channel bars, riparian woodland communities and unvegetated gravel. The number of land cover patches also tends to increase over time, thus indicating that the landscape is becoming more fragmented and composed of smaller land units within a more heterogeneous matrix. The loss of habitats due to erosion is illustrated in Figure 5.9b. The graph shows a decline in the mean area of coarse grassland from 3.31 ha in 1946 to 0.84 ha in 1994. The mean area of pasture has also declined over time, shown in Figure 5.9b and Appendix 15.3. The standard deviation for the mean area values are all high indicating a heterogeneous landscape with a complex mosaic of both large and small landscape patches showing considerable variation in area.

The active erosion also shows a loss of mean area of floodplain (agricultural) in Figure 5.15b. Approximately 2 ha of agricultural land have been lost due to erosion since 1946. The most notable changes in mean area over time are within the floodplain (semi-natural) and the point bar landform classes. The mean area of semi-natural floodplain doubled between 1946-1988 indicating

fewer landscape patches with larger interiors, and half of the mean area was subsequently lost between 1988-1994 inferring more landscape patches with smaller interiors and a more fragmented landscape mosaic. This gain and loss is also due to accretion of depositional features creating new floodplain areas, and loss due to erosion. The general trend is for an increase in the mean area of point bars. Channel area has changed considerably, however this may simply be a result of discharge levels at the time the aerial photography was flown.

The shape index results also show that the landscape mosaic has tended to become composed of more patches with smaller interiors over the study period. Not only do the shape indices suggest that the landscape has become more fragmented, but also that the landscape patches tend to increasingly deviate from isodiametric shapes. This creates complex patterns, however it also infers weaker plant community stability due to the interior-to-edge ratio (Forman and Godron, 1986). Isodiametric shapes are reported in ecology to be more stable and add to a more diverse landscape due to the ability of these patches to gain full development (Forman and Godron, 1981). Patches that strongly deviate from isodiametric shapes have limited interior area thus the edge-effect is a dominant characteristic of these patches. These transitional ecotones are typically species rich and of high habitat value (Forman and Godron, 1981). However, where the patch interior is small in relation to the perimeter, then full development of the plant community is restricted due to the presence of 'edge' species, ruderals and competitive flora. These patches do not offer the stability of isodiametric shapes and are more vulnerable to

disturbance. The land cover types deviating most from isodiametric shapes are the elongated features associated with the channel, such as cut-off channels and backwaters; this is also shown in the geodiversity analysis in Figure 5.17. The patch shapes of these land cover types have become more isodiametric over time. In terms of the area-to-perimeter ratios expressed by SI , the 1994 figures show the most extreme values. This suggests that the landscape has become more fragmented and is now composed mainly of small patches within a heterogeneous matrix. A reduction in patch size has not been coupled with a notable change in patch perimeter complexity. The standard deviation results for the shape indices show that there is very little variation in the shape of the landscape patch within each legend class for any given year.

Both *Betula* woodland and herb-rich grassland have altered over time from occurring as a few large patches within the landscape with complex perimeter shapes to being fragmented communities but with a more isodiametric pattern. Herb-rich grassland has been lost in part due to expansion of *Betula* woodland, but also as a result of scrub encroachment, particularly in the zone of recent channel abandonment in the Tomdachoille reach. Patches of *S. scoparius* scrub have become more fragmented over time and more isodiametric. This is due to the erosion of the former embankment where a dense community of *s. scoparius* has established and this species is also an early coloniser of gravel habitats.

In terms of biodiversity, several land cover types have increased in total area in comparison to the 1946 coverage. The expansion of the habitats however

has been primarily at the expense of herb-rich grassland. A large proportion of the herb-rich grassland was lost due to conversion to pasture post 1946. However, more areas of herb-rich grassland have been lost in the Tomdachoille reach due encroachment of scrub and *Betula* woodland. Many authors have shown that patch area holds a strong relationship with the species diversity of a given patch (Forman and Godron, 1981). The greatest rate of change is between 1946 and 1968. Since 1968 the total area of herb-rich grassland has increased due to colonisation and development of gravel habitats in the Ballinluig area. However the extent of herb-rich grassland is still less than in 1946. There has also been a net loss of cut-off channels since 1946 which provide important wetland habitats within the floodplain zones. This is primarily a result of isolation from the main channel and plant succession occurring. Riparian woodland cover has increased within the cut-off channels and also fringes the backwaters and abandoned channels. The total extent of riparian woodland has increased in comparison to 1946. This is directly due to new habitats being created by channel abandonment thus creating suitable niches for carr woodland establishment.

Within the Tomdachoille reach there has been an increase in the area of coarse grassland in contrast to 1946. However its rapid decline in area since 1971 emphasises the active erosion occurring on the river banks of this landscape patch. In contrast, when considering the whole reach there has been a net loss of coarse grassland. This is partly a result of erosion, but also due to the expansion of carr- and *Betula*-woodland. Areas of *S. scoparius* scrub have increased over time. This is due to it being a primary coloniser of the gravel

habitats, but also as a result of cyclic change. In the 1946 cover the remains of the embankment in the Tomdachoille reach is colonised by riparian woodland. This scrub community typically fluctuates between scrub and woodland community and reverted to *S. scoparius* scrub in the post 1946 period, and is still under this vegetation type to date.

In comparing Figures 5.1 and 5.8 with Figure 5.4 the loss or gain of species richness over the study period can be inferred. The highest species richness at Tomdachoille is within the floodplain, abandoned channel and abandoned point bar. Channel abandonment has led to an increase in species richness and the creation of species rich habitats. The mosaic of habitats produced by channel dynamics has also increased landscape diversity by providing new landscape patches. The creation of a backwater has led to the introduction of 14 species unique to this feature. The abandoned channel has enabled carr woodland development with 23 unique species, and there are 32 unique species within the floodplain (semi-natural) zone. Channel change has also led to the isolation of a point bar enabling succession to proceed and there are now 7 unique species to this habitat. These three geomorphic landforms and subsequent vegetation types has enabled the localised introduction of 13 rare species of which 3 are locally very rare at Tomdachoille. Due to the relatively recent creation of these features it can be implied that these species have been gained to the area over the study period. The extent of these rare species is probably less in the 1994 cover however in comparison to the 1988 cover due to scrub encroachment within the vicinity of the abandoned point bar. The creation of wetland habitats via channel change is of considerable ecological

importance due to the large scale destruction of these habitats at the national level. It is reported by Grime *et al.* (1990) that the persistence of *G. fluitans* is uncertain directly as a result of habitat loss and that its' abundance is declining. *E. fluviatile* is also in decline due to the loss of habitat, however a small *E. fluviatile* swamp is present in the 1988 and 1994 covers opposite Ballinluig Island, therefore possibly seeing the introduction of this species to the study area.

Provided scrub invasion does not achieve dominance within the isolated point bars, these communities typically develop into herb-rich grassland, the habitat type that has declined the most along the reach during the study period. However, at Tomdachoille, the abandoned point bar plant community is rapidly being invaded by scrub species, mainly *S. scoparius* and *U. europaeus*. Analysis in Chapter 3 revealed that the plant communities under this vegetation are very species poor. The abandoned point bar habitat presently hosts rare species which need protecting. Among these species are *R. canescens*, *T. drucei* and *Solidago virgaurea*. The latter species is reported to be close to extinction in lowland areas due to the loss of suitable habitat (Grime *et al.*, 1990).

The loss of herb-rich grassland could be resulting in a decline in the abundance of *Campanula rotundifolia*, *G. cruciata*, *G. verum*, *L. corniculatus*, *P. veris*, *R. minor* and *V. riviniana*. The latter is thought to be declining in grassland habitats due to poor dispersal (Grime *et al.*, 1990). However, this species is present in many of the plant communities within the study area and

therefore not under threat at the local scale. *C. rotundifolia* and *L. corniculatus* are in danger of decline however as a result of the loss of herb-rich grassland along the reach. These species are in decline as a result of land management, therefore these semi-natural habitats are of great importance for their preservation.

Channel change creating a new point bar opposite Tomdachoille has had the effect of locally raising landscape diversity by adding another point bar to the area which supports a variety of small mosaics of vegetation types accommodating 54 species of which 3 are locally rare. Rapid colonisation of this point bar has occurred in the 6-year period between 1988 and 1994. This succession has led to the establishment of dense carr woodland along the lower lying ground on the landward edge of the point bar and pioneer bryophytes and herbs colonising the more elevated areas of the point bar. This has raised landscape diversity locally as prior to channel change the land this side of the river was predominantly agricultural. The addition of a new landform also adds to overall landscape heterogeneity.

The Tomdachoille analysis in Chapter 3 revealed that the point bar has 10 unique species, of which 1 species is nationally rare, 4 are locally rare and 1 locally very rare. The total area of point bars is greater for all study years in comparison to 1946. However the total area of point bars has been declining since 1968. This is causing a loss of suitable habitat for the species assemblages these landforms support.

The total extent of semi-natural floodplain landforms has been declining since 1988. It can be inferred from analysis in Chapter 3 that these landforms can have approximately 32 unique species with 1 locally rare and 1 locally very rare species. The loss of this landform is a result of erosion, however floodplain under agriculture is also being eroded. This is resulting in depositional features along the river corridor thus resetting the succession for new species rich habitats to evolve. On the whole, the Ballinluig reach is very species rich. Species richness is likely to have increased over the study period as a result of the rapid colonisation of the vast areas of unvegetated gravel in 1946. This will have led to an estimated increase in species richness to approximately 79 in 1968 with the possibility of the establishment of 1 nationally rare species, 4 locally rare and 1 locally very rare plant. The subsequent stage of succession leads to a rapid rise in species richness with the addition of 4 species which are rare either nationally or locally and 1 very rare species.

In terms of the geomorphology of the study area, the primary change in landscape pattern is that the channel has become more sinuous over the study period. This is indicated in Figure 5.18 by an increase in the total area of point bars and the loss in area of lateral bars. Over longer time-scales of change, given in Figure 5.20, the number of point- and lateral bars varies considerably suggesting temporal change in the sinuosity of the channel. Between 1867 and 1900 the river appears to be fairly sinuous due to the high number of point bars and the low number of lateral bars. Sinuosity decreases between 1900 and 1946 where there is a notable increase in the number of lateral bars. The

number of point bars out numbers lateral bars from 1988 onwards showing an increase in sinuosity with active erosion and deposition occurring. The loss of lateral bars shown in Figure 5.18 is primarily a result of an increase in the area of point bars. The change in total area of these features is greatest between 1946 and 1968. Post 1968 the change in total area has been less over time in comparison to the 1946 cover. The decline in the total area of point bars has been due to stabilisation and accretion of these features and gradual isolation from the channel due to lateral migration, thus leading to the slow formation of a new floodplain zone.

The results in Figure 5.20a show mature islands have been present within this reach within the study period. The subsequent abandoned channels that have been created provide the complex landscape patterns that occur within this landscape. Figure 5.20a shows that mature islands were present with a 100 year time interval. Mid-channel bars are numerous along this reach. These features provide important habitats for colonies of gulls and create riffle features which are a habitat requirement for salmonids. Figure 5.20b emphasises how channel change has influenced the physical character of the landscape over time. The graph shows that there has been a considerable increase in the number of backwaters over the study period. The slight dip in 1968 is due to the channel splitting in the Tomdachoille reach creating a mature island. Subsequent channel abandonment has led to an increase in the number of backwaters. The number of cut-off channels has fluctuated over time, however very few occur in comparison to backwaters. Within this reach

the main channel tends to maintain connectivity with the abandoned channels at the downstream end.

5.5. Summary

Overall, the history of channel change along this reach has led to an increase in the total area of many of the ecologically valuable land cover types and has added to the geomorphic complexity of the landscape. A degree of congruence appears to exist between the geomorphic patterning and the resulting vegetation types. The temporal analysis has shown that there is a shifting mosaic of land cover types over time and the extent of each habitat patch fluctuates as a result. Channel and floodplain recovery since the abandonment of the embankments has led to an increase in most land cover types over approximately 100 years of development but at the loss of some ecologically important communities. The major changes in landscape pattern between 1946 and 1968 may also be a result of channel recovery following the construction of the Pitlochry dam during the 1950's. Despite the net loss of some ecologically important floodplain communities, the results reveal that provided a regime of disturbance and recovery is maintained the landscape will continue to maintain a mosaic of these habitat patches. This will protect loss of habitat due to unmanaged succession occurring within the floodplain whereby species rich habitats are lost due to scrub invasion.

Chapter 6: Discussion and Conclusions

6.1. Major outcomes of the research

6.1.1. Landscape diversity on a wandering gravel-bed river; the case of the River Tummel

Channel instability on the River Tummel is a major control on landscape diversity and nature conservation value. Without flood-induced channel change the vegetation would differ according to elevation and substrate size (these indeed being a function of past channel changes), but each vegetation unit would move towards climax vegetation. Previous research which has used the River Tummel as a fluvial research site has focused primarily on geomorphic processes of channel change, flooding events and mechanisms of embankment failure along the constrained reaches of the river. The major outcomes of the research presented in this thesis are summarised below:

- i. The deriving of quantitative results of the spatial and temporal patterns of landscape diversity within semi-natural areas of a wandering gravel-bed river valley floor.
- ii. Evaluation of the role of channel dynamics in creating the diverse mosaic of land cover types within semi-natural zones of the valley floor.
- iii. The analysis of temporal changes in floodplain landscape diversity and vegetation species richness using aerial photography and field studies.
- iv. Development of a protocol for the assessment of landscape diversity.

- v. Identification of the environmental controls and supporting floodplain habitats of a number of rare species.

This research has thus provided an added dimension to the knowledge base already established by providing detailed quantitative data on the spatial patterns of diversity within the semi-natural areas of the valley floor. Information on the geomorphic processes can now be linked to the spatial pattern of landscape diversity observed through a synthesis of the knowledge to date. The methodologies applied by Winterbottom (1995) and discussed in Chapter 5 could be combined to provide a holistic approach to assessing landscape process within the valley floor in order to model future channel change and its implications upon landscape diversity.

Studies on the River Tummel system have revealed the river to maintain high rates of fluvial activity for a temperate environmental setting. This research has evaluated the role of the channel dynamics in creating the diverse mosaic of habitat patches that occur within the semi-natural zones. The results of this study also emphasise the importance of a mosaic of fluvial landforms for creating habitats for rare species in that rare species were most commonly found in the backwater, point bar, abandoned channel and abandoned point bar landforms.

Temporal analysis of patterns of change in habitat patches has shown that the mosaic of habitat types has become more complex over time thus increasing habitat type richness within the valley floor. However, this increase in richness is at the expense of the evenness of patch distribution and habitat patches are

now considerably more fragmented in the post 1968 records. Changes in area, shape and connectivity of patches lead to changes in species richness, distribution and persistence of populations (Franklin and Forman, 1987). Therefore it may be concluded that understanding the ecological principles of changing pattern is important for nature conservation and landscape planning (Hulshoff, 1995).

Historical analysis dating back 250 years suggests that the Tummel valley floor was once dominated by the semi-natural habitat types that presently occur as relatively small and scattered fragments. These semi-natural areas occur where the river has historically been left partially unconstrained or where the straight-jacketing of the river by flood embankments ceased due to repeated breaching. Thus river regulation has significantly reduced the landscape diversity value within this valley. However, cultural land use is protected whilst also allowing zones for nature conservation along this river. Future floodplain management should adopt a similar approach as suggested by Gilvear et al. (1995a) whereby 'washlands' (where fluvial processes are allowed to dominate) and 'drylands' (where human activity is prioritised) are allocated within the floodplain.

Both geo- and pedo-diversity lead to habitat mosaicism and influence the pattern of plant communities which develop. The spatial distribution of species has been found to vary according to geomorphic units within the valley floor (Tabacchi *et al.*, 1996). However little research has been directed into quantifying the spatial and temporal patterns of geomorphic and

pedological heterogeneity and the integration of diversity results to derive an overall assessment of landscape diversity within alluvial valley floors. This research has contributed to research into floodplain diversity patterns via the main aim of this research. That is to investigate the spatial and temporal patterns of geodiversity, pedodiversity and biodiversity (flora only) within alluvial valley floor landscapes in order to provide a more comprehensive evaluation of landscape diversity. The shortfall of the research is through the difficulty in assessing past spatial variation in pedodiversity as it is difficult to map pedological variation within dynamic alluvial valley floors without field investigation and quantitative data. However, depending on the degree of accuracy required, there is the potential of mapping crude taxonomic boundaries on wandering gravel-bed rivers from historical aerial photograph records based on particle size texture and estimates of the degree of pedological development inferred from the stage of vegetation development.

Riparian and floodplain habitats are among the most threatened habitats due to the intense demand for land nationally for development needs. There is a distinct urgency for floodplain zones to be protected and rehabilitated where possible. Thus the allocation of washlands and drylands will enable cultural landuse within the floodplain whilst preserving or restoring ecological niches for wetland communities. With the European directives on biodiversity in place and the forthcoming Water Framework Directive, effort should be targeted into promoting the preservation of river systems and improvements of habitat quality. Such an effort, however, has to be based on reliable scientific

understanding of river ecosystems and hence the need for research such as found within this thesis.

6.2. Wider implications and major outcomes of the research

6.2.1. Evidence for accepting or rejecting the null hypotheses

6.2.1a. Hypothesis 1a: Geomorphic landform heterogeneity is a major control on the botanical and pedological diversity within semi-natural zones within alluvial valley floors

The research has shown that the patterns of diversity of the landscape components are highly complex in dynamic riverine environments with a long history of channel change. However, the patterns of landscape diversity do tend to be structured within the geomorphic land units within the valley floor thus leading to the acceptance of the alternative hypothesis stated above. Where the geomorphic heterogeneity was lower, the research revealed that the diversity of substrate types and plant communities was also lower.

6.2.1b. Hypothesis 1b: Plant community type, vegetation composition and species diversity respond to an environmental gradient of elevation, substrate particle size and soil depth within alluvial valley floors

The analysis proved this hypothesis to hold true therefore the null hypothesis is rejected as strong correlations were derived between the species data and indices with elevation, substrate particle size and soil profile depth.

6.2.1c. Hypothesis 2: The scale and pattern of botanical and pedological variation mirrors the scale and patterns of geomorphic landforms within alluvial valley floors

The outcomes of this research do not support the hypothesis stated above, therefore the null hypothesis should be accepted. The spatial arrangement of botanical and pedological heterogeneity is found to vary within the meso-scale landform types. Thus other factors, or micro-scale landforms, are important in controlling the spatial arrangement of pedological and plant community development within the land units. These factors could relate to the distance from, relative position and connectivity of the landform with the main river channel which will in turn influence the frequency of inundation, and the time since fluvial disturbance.

6.2.1d. Hypothesis 3: Partial stabilisation of the floodplain land units as a result of river regulation increases landscape diversity and botanical diversity within floodplain environments

The analysis revealed that landscape richness has indeed increased rapidly as a result of partial stabilisation of the floodplain landforms. However, this increase in richness has been at the expense of a loss of evenness of the landscape patches. This has led to a more fragmented landscape with small patches as opposed to a landscape dominated by early successional stages within the semi-natural zones, of which these patches were relatively large and isodiametric in shape. The frequent disturbance prior to river regulation however restricted the development of carr woodland, which has significantly

increased in coverage in the latter half of the 20th century. The constraining of the channel has had the impact of reducing the physical diversity of the valley floor in that fewer mid-channel bars and mature islands are present within the valley.

6.3. Relationships of the findings to the scientific literature

6.3.1. Channel change

The findings of this research has revealed many relationships which hold congruence with the findings of other authors researching floodplain dynamics and the spatial organisation of plant communities within river valley floors. For example the results are in agreement with findings of Bornette and Amoros (1996), Chiarello *et al.* (1993) and Nilsson *et al* (1991) that landscape diversity patterns within alluvial valley floors are directly linked to channel dynamics and the spatial organisation of land units and variations in floodplain substrate particle size. The spatio-temporal heterogeneity typical of semi-natural floodplains makes them among the most species rich environments in temperate zones (Ward *et al.* 1999).

6.3.2. Substrate particle size and inundation

Plant community type and floristic diversity proved to hold strong correlations with pedological and topographic heterogeneity. The pedological properties influencing the spatial patterns of plant community type and composition are in agreement with Cellot *et al.* (1994) and Nilsson *et al.* (1991) in that substrate particle size plays an important role in colonisation. Cellot *et al.* (1994) also reported OMC to have an important influence upon the spatial patterns of plant communities within floodplain environments. This relationship was not found to be of major influence within this research. However, the degree of soil profile development was found to be a significant variable whereby plant communities tend to be arranged not only according to elevation and the particle size matrix, but also along a gradient of increasing soil depth.

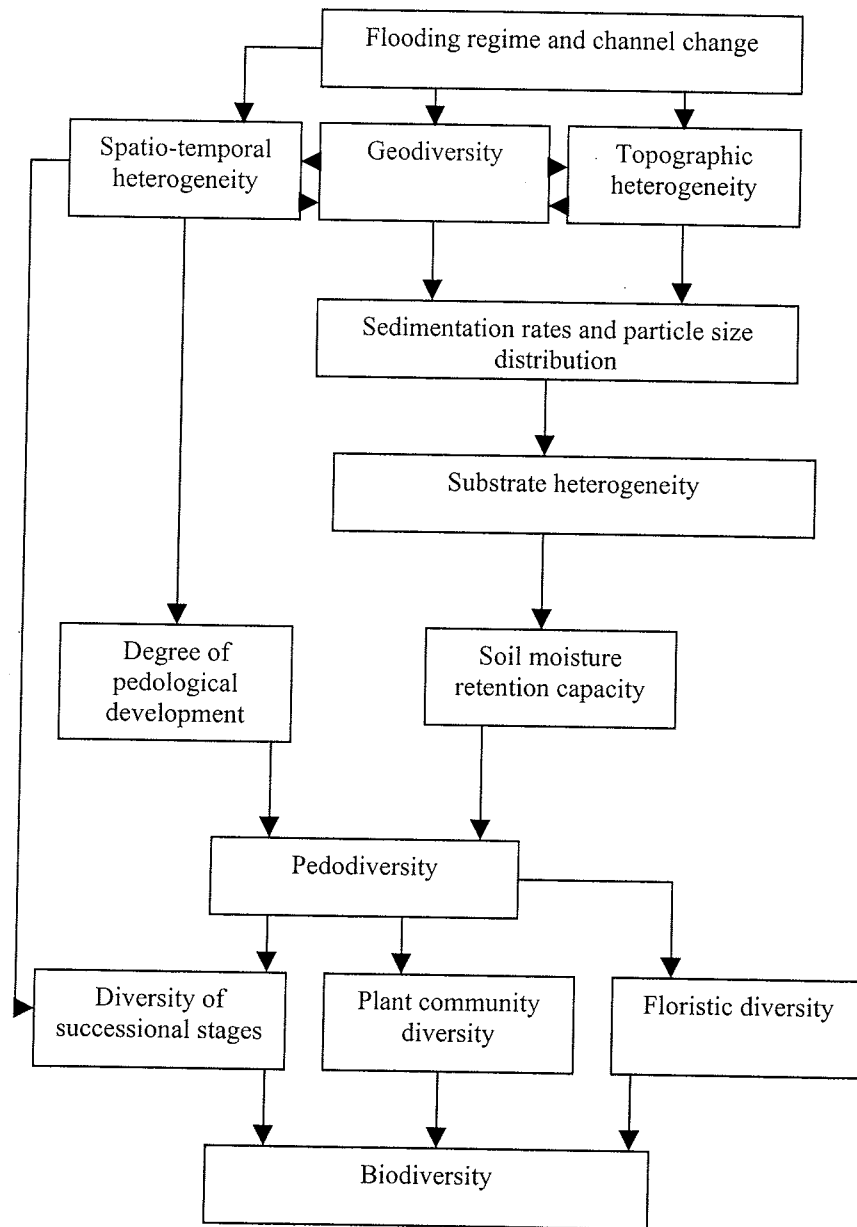
The spatial distribution of the key variables shown to influence the spatial organisation of species and plant communities are related to each other in that elevation will influence substrate deposition patterns and drainage, and substrate size will in turn influence the moisture retention capacity. These variables will determine the frequency of inundation which in turn influences the spatial patterns of vegetation development (Wassen, 1997). Hydrological-geomorphological-ecological interactions in the landscape are thus of paramount importance. Areas prone to flooding also provide ecologically important habitats as they create a niche for species with physiological

adaptations which have been deprived of suitable habitats through the history of catchment management practices.

6.3.3. Elevation and inundation

Baker (1990) found no significant relationship between species richness and elevation, in part because trees and shrub richness decreases with an increase in elevation and the loss of riparian habitat causes a loss of species richness. The results of this study found a relationship between species and elevation and revealed a negative correlation between tree cover and elevation. This reinforces the need to preserve low-lying fluvial landforms and allow the establishment of riparian woodland along river corridors to locally enhance species richness. In contrast to the findings of Baker (1990), Menges and Waller (1983) demonstrate how floodplain herbs are very sensitive to only very small differences in elevation and show that competitive plants colonise the more elevated areas of the floodplain through to less competitive but stress tolerant species at the lower elevations. These patterns were also reported by Coates (1915) whereby he described plant succession in relation to elevation differing on a 'descending scale of toughness and hardiness'. The primary controls on the maintenance of landscape diversity within alluvial valley floors are summarised in Figure 6.1.

Figure 6.1: Simplified flow diagram of the relationships between geomorphic and pedological heterogeneity in creating biodiversity within alluvial valley floors.



6.3.4. Timescales of change and development

Active geomorphic processes cause a shifting mosaic of habitats which enhances temporal diversity due to changes in the distribution and extent of landscape patches. The importance of geomorphic heterogeneity in creating landscape diversity is consistent with the findings of the amateur naturalist Coates (1915) on the Tummel floodplain and also with studies on other Scottish river systems such as the scientific work of Forster and Green (1985) on the River Dee and Gilvear *et al.* (2000) on the River Feshie. The research revealed that the patterns of plant succession on the River Tummel also show similar trends to those described on the River Feshie by Gilvear *et al.* (2000). On the Feshie a low level of disturbance for five years is sufficient for heath/grassland communities to develop and a period of 15-25 years is required for woodland establishment. Similar time-scales of development were also observed in the temporal analysis of vegetation development in Chapter 5. Habitat patches with the highest diversity tend towards those that have been colonised for about 20 years.

6.4. Floodplain management and nature conservation

Wide-scale flooding events within the UK and the rest of Europe over recent years, such as the 'Easter floods 2000' in the UK, have raised awareness of the functioning and management of floodplain environments. In addition EU directives on biodiversity and the forthcoming Water Framework Directive also address the functioning and management of riverine systems. Member

states will soon be required to set habitat quality targets for the management of river systems. Therefore detailed understanding of riverine habitats is fundamental to the implementation of realistic and appropriate habitat goals within floodplain environments. A further need is to translate the knowledge of floodplain functioning and management needs to the district council level in order to ensure that environmentally sensitive and sustainable management schemes are adopted within Local Biodiversity Action Plans (LBAPS) and regional planning.

In light of the recognition of the ecological value of floodplain environments and increased political will to protect riverine systems, floodplain management needs to be focused on highlighting zones of high landscape diversity and to prioritise the largest areas with greatest connectivity and habitat quality for nature conservation (Nilsson, 1992). In addition the demand for agricultural use of floodplains has declined in recent years due to the excess of agricultural land within the EU (c.f. Harper *et al.*, 1995). This provides an ideal opportunity to restore or rehabilitate river and floodplain dynamics, to reinstate connectivity and thus restoring ecosystem integrity ultimately creating habitats of high nature conservation value. River corridor rehabilitation could make a major contribution to providing for the increasing demands for recreation, amenity and nature conservation. This research has shown that a rich mosaics of habitats of high diversity value can be naturally restored over relatively short time-scales (approximately 100 years) on wandering gravel bed rivers with no or little financial cost. In addition for successful restoration or rehabilitation schemes it is essential to understand the

existing semi-natural fragments of floodplain habitats in order to determine the essential habitat requirements. This research has studied the spatial patterns of diversity, the structure of the vegetation types and the interrelationships between the components of landscape diversity. Such information can be extrapolated and be incorporated into developing essential habitat requirements for rehabilitation schemes.

Restoration is high on the agenda of many countries (Hughes, 1997; Petts, 1994; Ward *et al.*, 1999). Within Europe there is legislation requiring member states to conserve the flora and fauna and natural beauty of the landscape and enhance wherever possible. The Water Framework Directive will further support the drive towards nature conservation once implemented. Ward *et al.* (1999) emphasise the need to implement sound ecological river-floodplain management in order to prevent succession occurring along a single pathway without rejuvenation thus requiring detailed knowledge of the functioning of these systems.

6.5. Methodological development for assessing floodplain landscape diversity

The second main aim of the research project described herein was the development of a protocol for the assessment of landscape diversity within alluvial valley floors. This was achieved by determining the merits and limitations of the various analytical techniques used and the different methodological approaches possible. A flow chart describing the methodological approach formulated to analyse floodplain habitat diversity is

given in Figure 6.2. The methodology is centred around aerial photograph interpretation and mapping together with field survey and is likely to be transferable most river systems. Only in some remote areas will the absence of sequential sets of aerial photographs prevent an historical analysis to be undertaken. Vegetation types, patch boundaries and geomorphic land units can easily and rapidly be mapped from aerial photographs and subsequently groundtruthed provided the most recent aerial photographs are from recent years and no major disturbance has occurred in the timespan between the present day and the date of the photography. Pedological boundaries can also be mapped on the basis of substrate size by defining a boundary between coarse substrates (boulders, cobbles, gravel) from finer substrate (sands and silts) and also inferring variations in soil profile depth based on the degree of vegetation development.

Conceptual models of landscape diversity are presented in Figure 6.3. This flow diagram assumes that the intermediate disturbance hypothesis holds true for landscape diversity within alluvial valley floors based on the degree of stability of the channel. The intermediate disturbance hypothesis could be tested using the methodology proposed for evaluating landscape diversity on different river systems of similar scale but with differing degrees of stability/instability.

Figure 6.2: Protocol for the assessment of floodplain landscape diversity within alluvial valley floors based on aerial photograph examination and landscape patch analysis.

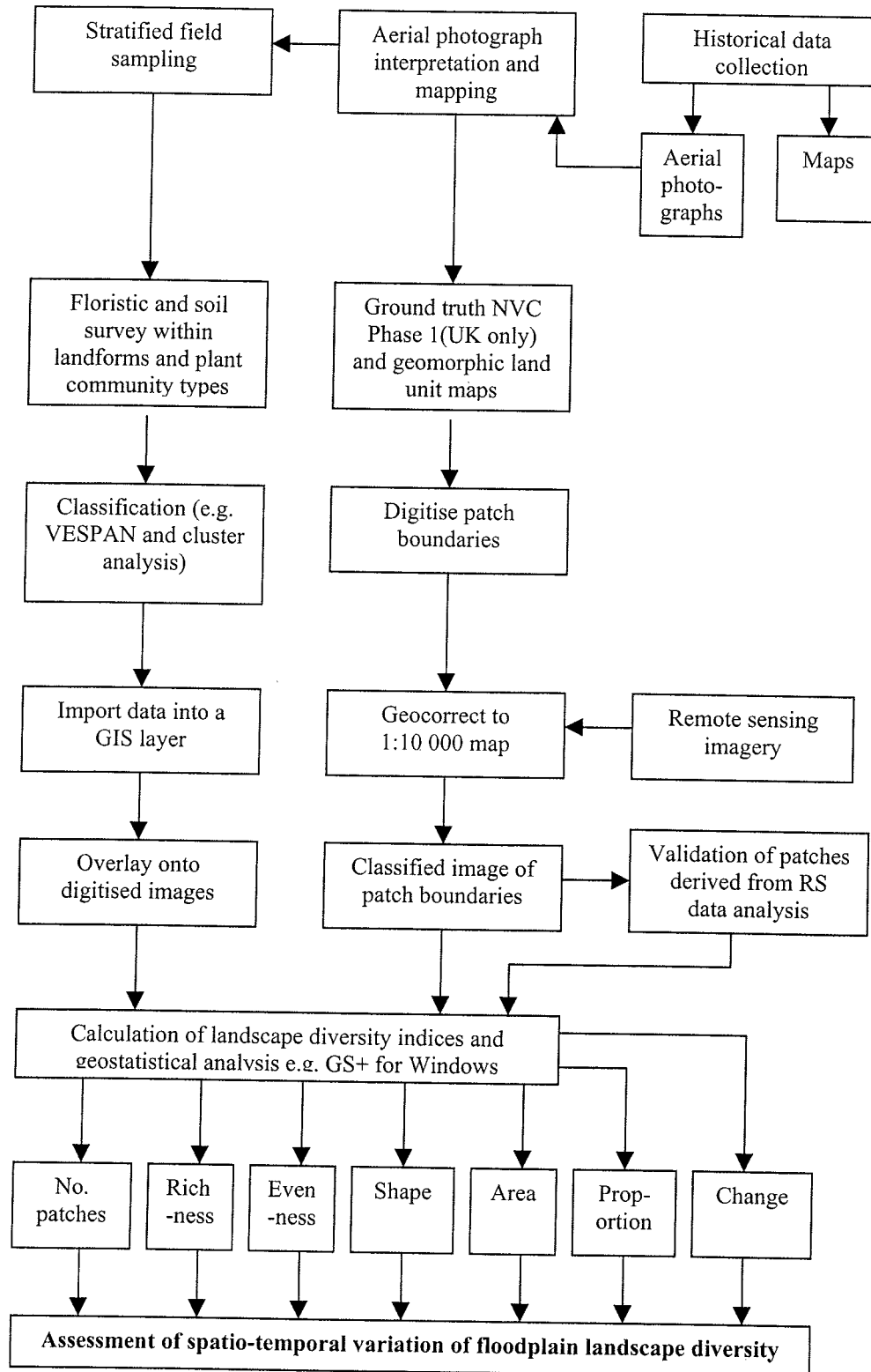
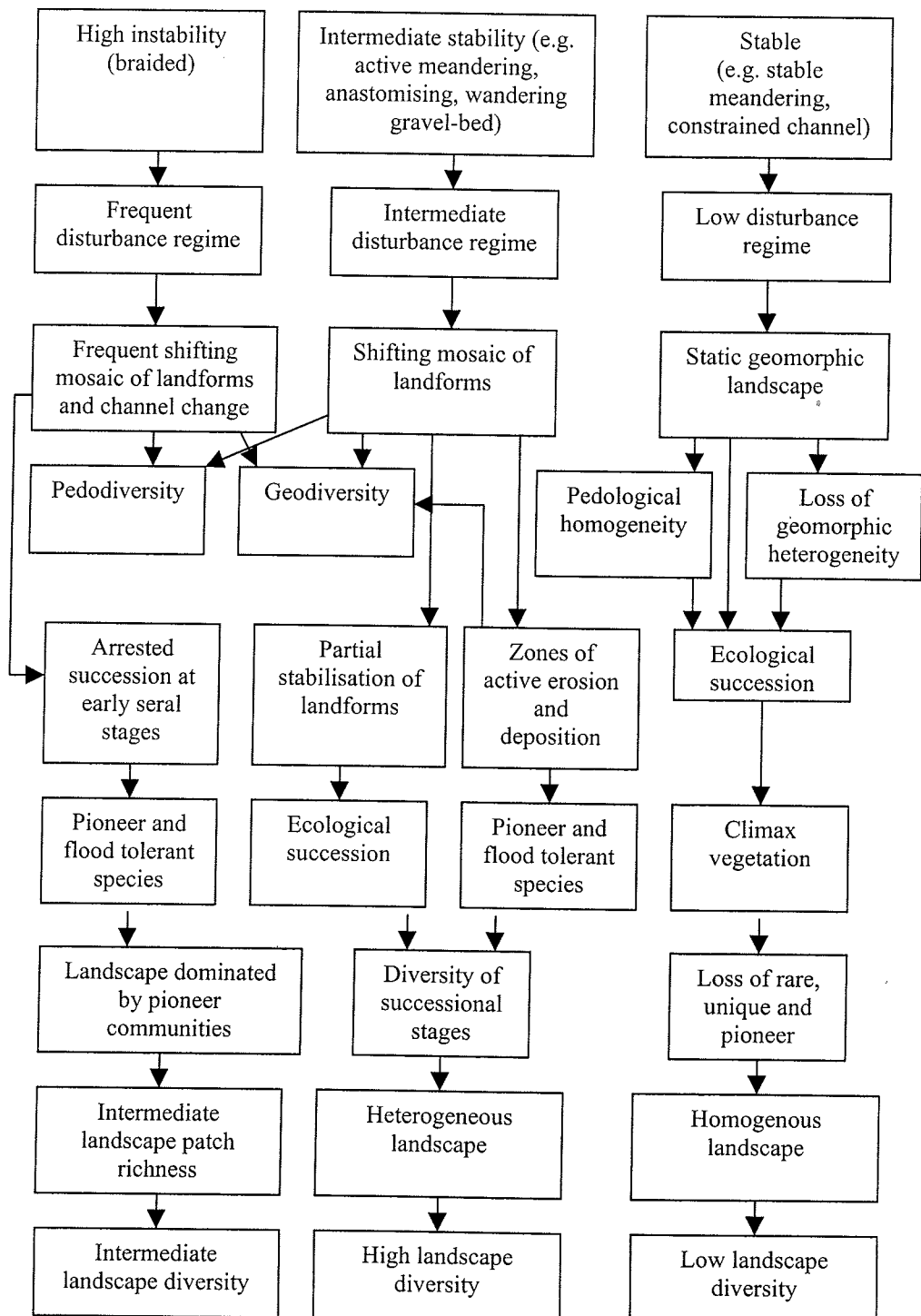


Figure 6.3: Conceptual model of the role of varying degrees of channel stability/instability on the patterns of landscape diversity within alluvial valley floors based on the assumption that the intermediate disturbance hypothesis holds true.



Various methodological and logistic difficulties were experienced throughout the duration of the field sampling, which can only be expected when undertaking fieldwork on dynamic river systems. The first major difficulties arose from the complexity of the vegetation types within the study area, in particular the density of growth. The dense carr woodland and scrub made visibility and access difficult for the location of sampling points. It is such field-based difficulties that favour the automated assessment of such environments through the use of aerial photography and remote sensing data. Secondly, high rainfall and consequently high flows throughout the second and third field season further restricted access and created difficulties for field-based studies. This again promotes the use of remote sensing techniques for floodplain studies. Remote sensing also has the added benefit of being able to evaluate landscape patterns over much larger spatial scales.

Although geostatistical analysis yielded useable results, such dynamic landscapes with high levels of spatial heterogeneity over relatively short distances do not lend themselves to the effective application of geostatistics. This is due to the presence of non-stationarity within the data as a result of anisotropic variation brought about by geomorphic heterogeneity. Within the context of British rivers the scale of the geomorphic landforms are typically too small for the effective application of geostatistics as a means of introducing optimal sampling strategies. This is because intense sampling needs to be undertaken over very short distances firstly to derive a large enough data set required for building semivariograms, and secondly to incorporate the high degree of heterogeneity in order to model spatial

dependence. However, on larger river systems found within the continents geostatistics may be a useful tool for minimising sampling within floodplain environments. The scale of geomorphic features are considerably greater on large continental river systems than on British rivers, therefore this may reduce the problem of anisotropy within the semivariogram models. The application of geostatistics to the analysis of heterogeneity within alluvial valleys could therefore be further tested on larger river systems.

The kriging results revealed that the sampling intensity (15.5m) was adequate for incorporating the degree of spatial heterogeneity within the study area. These results suggest that a less intense sampling strategy for determining the spatial patterns of heterogeneity would introduce too much variance into the results. An increase in variance would therefore lessen the ability to produce robust statistical models from the data.

6.6 Further research

Current and forthcoming legislation focusing on the management of river systems gives impetus for further research into the ecological functioning of fluvial environments. This research has provided strong predictive models which can be developed and improved in order to model floodplain ecosystem functioning on other river systems. More specifically the following areas of research could prove fruitful.

- (i) The proposed protocol for the assessment of landscape diversity within alluvial valley floors could be tested on different rivers of

similar scale but with differing stability in order to determine the role of channel stability in creating landscape diversity.

- (ii) Research into the physical, pedological and biological processes controlling diversity to complement knowledge on the patterns of spatial heterogeneity.

For example substrate heterogeneity proved to be a major control on the spatial patterns of species richness, but little is known about rates and patterns of sedimentation on many river types and how substrate stability affects vegetation colonisation and survival. Further work on the role of coarse woody debris in influencing sedimentation, and thus providing a nucleus for colonisation is another area where research could prove fruitful. Further research could also be focused on understanding the processes operating in creating the conditions suitable for the presence of the rare species in order to manage rivers effectively to incorporate and sustain their presence within catchments.

- (iii) Assessing geomorphic processes and spatial and temporal patterns of diversity within a GIS framework and testing the methodology on rivers over a range of spatial scales and differing morphologies.

This can be achieved through the combination of the methodologies for landscape diversity assessment with existing theoretical models of patterns and rates of channel change. The outcomes of such research could be applied to environmental impact assessment by predicting the impact of channel works or other planning applications on the ecological integrity and diversity of the valley floor.

(iv) Re-analysis of the data to compare the results of statistical analyses when taking autocorrelation into account.

(v) Testing the validity of using remote sensing imagery for the assessment of landscape diversity and channel change dynamics.

Analysis could also be undertaken to determine the most efficient scale of resolution of remote sensing data for fluvial and floodplain dynamics research. Such research has the potential of quantifying the spatial pattern of habitat quality at the catchment, regional and national scale.

(vi) Long-term monitoring of river systems to examine the rates of change to aid the understanding of the functional and temporal dynamics of fluvial systems.

Overall, research into floodplain functioning should continue with the aim towards producing robust scientific models which explain and predict floodplain landscape diversity in differing environmental settings and development scenarios. Such models if developed will prove to be very valuable for sustainable river and floodplain management and for the protection of biodiversity.

References

- Allan, J. D.; Erickson, D. L. and Fay, J. (1997) The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37: 149-161.
- Allen, T.F.H. and Starr, T.B., (1982). *Hierarchy: Perspectives for ecological complexity*. University of Chicago Press, Chicago.
- Amoros, C., Roux, A.L. and Reygrobellet, J.L., (1987). A method for applied ecological studies of fluvial hydrosystems. *Regulated Rivers: Research and Management*, 1: 17-36.
- Amoros, C. (1991) Changes in side-arm connectivity and implications for river system management. *Rivers* 2 (2): 105-112.
- Amoros, C., Gibert, J. and Greenwood, M.T., (1996). Interactions between units of the fluvial hydrosystem. In: G.E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.
- Amoros, C. and Wade, P.M., (1996). Ecological successions. In: G.E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.
- Andersson, E.; Nilsson, C. and Johansson, M. E. (2000) Effects of river fragmentation on plant dispersal and riparian flora. *Regulated Rivers: Research and Management* 16: 83-89.
- Anderson, M.; Walling, D. and Bates, P. (1996) *Floodplain processes*. Wiley.
- Aspinall, R.J., 1996. Some issues in measuring and modelling (bio)diversity. In: I.A. Simpson and P. Dennis (Editors), *The Spatial Dynamics of Biodiversity. Towards an understanding of spatial patterns and processes in the landscape*. Proceedings of the fifth annual IALE (UK) conference. IALE (UK), University of Stirling.
- Asselman, N.E.M. and Middelkoop, H., (1995). Floodplain sedimentation: Quantities, patterns and process. *Earth Surface Processes and Landforms*, 20: 481-495.
- Augustin, N. H.; Mugglestone, M. A. and Buckland, S. T. (1996) An autologistic model for the spatial distribution of wildlife *Journal of Applied Ecology* 33: 339-347.
- Avery, B. W. and Bascomb, C. L. (Editors) (1982) *Soil survey and laboratory methods*. Soil Survey Monograph, No. 6, Harpenden.
- Baker, V. R., Kochel, R. C., Patton, P. C. and Pickup, G., (1983). Palaeohydrologic analysis of Holocene flood slack-water sediments. *Special Publication of the International Association of Sedimentology*. 6: 229-239.

- Baker, V. R. (1989) *Magnitude and frequency of palaeofloods*. In: K. Beven and P. Carling. *Floods: Hydrological, sedimentological and geomorphological implications*. John Wiley and Sons, Chichester.
- Baker, W. L. (1989) A review of models of landscape change. *Landscape Ecology* 2 (2): 111-133.
- Baker, W. L. (1990) Species richness of Colorado riparian vegetation *Journal of Vegetation Science* 1: 119-124.
- Banášová, V., Otahelová, H., Jarolímek, I., Zaliberová, M. and Husák, S. (1994) Morava River floodplain vegetation in relation to limiting ecological factors *Ekológia (Bratislava)* 13 (3): 247-262.
- Barrat-Segretain, M. H. and Amoros, C. (1996) Recovery of riverine vegetation after experimental disturbance: a field test of the patch dynamics concept. *Hydrobiologia* 321: 53-68.
- Bascomb, C.L., (1982). Physical and chemical analyses of < 2mm samples. In: B.W. Avery and C.L. Bascomb (Editors), *Soil survey laboratory methods*. Soil Survey Technical Monographs, Harpenden.
- Bashenina, N.V., (1978). Methods of analysis in geomorphological mapping. In: J. Demek and C. Embleton (Editors), *Guide to medium-scale geomorphological mapping*. IGU Commission of Geomorphological Survey and Mapping, Brno.
- Bayley, P.B., (1991). The flood pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers: Research and Management*, 6: 75-86.
- Bedward, M.; Keith, D. A. and Pressey, R. L. (1992) Homogeneity analysis: Assessing the utility of classifications and maps of natural resources. *Australian Journal of Ecology* 17: 133-139.
- Benningfield, G. (1993) *Benningfield's woodlands*. Viking Penguin Group.
- Beven, K. and Carling, P., (1989). *Floods: Hydrological, sedimentological and geomorphological implications*. John Wiley and Sons, ltd, Chichester.
- Bilby, R. E. and Likens, G. E. (1980) Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61 (5): 1107-1113.
- Billings, W. D., Golley, F., Lange, O. L., Olsen, J. S. and Remmert, H., (1991). *Ecological Studies: Analysis and Synthesis*. Springer Verlag, New York.
- Blank, R. R., Svejcar, T. J. and Riegel, G. M., (1995). Soil genesis and morphology of a montane meadow in the northern Sierra Nevada Range. *Soil Science*, 160 (2): 136-152.

- Boon, P. J. (1992) Essential elements in the case for river conservation. In: P. J. Boon; P. Calow and G. E. Petts (Editors) *River conservation and Management*. Wiley, Chichester, pp 11-34.
- Bornette, G. and Amoros, C. (1991) Aquatic vegetation and hydrology of a braided river floodplain. *Journal of Vegetation Science* 2: 497-512.
- Bornette, G.; Amoros, C. and Chessel, D. (1994) Effect of allogenic processes on successional rates in former river channels. *Journal of Vegetation Science* 5: 237-246.
- Bornette, G. and Large, A. R. G. (1995) Groundwater-surface water ecotones at the upstream part of confluences in former river channels. *Hydrobiologia* 310: 123-137.
- Bornette, G. and Amoros, C. (1996) Disturbance regimes and vegetation dynamics: role of floods in riverine wetlands. *Journal of Vegetation Science* 7: 615-622.
- Bornette, G., Amoros, C. and Rostan, J. C. (1996) River incision and vegetation dynamics in cut-off channels *Aquatic Sciences* 58/1: 31-51.
- Bornette, G.; Amoros, C.; Piégay, H.; Tachet, J. and Hein, T. (1998) Ecological complexity of wetlands within a river landscape. *Biological Conservation* 85: 35-45.
- Bravard, J. P.; Amoros, C. and Pautou, G. (1986) Impacts of civil engineering works on the succession of communities in a fluvial system: a methodological and predictive approach applied to a section of the Upper Rhône River. *Oikos*, 47, 92-111.
- Bravard, J. P., Roux, A. L., Amoros, C. and Reygrobellet, J. L., (1992). The Rhône River: A large alluvial temperate river. In: P. Calow and G.E. Petts (Editors), *The Rivers Handbook Volume 1*. Blackwell Scientific Publications, Oxford.
- Bravard, J. P. and Gilvear, D. J. (1996) Hydrological and geomorphological structure of hydrostreams. In: G.E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.
- Bravard, J. P. and Petts, G. E., (1996). Human impacts on fluvial hydrosystems. In: G.E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.
- Breimer, R. F.; Van Kekem, A. J. and Van Reuler, H. (1986) *Guidelines for soil survey and land evaluation in ecological research*. UNESCO, Paris.
- Bremner, A. (1939) The late glacial geology of the Tay Basin from Pass of Birnam to Grandtully and Pitlochry. *Transactions of the Edinburgh Geological Society*. 13: 473-483.

- Brookes, A. (1988) *Channelized Rivers* John Wiley and Sons, Chichester.
- Brown, A.; Birks, H. J. B. and Thompson, D. B. A. (1993) A new biogeographical classification of the Scottish uplands. II. Vegetation-environment relationships. *Journal of Ecology* 81: 231-251.
- Brown, A. G.; Stone, P. and Harwood, K (1995) The biogeomorphology of a wooded anastomosing river: The Gearagh on the River Lee in County Cork, Ireland. *Occasional paper for the Department of Geography, University of Leicester* No. 32. Unpublished.
- Bryant, R. G. and Gilvear, D. J. (1999) Quantifying geomorphic and riparian land cover changes either side of a large flood event using airborne remote sensing: River Tay, Scotland. *Geomorphology* 29: 307-321.
- Burgess, T. M. and Webster, R. (1980a) Optimal interpolation and isarithmic mapping of soil properties. I. The semi-variogram and punctual kriging. *Journal of Soil Science* 31: 315-331.
- Burgess, T. M. and Webster, R. (1980b) Optimal interpolation and isarithmic mapping of soil properties. II. Block kriging. *Journal of Soil Science* 31: 333-341.
- Burrough, P. A. (1981) Fractal dimensions of landscapes and other environmental data. *Nature* 294: 240-242.
- Burrough, P. A. (1993) The technological paradox in soil survey: new methods and techniques of data capture and handling. *ITC Journal* 1: 15-22.
- Buzer, S., 1995. A landscape ecology approach to modelling natural disturbance. In: G.H. Griffiths (Editor), *Landscape Ecology: Theory and Applications*. Proceedings of the fourth annual IALE (UK) conference. IALE (UK), University of Reading.
- Calow, P. and Petts, G. E. (Editors) (1992). *The Rivers Handbook Volume 1*. Blackwell Scientific publications, Oxford.
- Calow, P. and Petts, G. E., (1994). *The Rivers Handbook Volume 2*. Blackwell Scientific Publications, Oxford.
- Cellot, B.; Dole-oliver, M. J.; Bornetter, G. and Pautou, G. (1994) Temporal and spatial environmental variability in the upper Rhône river and its floodplain. *Freshwater Biology* 31: 311-325.
- Chiarello, E.; Jolion, J. M. and Amoros, C. (1993) Model of spatial organisation of vegetation in river floodplains. *Acta Stereologica* 12/2: 255-261.

- Claret, C.; Marmonier, P.; Boissier, J. M.; Fontvieille, D. and Blanc, P. (1997) Nutrient transfer between parafluvial interstitial water and river water: influence of gravel bar heterogeneity. *Freshwater Biology* 37: 657-670.
- Cleve, K. V., Viereck, L. A. and Dyrness, C. T., (1996). State factor control of soils and forest succession along the Tanana River in interior Alaska, USA. *Arctic and Alpine Research*, 28 (3): 388-400.
- Coates, H. C., (1906). The evolution of a Haughland, as illustrated in the camping-ground of the Boys' Brigade at Ballinluig. *Proceedings of the Perthshire Society of Natural Science*.
- Coates, H. C., (1915). The evolution of plant life on a Haughland. *Transactions of the Perthshire Society of Natural Science*.
- Conchou, O. and Pautou, G. (1987) Modes of colonisation of an heterogeneous alluvial area on the edge of the Garonne River by *Phalaris arundinacea* L. *regulated Rivers: research and management* 1 (1): 37-48.
- Connor, E. F. and Simberloff, D. (1979) The assembly of species communities: chance or competition? *Ecology* 60 (6): 1132-1140.
- Cooke, R. U. and Doornkamp, J. C., (1974). *Geomorphology in environmental management*. Oxford University Press, Oxford.
- Coombes, A. J. (1992) *Trees. The visual guide to over 500 species of tree from around the world*. Dorling Kindersley Limited.
- Cressie, N. A. C. (1991) *Statistics for spatial data*. John Wiley, New York.
- Dargie, T. C. D. (1993) *Sand dune vegetation survey of Great Britain. A national inventory. Part II: Scotland*. Joint Nature Conservation Committee.
- Davidson, D. A. and Watson, A. I., (1995). Spatial variability in soil moisture as predicted from airbourne thematic mapper (ATM) data. *Earth Surface Processes and Landforms*, 20: 219-230.
- Décamps, H.; Joachim, J. and Lauga, J. (1987) The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S. W. France. *Regulated Rivers: Research and Management*. 1: 301-316.
- Décamps, H.; Fortuné, M.; Gazelle, F. and Pautou, G (1988) Historical influence of man on the riparian dynamics of a fluvial landscape *Landscape Ecology* 1 (3):163-173.
- Décamps, H. and Tabacchi, E., (1993). Species richness along river margins. In: P.S. Giller, A.G. Hildrew and D. Raffaelli (Editors), *Aquatic ecology: Scale, pattern, and process*. John Wiley and Sons, ltd, Chichester.

- Delcourt, H. R. and Delcourt, P. A. (1982) Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1: 153-175.
- Di, H. J.; Trangmar, B. B. and Kemp, R. A. (1989) Use of geostatistics in designing sampling strategies for soil survey. *Soil Science society of America Journal*. 53 (4): 1163-1167.
- Dirkx, G. H. P. (1997) Historical ecology of river and stream valleys. In: *Landscape Ecology: things to do. Proactive thoughts for the 21st century*, Amsterdam. 25th Anniversary of the Dutch Association for Landscape Ecology, WLO.
- Dolédec, S. and Statzner, B. (1994) Theoretical habitat templates, species traits, and species richness: 548 plant and animal species in the upper Rhône River and its floodplain. *Freshwater Biology* 31 (3): 523-538.
- Drost, H. J. (1997) The Danube Delta as a reference area for ecological restoration in the Netherlands. In: *Landscape Ecology: things to do. Proactive thoughts for the 21st century*, Amsterdam. 25th Anniversary of the Dutch Association for Landscape Ecology, WLO.
- Dunn, C. P., Sharpe, D. M., Guntenspergen, G. R., Steams, F. and Yang, Z., (1991). Methods for analysing temporal changes and landscape pattern. In: M.G. Turner and R.H. Gardner (Editors), *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity*. Springer Verlag, New York.
- Farina, A. (1993) Editorial comment: From global to regional landscape ecology. *Landscape Ecology* 8 (3): 153-154.
- Ferguson, R. I. and Werrity, A., (1983). Bar development and channel changes in the gravelly River Feshie, Scotland. *Special Publication of the International Association of Sedimentologist*, 6: 181-193.
- Fitter, R.; Fitter, A. and Blamey, M. (1985) *Wild flowers of Britain and northern Europe*. Harper Collins Publishers.
- Fitter, R.; Fitter, A. and Farrer, A. (1984) *Grasses, sedges, rushes and ferns of Britain and Northern Europe*. Harper Collins Publishers.
- Forman, R. T. T. and Godron, M., (1981). Patches and structural components for a landscape ecology. *BioScience*, 31 (10): 733-740.
- Forman, R. T. T. and Godron, M., (1986). *Landscape ecology*. John Wiley and Sons, ltd, New York.
- Forman, R.T.T., (1995). Some general principles of landscape and regional ecology. *Landscape Ecology*, 10: 133-142.

- Forster, J. A. and Green, J. (1985) Vegetation of the valley floor of the River Dee. In: D. Jenkins (Editor) *The Biology and Management of the River Dee*. ITE Symposium. NERC, 56-63.
- Franklin, J. F. and Forman, R. T. T., (1987). Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecology*, 1 (1): 5-18.
- French, D. D., (1994). Hierarchical Richness Index (HRI): A simple procedure for scoring 'richness', for use with grouped data. *Biological Conservation*, 69 (2): 207-212.
- Fry, G. L. A. and Sarlov Herlin, I., 1995. Landscape design; how do we incorporate ecological, cultural and aesthetic values in design principles? In: G. H. Griffiths (Editor), *Landscape Ecology: Theory and Applications*. Proceedings of the fourth annual IALE (UK) conference. IALE (UK), University of Reading.
- Fry, G. L. A., 1996. A landscape perspective of biodiversity; indices, models and planning. In: I. A. Simpson and P. Dennis (Editors), *The Spatial Dynamics of Biodiversity*. Towards an understanding of spatial patterns and processes in the landscape. Proceedings of the fifth annual IALE (UK) conference. IALE (UK), University of Stirling.
- Gardner, R. H.; Milne, B. T.; Turner, M. G. and O'Neill, R. V. (1987) Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* 1 (1): 19-28.
- Gärling, T.; Böök, A. and Lindberg, E. (1984) Cognitive mapping of large-scale environments. The interpretation of action plans, acquisition, and orientation. *Environment and Behaviour* 16 (1): 3-34.
- Gellert, J.F., (1978). General principles of medium-scale geomorphological mapping. In: J. Demek and C. Embleton (Editors), *Guide to medium-scale geomorphological mapping*. IGU Commission of Geomorphological Survey and Mapping, Brno.
- Gerrard, J. (1992) *Soil geomorphology. An integration of pedology and geomorphology*. Chapman and Hall, London.
- Gilvear, D. J. and Harrison, D. J., (1991). Channel change and the significance of floodplain stratigraphy: 1990 Flood event, lower River Tay, Scotland. *Earth Surface Processes and Landforms*, 16 (8): 753-761.
- Gilvear, D. J. and Winterbottom, S. J. (1992) Channel changes and flood events since 1783 on the regulated River Tay, Scotland. *Regulated Rivers: Research and Management*. 7: 247-260.

- Gilvear, D. J. (1993) River management and conservation issues on formerly braided river systems; the case of the River Tay, Scotland. In: J. L. Best and C. S. Bristow (Editors) *Braided Rivers*. Geological Society Special Publication 75: 231-240.
- Gilvear, D. J. (1994). River flow regulation. In: P. S. Maitland, P. J. Boon and D. S. McLusky (Editors), *The fresh waters of Scotland. A natural resource of international significance*. John Wiley and Sons, ltd, Chichester.
- Gilvear, D. J.; Davies, J. and Winterbottom, S. J. (1994) Mechanisms of flood embankment failure during large flood events; River Tay, Scotland. *Quarterly Journal of Engineering Geology* 27: 319-332.
- Gilvear, D. J.; Maitland, P.; Peterken, G. and Hanley, N. (1995a) Wild Rivers, Phase 1 technical paper. Report to WWF, Scotland.
- Gilvear, D. J., Waters, T. M. and Milner, A. M., (1995b). Image analysis of aerial photography to quantify changes in channel morphology and instream habitat following placer mining in interior Alaska. *Freshwater Biology*, 34: 389-398.
- Gilvear, D. J. and Bravard, J. P., (1996). Geomorphology of temperate rivers. In: G. E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London. Pp 68-97.
- Gilvear, D. J. and Winterbottom, S. J. (1998) Changes in channel morphology, floodplain landuse and flood damage on the Rivers Tay and Tummel over the last 250 years: Implications for floodplain management. In: R. Bailey, P. Jose and B. R. Sherwood (Editors), *United Kingdom Floodplains*. Westbury, Otley, pp. 93-116.
- Gilvear, D. J.; Cecil, J. and Parsons, H. (2000) Channel change and vegetation diversity on a low-angle alluvial fan: River Feshie Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10: 53-71.
- Givnish, T. J. (1982) On the adaptive significance of leaf height in forest herbs. *The American Naturalist* 120 (3): 353-381.
- Grace, J., (1991). Physical and ecological evaluation of heterogeneity. *Functional Ecology*, 5: 192-201.
- Grant, G. E. and Swanson, F. J., (1995). Morphology and process of valley floors in mountain streams, Western Cascades, Oregon. Natural and anthropogenic influences in fluvial geomorphology. *Geophysical Monograph*, 89.
- Green, E. E. (1997) Habitat management news. Management of grassland on airfields. *British Wildlife* 9 (2): 110-111.

- Gregory, S. V.; Swanson, F. J.; McKee, W. A. and Cummins, K. W. (1991) An ecosystem perspective of riparian zones. *BioScience* 14 (8): 540-551.
- Greig-Smith, P. (1983) *Quantitative plant ecology. Studies in ecology, volume 9. Third edition.* Blackwell Scientific Publications.
- Gréville, F. And Muller, S. (1997) The floodplain ecosystems of the French Meuse as a reference for its downstream restoration. In: *Landscape Ecology: things to do. Proactive thoughts for the 21st century*, Amsterdam. 25th Anniversary of the Dutch Association for Landscape Ecology, WLO.
- Grime, J. P.; Hodgson, J. G. and Hunt, R. (1990) *The abridged comparative plant ecology.* Chapman and Hall, London.
- Grubb, P. J., (1977). The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Review*, 52: 107-145.
- Gurnell, A. M., Angold, P. and Gregory, K. J., (1994). Classification of river corridors: Issues to be addressed in developing an operational methodology. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 4: 219-231.
- Gustafson, E. J. and Gardner, R. H., (1996). The effect of landscape heterogeneity on the probability of patch colonisation. *Ecology*, 77 (1): 94-107.
- Haines-Young, R. and Chopping, M., (1996). Quantifying landscape structure: A review of landscape indices and their application to forested landscapes. *Progress in Physical Geography*, 20 (4): 418-445.
- Halley, J. M.; Oldham, R. S. and Arntzen, J. W. (1996) Predicting the persistence of amphibian populations with the help of a spatial model *Journal of Applied Ecology* 33: 455-470.
- Hanson, J. S., Malanson, G. P. and Armstrong, M. P., (1990). Landscape fragmentation and dispersal in a model of riparian forest dynamics. *Ecological Modelling*, 49: 277-296.
- Harmon, M. E.; Franklin, J. F.; Swanson, F. J.; Sollins, P.; Gregory, S. V.; Lattin, J. D.; Anderson, N. H.; Cline, S. P.; Aumen, N. G.; Sedell, J. R.; Lienkaemper, G. W.; Cromack, J. R. K.; and Cummins, K. W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.
- Harper, D.; Smith, C.; Barham, P and Howell, R. (1995) The ecological basis for the management of the natural river environment. In: D. M. Harper and A. J. D. Ferguson (Editors) *The ecological basis for river management.* John Wiley and Sons Ltd.

- Harvey, A. M. and Renwick, W. H., (1987). Holocene alluvial fan and terrace formation in the Bowland Fells, Northwest England. *Earth Surface Processes and Landforms*, 12: 249-257.
- Harvey, A. M., Alexander, R. W. and James, P. A., (1984). Lichens, soil development and the age of Holocene valley floor landforms: Howgill Fells, Cumbria. *Geografiska annaler*, 66 A (4): 353-368.
- Heiler, G.; Hein, T. and Schiemer, F. (1995) Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. *Regulated Rivers: Research and Management* 11: 351-361.
- Hill, M. O., (1979). *DECORANA: A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. New York Section of Ecology and Systematics, Ithaca.
- Hill, M. O., (1979). *TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classifying the individuals and attributes*. New York Section of Ecology and Systematics, Cornell University, Ithaca.
- Hobbs, R. J. and Saunders, D. A., (1990). Nature conservation: The role of corridors. *Ambio*, 19 (2): 94-95.
- Hobbs, R. J., Saunders, D. A. and Arnold, G. W., (1993). Integrated landscape ecology: A western Australian perspective. *Biological Conservation*, 64: 231-238.
- Hubbard, C. E. (1984) *Grasses. A guide to their structure, identification, uses and distribution in the British Isles*. Penguin Books.
- Hughes, F. M. R. (1997) Floodplain biogeomorphology *Progress in Physical Geography* 21 (4): 501-529.
- Huggett, R. J. (1975) Soil landscape systems: a model of soil genesis. *Geoderma* 13: 1-22.
- Hulshoff, R. H., (1995). Landscape indices describing a Dutch landscape. *Landscape Ecology*, 10 (2): 101-111.
- Hurlbert, S. H. (1971) The nonconcept of species diversity: A critique and alternative parameters. *Ecology* 52 (4): 577-586.
- Hynes, H. B. N. (1975) The stream and its valley. *Verh. Int. Ver. Limnol.*, 19: 1-15.
- Ibàñez, J. J., Jimenez Ballesta, R. and Garcia Alvarez, A., (1990). Soil landscapes and drainage basins in mediterranean mountain areas. *Catena*, 17: 573-583.

- Ibàñez, J. J., De-Alba, S., Bermudez, F. F. and Garcia-Alvarez, A., (1995). Pedodiversity: concepts and measures. *Catena*, 24: 215-232.
- Ibàñez, J. J., 1996. *An introduction to pedodiversity analysis*, European Society for Soil Conservation Newsletter 1.
- Isaaks, E. H. and Srivastava, R. M. (1989) *An introduction to applied geostatistics*. Oxford University Press, New York.
- Iverson, L. R., (1988). Land-use changes in Illinois, USA: The influence of landscape attributes on current and historic land use. *Landscape Ecology*, 2 (1): 45-61.
- Johnson, L. B. and Gage, S. H. (1997) Landscape approaches to the analysis of aquatic ecosystems. *Freshwater Biology* 37: 113-132.
- Jongman, R. H. G., (1992). Vegetation, river management and land use in the Dutch Rhine floodplains. *Regulated Rivers: Research and Management*, 7 (3): 279-289.
- Junk, W. J., Bayley, P. B. and Sparks, R. E., (1989). The flood pulse concept in river-floodplain systems. Proceedings of the International Large River Symposium. *Canadian Special Publication of Fisheries and Aquatic Science*. 106: 110-127.
- Kalliola, R. and Puhakka, M. (1988) River dynamics and vegetation mosaicism: a case study of the River Komajohka, northernmost Finland. *Journal of Biogeography* 15: 703-719.
- Keller, E. A. and Capelli, M. H., (1992). Ventura River flood of February 1992: a lesson ignored? *Water Resources Bulletin*, 28: 813-832.
- Kent, M. and Coker, P. (1992) *Vegetation description and analysis*. John Wiley and sons Ltd, Chichester.
- King, A. W., (1991). Translating models across in the landscape. In: M.G. Turner and R.H. Gardner (Editors), *Quantitative methods in landscape ecology*. Springer Verlag, New York.
- Kinnes, L. (1987) *Tomdachoille Island SSSI Habitat Survey*. Scottish Natural Heritage Report ref: NN95/2.
- Klinger, L. F., (1996). Coupling of soils and vegetation in peatland succession. *Arctic and Alpine Research*, 28 (3): 380-387.
- Knapp, A. W. (Ed) (1984) *Sampling methods and taxon analysis in vegetation science*, Junk, The Hague.

- Kondolf, G. M. and Sale, M.J., (1985) Application of historical channel stability analysis to instream flow studies. In: F. W. Olsen, R. G. White and R. H. Hamre (Editors), *Proceedings of the Symposium on Small Hydropower and Fisheries*. American Fisheries Society, Denver, pp. 184-194.
- Kondolf, G. M. and Larson, M., (1995). Historical channel analysis and its application to riparian and aquatic habitat restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5: 109-126.
- Kozłowski, T. T., (1984). Plant responses to flooding of soil. *BioScience*, 34 (3): 162-167.
- Krebs, C. J. (1989) *Ecological Methodology*. Harper and Row, 328-369.
- Krebs, L.; Corbonnois, J. and Muller, S. (1997) Alluvial meadows and groundwater quality in the upper course of the river Meuse. In: *Landscape Ecology: things to do. Proactive thoughts for the 21st century*, Amsterdam. 25th Anniversary of the Dutch Association for Landscape Ecology, WLO.
- Krummel, J. R., Gardner, R. H., Sugihara, G., O'Neill, R. V. and Coleman, P. R., (1987). Landscape patterns in a disturbed environment. *Oikos*, 48 (3): 321-324.
- Kupfer, J. A., (1995). Landscape ecology and biogeography. *Progress in Physical Geography*, 19 (1): 18-34.
- Landon, N.; Piégay, H. and Bravard, J. P. (1998) The Drôme river incision (France): from assessment to management. *Landscape and Urban Planning* 43: 119-131.
- Langlade, L. R. and Décamps, O. (1994) Plant colonisation on river gravel bars: the effect of litter accumulation. *Comptes Rendus Academie des sciences serie III*: 899-905.
- Large, A. R. G. and Petts, G. E., (1994). Rehabilitation of river margins. In: P. Calow and G. E. Petts (Editors), *The Rivers Handbook Volume 2*. Blackwell Scientific Publications, Oxford.
- Large, A. R. G.; Prach, K.; Bickerton, M. A. and Wade, P. M. (1994) Alteration of patch boundaries on the floodplain of the regulated River trent. *Regulated rivers: Research and Management*. 9: 71-78.
- Large, A. R. G., Pautou, G. and Amoros, C., (1996). Primary production and primary producers. In: G.E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.
- Lark, R. M. and Beckett, P. H. T. (1995) A regular pattern in the relative areas of soil profile classes and possible applications in reconnaissance soil survey. *Geoderma* 68 (1-2): 27-37.

- Larson, P., (1994). Restoration of river corridors: German experiences. In: P. Calow and G.E. Petts (Editors), *The Rivers Handbook Volume 2*. Blackwell Scientific Publications, Oxford.
- Lavorel, S., Gardner, R. H. and O'Neill, R. V., (1993). Analysis of patterns in hierarchically structured landscapes. *Oikos*, 67 (3): 521-528.
- LeRoy Poff, N and Ward, J. V. (1990) Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14 (5): 629-645.
- Lewin, J. and Manton, M. M. M., (1975). Welsh floodplain studies: the nature of floodplain geometry. *Journal of Hydrology*, 25: 37-50.
- Lewin, J., (1978). Floodplain geomorphology. *Progress in Physical Geography*, 2 (3): 408-437.
- Lewin, J., (1992). Floodplain construction and erosion. In: P. Calow and G. E. Petts (Editors), *The Rivers Handbook Volume 1*. Blackwell Scientific Publications, Oxford.
- Liébault, F.; Clément, P.; Piégay, H. and Landon, N. (1999) Assessment of bedload delivery from tributaries: The Drôme River Case, France. *Arctic, Antarctic and Alpine Research* 31(1): 108-117.
- Lorenz, C. M.; Gilbert, A. J. and Cofino, W. P. (1997) Sustainable management of transboundary rivers. Relating environmental quality to environmental functions and cause-effect chains. In: *Landscape Ecology: things to do. Proactive thought for the 21st century*, Amsterdam. 25th Anniversary of the Dutch Association for Landscape Ecology, WLO.
- Macklin, M. G. and Smith, R. S., (1990). Historic riparian vegetation development and alluvial Metallophyte plant communities in the Tyne Basin, North-east England. In: J.B. Thornes (Editors), *Vegetation and Erosion*. John Wiley and Sons, Ltd, Chichester.
- Macklin, M. G., Rumsby, B. T. and Heap, T., (1992). Flood alluviation and entrenchment: Holocene valley-floor development and transformation in the British uplands. *Geological Society of America Bulletin*, 104: 631-643.
- Magurran, A. (1988) *Ecological Diversity and its Measurement*. Croom Helm, London.
- Malanson, G. P. and Butler, D. R. (1991) Floristic variation among gravel bars in a subalpine river, Montana, USA. *Arctic and Alpine Research* 23 (3): 273-278.
- Malanson, G. P., (1993). *Riparian Landscapes*. Cambridge University Press, Cambridge.

- Malloch, A. J. C. (1997a) VESPAN III. A computer package to handle and analyse multivariate and species distribution data for WINDOWS NT and WINDOWS 95. Unit of Vegetation Science, University of Lancaster.
- Malloch, A. J. C. (1997b) MATCH version 2 for WINDOWS/95 and WINDOWS/NT. Unit of Vegetation Science, University of Lancaster.
- Mandelbrot, B. B. (1977) *The fractal geometry of nature*. W. H. Freeman and Company, New York.
- Margalef, R. (1975) Diversity, stability and maturity in natural ecosystems. In: W. H. Van Dobben and R. H. Lowe-McConnell (Editors) *Unifying Concepts in Ecology*. Junk, The Hague, 152-60.
- Marston, R. A.; Girel, J.; Pautou, G.; Piégay, H.; Bravard, J.; and Arneson, C. (1995) Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France. *Geomorphology* 13: 121-131.
- McBratney, A. B.; Webster, R. and Burgess, T. M. (1981) The design of optimal sampling schemes for local estimation and mapping of regionalised variables – I. *Computers and Geosciences* 7(4): 331-334.
- McBratney, A.B., (1992). On variation, uncertainty and informatics in environmental soil management. *Australian Journal of Soil Research*, 30: 913-935.
- McEwen, L. J., (1989). River channel changes in response to flooding in the Upper River Dee catchment, Aberdeenshire, over the last 200 years. In: K. Beven and P. Carling (Editors), *Floods: Hydrological, sedimentological and geomorphological implications*. John Wiley and Sons, Ltd, Chichester.
- Meisel, J. E. and Turner, M. G. (1998) Scale detection in real and artificial landscapes using semivariance analysis. *Landscape Ecology* 13: 247-362.
- Menges E. S. and Waller, D. M. (1983) T strategies in relation to elevation and light in floodplain herbs *The American Naturalist* 4: 454-473.
- Meshalkina, J. L.; Stein, A. and Dmitriev, Ye. A. (1995) Spatial variability of penetration data on Russian plots in different land use. *Soil Technology* 8 (1): 43-59.
- Metzger, J. P. and Muller, E., (1996). Characterising the complexity of landscape boundaries by remote sensing. *Landscape Ecology*, 11 (2): 65-77.
- Miller, J. R.; Schulz, T. T.; Hobbs, N. T.; Wilson, K. R.; Schrupp, D. L. and Baker, W. L. (1995). Changes in the landscape structure of a southeastern Wyoming riparian zone following shifts in stream dynamics. *Biological Conservation*, 72 (3): 371-379.

- Mills, J. (1994) GIS-based spatial analysis of channel and vegetation responses to dynamics below-dam river flows. Papers and Proceedings of Applied Geography Conferences, State University of New York at Binghamton, Vol. 17: 57-62.
- Milne, J. A. (1982) River channel change in the Harthope Valley, Northumberland since 1897. *University of Newcastle Upon Tyne, Department of Geography Research Series No. 13.*
- Milne, B.T., (1991). Lessons from applying fractal models to landscape patterns. In: M. G. Turner and R. H. Gardner (Editors), *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity.* Springer Verlag, New York.
- Milner, A. M., (1994). System recovery. In: P. Calow and G. E. Petts (Editors), *The Rivers Handbook Volume 2.* Blackwell Scientific Publications, Oxford.
- Mitchell, A. (1974) *A field guide to the trees of Britain and Northern Europe.* Collins.
- Moore, P. and Cobby, J. (1998) *Introductory statistics for environmentalists.* Prentice Hall, Europe.
- Murphy, R. E., (1967). A spatial classification of landforms based on both genetic and empirical factors- a revision. *Association of American Geographers*, 57: 185-186.
- Naiman, R. J., Décamps, H., Pastor, J. and Johnston, C. A. (1988) The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* 7: 289-306.
- Naiman, R. J. and Décamps, H. (1990) *The Ecology and management of Aquatic-terrestrial Ecotones.* The Parthenon Publishing Group. Man and the Biosphere series vol. 4.
- Nanson, G. C. and Croke, J. C., (1992). A genetic classification of floodplains. *Geomorphology*, 4: 459-486.
- Nature Conservancy council (1990) Handbook for Phase 1 habitat survey. A technique for environmental audit. Field Manual. Nature Conservancy Council.
- Nash, M. H. and Daugherty, L. A. (1990) Statistical comparison of soil map-unit boundaries. *Soil Science Society of America Journal* 54 (6): 1677-1681.
- Nassauer, J. I., (1995). Culture and changing landscape structure. *Landscape Ecology*, 10 (4): 229-237.

- Naveh, Z. (1994) From biodiversity to ecodiversity: A landscape ecology approach to conservation and restoration. *Restoration Ecology* 2 (3): 180-189.
- Naveh, Z., (1995). From biodiversity to ecodiversity: New tools for holistic landscape conservation. *International Journal of Ecological and Environmental Sciences*, 21: 1-16.
- Nestler, J. and Sutton, V. K. (2000) Describing scales of features in river channels using fractal geometry concepts. *Regulated rivers: Research and Management*. 16: 1-22.
- Nilsson, C., Grelsson, G., Johansson, M., Sperens, U. (1989) Patterns of plant species richness along riverbanks *Ecology* 70 (1): 77-84.
- Nilsson, C., Ekblad, A., Gardfjell, M., Carlberg, B. (1991) Long-term effects of river regulation on river margin vegetation *Journal of Applied Ecology* 28: 963-987.
- Nilsson, C. (1992) Conservation management of riparian communities. In: L. Hanson (Editor) *Ecological principles of nature conservation. Applications in temperate and boreal forests*. Elsevier, London, 352-372.
- Nilsson, C., (1996). Remediating river margin vegetation along fragmented and regulated rivers in the North: What is possible? *Regulated Rivers: Research and Management*, 12 (4 and 5): 415-431.
- Nilsson, C. and Brittain, J.E., (1996). Remedial strategies in regulated rivers: Introductory remarks. *Regulated Rivers: Research and Management*, 12 (4 and 5): 347-351.
- Noss, R. F., (1983). A regional landscape approach to maintain diversity. *BioScience*, 33 (11): 700-706.
- Noss, R. F., (1990). Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology*, 4 (4): 355-364.
- Odum, E. P., (1971). *Fundamentals of ecology*. W. B. Saunders Co, Philadelphia.
- Oliver, M. A. and Webster, R., (1991). How geostatistics can help you. *Soil Use and Management*, 7: 206-217.
- Olsen, E. R., Ramsey, R. D. and Winn, D. S., (1993). A modified fractal dimension as a measure of landscape diversity. *Photogrammetric Engineering and Remote Sensing*, 59 (10): 1517-1520.
- O'Neill, R. V.; Krummel, J. R.; Gardner, R. H.; Sugihara, G.; Jackson, B.; DeAngelis, D. L.; Milne, B. T.; Turner, M. G.; Zygmunt, B.; Christensen, S. W.; Dale, V. H. and Graham, R. L. (1988). Indices of landscape pattern. *Landscape Ecology*, 1 (3): 153-162.

- Ostendorf, B., (1996). Modelling the influence of hydrological processes on spatial and temporal patterns of CO₂ soil efflux from an Arctic Tundra catchment. *Arctic and Alpine Research*, 28 (3): 318-327.
- Pautou, G. and Décamps, H. (1985) Ecological interactions between the alluvial forests and hydrology of the Upper Rhône. *Arch. Hydrobiol.*, 104, 13-37.
- Pautou, G. and Arens, M. F. (1994) Theoretical habitat templates, species traits, and species richness: floodplain vegetation in the Upper Rhône River. *Freshwater Biology* 31: 507-522.
- Peet, R. K. (1974) The measurement of species diversity *Annual Review of Ecology and Systematics* 5: 285-307.
- Peterson, R. C. Jr, Madsen, B. C. and Wilzbach, M. A. (1987) Stream management: emerging global similarities. *Ambio*, 16: 166-79.
- Pettitt, A. N. and McBratney, A. B. (1993) Sampling designs for estimating spatial variance components. *Applied Statistics* 42 (1): 185-209.
- Petts, G. E. (1984) *Impounded Rivers* John Wiley and Sons, Chichester.
- Petts, G. E. and Foster, I. D. L., (1985). *Rivers and landscape*. Edward Arnold, London.
- Petts, G. E., (1989). Historical change in large European alluvial rivers. In: G. E. Petts and H. Muller (Editors), *Historical change in large European alluvial rivers*. John Wiley and Sons ltd, Chichester.
- Petts, G. E., (1994). Rivers: Dynamic components of catchment ecosystems. In: P. Calow and G. E. Petts (Editors), *The Rivers Handbook Volume 2*. Blackwell Scientific Publications, Oxford.
- Petts, G. E., (1996). Water allocation to protect river ecosystems. *Regulated Rivers: Research and Management*, 12: 353-365.
- Petts, G. E. and Amoros, C. (Editors) (1996a). *Fluvial Hydrosystems*. Chapman and Hall, London.
- Petts, G. E. and Amoros, C. (1996b) The fluvial hydrosystem. In: G. E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.
- Petts, G. E. and Bravard, J. P., (1996). A drainage basin perspective. In: G. E. Petts and C. Amoros (Editors), *Fluvial hydrosystems*. Chapman and Hall, London.

- Piégay, H (1993) Nature, mass and preferential sites of coarse woody debris deposits in the lower Ain Valley (Mollon Reach), France. *Regulated Rivers: Research and Management* 8: 359-372.
- Piégay, H. and Bravard, J. P. (1997) Response of a mediterranean riparian forest to a 1 in 400 year flood, Ouveze River, Drome-Vaucluse, France. *Earth Surface Processes and Landforms* 22: 31-43.
- Piégay, H.; Cuaz, M.; Javelle, E. and Mandier, P. (1997) Bank erosion management based on geomorphological, ecological and economic criteria on the Galaure River, France. *Regulated Rivers: Research and Management* 13: 433-448.
- Piégay, H. and Gurnell, A. M. (1997) Large woody debris and river geomorphological pattern: examples from S. E. France and S. England. *Geomorphology* 19: 99-116.
- Piégay, H. and Landon, N. (1997) Promoting ecological management of riparian forests on the Drôme River, France. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 7: 287-304.
- Piégay, H. and Salvador, P. G. (1997) Contemporary floodplain forest evolution along the middle Ubaye River, Southern Alps, France. *Global Ecology and Biogeography Letters* 6: 397-406.
- Piégay, H.; Thévenet, A. and Citterio, A. (1999) Input, storage and distribution of large woody debris along a mountain river continuum, the Drôme River, France. *Catena* 35: 19-39.
- Pons, L. J. and Zonneveld, I. S., (1965). *Soil ripening and soil classification. Initial soil formation of alluvial deposits with a classification of the resulting soils*. Wageningen, The Netherlands.
- Potter, S (1991) *The effect of river management on the structure and diversity of the River Tay and Tummel floodplain habitats*. M.Sc dissertation, University of Stirling.
- Prach, K., Kucera, S. and Klimesova, J., (1990). Vegetation and land use in the Luznice River floodplain and valley in Austria and Czechoslovakia. *Wetland Ecology and Management: Case Studies*: 117-125.
- Prach, K., (1994). Vegetation succession on river gravel bars across the Northwestern Himalayas, India. *Arctic and Alpine Research*, 26 (4): 349-353.
- Qi, Y. and Wu, J. (1996) Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. *Landscape Ecology* 11 (1): 39-49.

- Raven, P. J.; Holmes, N. T. H.; Dawson, F. H.; Fox, P. J. A.; Everard, M.; Fozzard, I. R. and Rouen, K. J. (1998) *River Habitat Quality. The physical character of rivers and streams in the UK and Isle of Man*. Environment Agency, Bristol.
- Rex, K. D. and Malanson, G. P., (1990). The fractal shape of riparian forest patches. *Landscape Ecology*, 4: 249-258.
- Rice, P. M.; Fox, H. R. and Moore, H. M. (1995) Landscape ecology of the Souss-Massa National Park Southern Morocco, and applications for endangered species conservation. In: G. H. Griffiths (ed) Proceedings of the fourth annual IALE (UK) conference, University of Reading, September 1995.
- Richards, K., (1987). Fluvial geomorphology. *Progress In Physical Geography*, 11 (3): 432-457.
- Risser, P. G., Karr, J. R. and Forman, R. T. T., (1984). *Landscape ecology: Directions and approaches*. Illinois Natural History Survey Special Publication 2, Champaign.
- Rivoirard, J., (1994). *Introduction to disjunctive kriging and non-linear geostatistics*. Oxford University Press, New York.
- Roberts, J. and Ludwig, J. A. (1991) Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray, Australia *Journal of Ecology* 79: 117-127.
- Robertson, G. P. (1987) Geostatistics in ecology: interpreting with known variance. *Ecology* 68: 744-748.
- Robertson, K. M. and Augspurger, C. K. (1999) Geomorphic processes and spatial patterns of primary forest succession on the Bogue Chitto River, USA. *Journal of Ecology* 87(6): 1052-1063.
- Robertson-Rintoul, M.S.E., (1986). A quantitative soil-stratigraphic approach to the correlation and dating of post-glacial river terraces in Glen Feshie, Western Cairngorms. *Earth Surface Processes and Landforms*, 11 (6): 605-617.
- Robinson, J.G., (1993). The limits to caring: Sustainable living and the loss of biodiversity. *Conservation Biology*, 7 (1): 20-28.
- Rodwell, J. S. (1991a) *British Plant Communities: Volume 1 Woodlands and scrub*. Cambridge University Press.
- Rodwell, J. S. (1991b) *British Plant Communities: Volume 2 Mires and heaths*. Cambridge University Press.
- Rodwell, J. S. (1992) *British Plant Communities: Volume 3 Grasslands and montane communities*. Cambridge University Press.

- Rodwell, J. S. (1995a) *British Plant Communities: Volume 4 Aquatic communities, swamp and tall-herb fens*. Cambridge University Press.
- Rodwell, J.S., (1995b). *Handbook for using the National Vegetation Classification. A technique for vegetation survey*. Joint Nature Conservation Committee.
- Rogowski, A. S. and Wolf, J. K. (1994) Incorporating variability into soil map unit delineations. *Soil Science Society of America Journal* 58 (1): 163-174.
- Romme, W. H. and Knight, D. H., (1982). Landscape diversity: The concept applied to Yellowstone Park. *BioScience*, 32 (8): 664-670.
- Rose, F. (1981) *The wild flower key. British Isles-N. W. Europe*. Frederick Warne & Co.
- Rossi, R. E.; Mulla, D. J.; Journel, A. G. and Franz, E. H. (1992) Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecological monographs* 62 (2): 277-314.
- Routledge, R. D. (1977) On Whittaker's components of diversity. *Ecology* 58: 1120-1127.
- Rowel, D. L., (1994). *Soil science methods and applications*. Longman Scientific and Technical, Essex.
- Rowntree, K. M. and Dollar, E. S. J. (1999) Vegetation controls on channel stability in the Bell river, Eastern Cape, South Africa. *Earth Surface Processes and Landforms* 24: 127-134.
- Rumsby, B. T. and Macklin, M. G. (1994). Channel and floodplain response to recent abrupt climate change: The Tyne Basin, Northern England. *Earth Surface Processes and Landforms*, 19: 499-515.
- Ruzicka, V., (1993). Stony debris ecosystems- sources of landscape diversity. *Ecology (Bratislava)*, 12 (3): 291-298.
- Salo, J (1990) External processes influencing origin and maintenance of inland water-land ecotones. In: R. J. Naiman and H. Décamps (Editors) *The ecology and management of aquatic-terrestrial ecotones*. pp. 37-64. UNESCO, Paris, Parthenon, Carnforth, UK.
- Sanders, J. (1996) *A management plan for the lower River Tummel, Perthshire, Scotland* M.Sc dissertation, University of Stirling.

- Scatena, F. N. (1995) Relative scales of time and effectiveness of watershed processes in a tropical montane rain forest of Puerto Rico. In: J. E. Costa; A. J. Miller; K. W. Potter and P. R. Wilcock (Editors) *Natural and anthropogenic influences in fluvial geomorphology*. Geophysical Monograph 89, American Geophysical Union, Washington.
- Schumm, S. A., (1977). *The fluvial system*. Wiley, New York.
- Schwarz, W. L., Malanson, G. P. and Weirich, F. H., (1996). Effect of landscape position on the sediment chemistry of abandoned channel wetlands. *Landscape Ecology*, 11 (1): 27-38.
- Scott, D. (1974) *Description of relationships between plants and environment*. In: B. R. Strain & W. D. Billings (Editors) *vegetation and Environment*, Junk, The Hague.
- Sear, D. A., (1994). River restoration and geomorphology. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 4 (2): 169-177.
- Shaver, G. R., Laundre, J. A., Giblin, A. E. and Nadelhoffer, K. J., (1996). Changes in live plant biomass, primary production, and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research*, 28 (3): 363-379.
- Sheremet, B. V. and Afanas'yeva, T. V., (1993). New principles for the classification of alluvial soils. *Eurasian Soil Science*, 24 (6): 18-27.
- Sklar, F. H. and Costanza, R., (1991). The development of dynamic spatial models for landscape ecology: A review and prognosis. In: M.G. Turner and R.H. Gardner (Editors), *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity*. Springer Verlag, New York.
- Smart, P. F. M. and Grainger, J. E. A. (1974) Sampling for vegetation survey: some aspects of the behaviour of unrestricted, restricted, and stratified techniques. *Journal of Biogeography* 1: 193-206.
- Smith, R. A. H.; Stewart, N. F.; Taylor, N. W. and Thomas, R. E. (1992) *Checklist of the plants of Perthshire*. Perthshire Society of Natural Science.
- Smith, R. F. and Boardman, J., (1989). The use of soil information in the assessment of the incidence and magnitude of historical flood events in Upland Britain. In: K. Beven and P. Carling (Editors), *Floods: Hydrological, sedimentological and geomorphological implications*. John Wiley and Sons, Ltd, Chichester.
- Smith, R. D.; Sidle, R. C. and Porter, P. E. (1993) Effects on bedload transport of experimental removal of woody debris from a forest gravel-bed stream. *Earth Surface Processes and Landforms* 18: 455-468.

- Sneddon, P. and Randall, R. E. (1993) *Coastal vegetated shingle structures of Great Britain*. Joint Nature Conservancy Council.
- Sparks, R. E.; Bayley, P. B.; Kohler, S. L. and Osborne, L. L. (1990) Disturbance and recovery of large floodplain rivers. *Environmental Management* 14 (5): 699-709.
- Šrutek, M. (1993) Distribution of the stands with *Urtica dioica* L. along the Luznice River floodplain on the border between Austria and Czechoslovakia and land management. *Vegetatio* 106: 73-87.
- Stace, C. (1997) *New flora of the British Isles. Second edition*. Cambridge University Press.
- Statzner, B.; Resh, V. H. and Roux, A. L. (1994) The synthesis of long-term ecological research in the context of concurrently developed ecological theory: design of a research strategy for the upper Rhône River and its floodplain. *Freshwater Biology* 31: 253-263.
- Stromberg, J. C. and Patten, D. T. (1992) Riparian vegetation instream flow requirements: a case study from a diverted stream in the eastern Sierra Nevada, California. *Environmental Management*, 14: 185-94.
- Swanson, F. J., Wondzell, S. M. & Grant, G. E. (1992) *Landform, disturbance and ecotones*. In: A. J. Hansen & F. DiCasri (Editors) *Landscape boundaries-consequences for biotic diversity and ecological flows*, Springer-Verlag.
- Tabacchi, E., Planty-Tabacchi, A. M., Salinas, M. J. and Decamps, H., (1996). Landscape structure and diversity in riparian plant communities: A longitudinal comparative study. *Regulated Rivers: Research and Management*, 12: 367-390.
- Tan, K. H. (1996) *Soil sampling, preparation and analysis*. Marcel Dekker, inc., New York.
- Ter Braak, C. J. F. (1987) The analysis of vegetation-environment relationships by canonical correspondence analysis *Vegetatio* 69: 69-77.
- Thevenet, A.; Citterio, A. and Piégay, H. (1998) A new methodology for the assessment of large woody debris accumulations on highly modified rivers (example of two French piedmont rivers). *Regulated Rivers: Research and Management* 14: 467-483.
- Thomes, J. B. (Editor) (1990). *Vegetation and Erosion*. John Wiley and Sons, Ltd, Chichester.
- Tipping, R. (1994) Fluvial chronology and valley floor evolution of the Upper Bowmont Valley, Borders region, Scotland. *Earth Surface Processes and Landforms* 19: 641-657.

- Tipping, R. (1995). Holocene evolution of a lowland Scottish landscape: Kirkpatrick Fleming. Part III, fluvial history. *The Holocene*, 5 (2): 184-195.
- Turner, M. G. (1989). Landscape Ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics*, 20: 171-197.
- Turner, M. G. (1990). Spatial and temporal analysis of landscape patterns. *Landscape Ecology*, 4 (1): 21-30.
- Turner, M. G. and Dale, V. H. (1991). Modelling landscape disturbance. In: M.G. Turner and R.H. Gardner (Editors) *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity*. Springer Verlag, New York.
- Turner, M. G. and Gardner, R. H. (Editors) (1991a). *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity*. Springer Verlag, New York.
- Turner, M. G. and Gardner, R. H. (1991b). Quantitative methods in landscape ecology: An introduction. In: M.G. Turner and R.H. Gardner (Editors), *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity*. Springer Verlag, New York.
- Turner, S. J., O'Neill, R. V., Conley, W., Conley, M. R. and Humphries, H. C. (1991). Pattern and scale: Statistics for landscape ecology. In: M.G. Turner and R.H. Gardner (Editors), *Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity*. Springer Verlag, New York.
- Urban, D. L., O'Neill, R. V. and Shugart, J., H. H. (1987). Landscape Ecology: A hierarchical perspective can help scientists understand spatial patterns. *BioScience*, 37 (2): 119-127.
- Van Cleve, K., Viereck, L. A. and Dyrness, C. T. (1996). State factor control of soils and forest succession along the Tanana River in Interior Alaska, USA. *Arctic and Alpine Research*, 28 (3): 388-400.
- Van der Maarel, E. (1988). Vegetation dynamics: Patterns in time and space. *Vegetatio*, 77: 7-19.
- Van Splunder, I. (1998) *Floodplain forest recovery. Softwood forest development in relation to hydrology, riverbank morphology and management*. Ph.D thesis, Universiteit Comeniuslaan 2 Nijmegen, Netherlands.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. and Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science*, 37: 130-137.

- Vasil'yev, S. V. (1990). Mapping the dynamics of floodplain landscapes. *Mapping Sciences and Remote Sensing*, 27 (3): 245-251.
- Walker, L. R. (1989). Soil nitrogen changes during primary succession on a floodplain in Alaska, USA. *Arctic and Alpine Research*, 21 (4): 341-349.
- Walker, P. H. (1989). Contributions to the understanding of soil and landscape relationships. *Australian Journal of Soil Resources*, 27: 589-605.
- Walling, D. E. and He. Q. (1997) Investigating spatial patterns of overbank sedimentation on river floodplains. *Water, Air and Soil Pollution* 99: 9-20.
- Ward, J. V. and Stanford, J. A. (1983) The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research and Management* 10: 159-168.
- Ward, J. V. (1998) Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83 (3): 269-278.
- Ward, J. V.; Tockner, K. and Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers: Research and Management* 15: 125-139.
- Wassen, M. J. (1997) Flood dynamics and vegetation development in river marginal floodplains: gaps in knowledge. In: *Landscape Ecology: things to do. Proactive thoughts for the 21st century*, Amsterdam. 25th Anniversary of the Dutch association for Landscape ecology, WLO.
- Webster, R. (1977a). *Quantitative and numerical methods in soil classification and survey. Monographs on soil survey*. Oxford University Press, Oxford.
- Webster, R. (1997b) Regression and functional relations. *European Journal of Soil Science* 48: 557-566.
- Webster, R. and Oliver, M. A. (1990) *Statistical methods in soil and land resource survey*. Oxford University Press, New York.
- Werrity, A., Brazier, V., Gordon, J. E. and McManus, J. (1994). Geomorphology. In: P. S. Maitland, P. J. Boon and D. S. McLusky (Editors), *The fresh waters of Scotland. A natural resource of international significance*. John Wiley and Sons, Ltd, Chichester.
- White, L. P. (1977). *Aerial photography and remote sensing for soil survey. Monographs on soil survey*. Oxford University Press, Oxford.
- Whittaker, R. H. (1972) Evolution and measurement of species diversity. *Taxon* 21: 213-51.
- Whittaker, R. H. (1975) *Communities and Ecosystems. Second edition*. Macmillan, New York

Wickham, J. D. and Norton, D. J. (1994). Mapping and analysing landscape patterns. *Landscape Ecology*, 9 (1): 7-23.

Wiens, J. A. (1992). What is landscape ecology, really? *Landscape Ecology*, 7 (3): 149-150.

Wolcott, J. and Church, M. (1991) Strategies for sampling spatially heterogeneous phenomena: the example of river gravels. *Journal of Sedimentary Petrology* 61 (4): 534-543.

Winterbottom, S. J. (1995) *An analysis of channel change on the Rivers Tay and Tummel, Scotland, using GIS and remote sensing techniques*. Unpublished PhD, University of Stirling.

Wondzell, S. M., Cunningham, G. L. and Bachelet, D., (1996). Relationships between landforms, geomorphic processes, and plant communities on a watershed in the Northern Chihuahuan Desert. *Landscape Ecology*, 11 (6): 351-362.

Wright, J. F.; Moss, D.; Armitage, P. D. and Furse, M. T. (1984) A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. *Freshwater Biology* 14: 221-256.

Wright, R. L., (1996). An evaluation of soil variability over a single bedrock type in part of southeast Spain. *Catena*, 27: 1-24.

www.environment-agency.gov.uk/info/floodplain.html.

Zube, E. H., (1984). Themes in landscape assessment theory. *Landscape Journal*, 3 (2): 104-110.

Appendix 1

Definitions of key words used in this thesis.

- Abandoned channel: A former river channel which is only periodically inundated during high flows.
- Abandoned point bar: A depositional feature created by the river, composed of the channel substrate which is no longer connected to the river due to channel change.
- Backwater: Remnant of a former channel, permanently inundated and connected to the main channel at the downstream end.
- Biodiversity: The number (richness) and distribution (evenness) of species (flora only) and plant communities within the study area, and the shape of the patches of the plant community types.
- Connectivity: Connectivity refers to the interactions and linkages of the fluvial hydrosystem in the longitudinal, lateral, and vertical dimensions.
- Diversity: The number (richness) and distribution (evenness) of the components of the landscape (i.e. flora, soil/substrate types and landforms), and the shape of the patches of the landscape components. Diversity in this study incorporates analysis down to the species level (alpha diversity) as well as analysing the diversity of and between defined assemblages of the data, e.g. plant community, landform, soil group (beta diversity).

- Ecotone: The transition between two or more contrasting landscape patches. The term ecotone is applicable to all structural and biotic components of the landscape.
- Embankment: An artificial feature created to increase the capacity of the channel during high flows thus preventing water spilling onto the floodplain.
- Floodplain: The relatively flat land lying either side of a river beyond the first major break in slope from the river bank. The floodplain in this thesis is examined at the meso-scale, thus does not incorporate the micro-scale biotopes of former alluvial features which it is composed of.
- Geodiversity: The number (richness) and distribution (evenness) of the variety of geomorphic land units within the study area, and the shape of the patches of the land units.
- Pedodiversity: The number (richness) and distribution (evenness) of the variety of pedological units within the study area, and the shape of the patches of the pedological units.
- Point bar: A depositional feature created by the river found on the inside of a meander bend composed of the channel substrate.
- Riparian zone: Reference to the vegetation and the land that occurs along the banks of the river.

Appendix 2

Appendix 2.1: Criteria for the selection of study areas

FLOODPLAIN FEATURES	BRAIDED CHANNELS	WANDERING GRAVEL BED CHANNELS	MEANDERING CHANNELS
FLUVIAL/ GEOMORPHIC FEATURES	Shifting channels	Evidence of channel adjustment and channel avulsion	River migration
	Abandoned channels and palaeochannels	Abandoned channels and backwaters	Abandoned channels, meander cut-offs, ox-bow lakes, infilled ox-bows
	Bank erosion	Bank erosion, deposition, and channel movements	Undercutting of banks and deposition
	Gravel bars, islands	Shifting gravel bars and islands	Point bars on meander bends
	Evidence of deposition on the floodplain		
	Complex floodplain stratigraphy and topography resulting from channel dynamics		
VEGETATION	Mosaic of plant communities at different successional stages		Mosaic of plant communities
	Variety of land use or land cover pattern, semi-natural habitats and cultural land use		
SOILS	Area of the floodplain with an absence of ploughing		
HISTORICAL	Historical records available for the site, monitoring of the site, aerial photographs available		

Table 2.2: Criteria for the selection of study areas based primarily on geomorphic features.

VALLEY FEATURES	SITE DETAILS
Valley shape	
Valley width	
Floodplain width	
Landforms	
Land use	
Vegetation	
Plant succession	
Discharge	
General description	
Other features	

Table 2.3: Floodplain and Channel Features

VALLEY FEATURES	PRESENT /ABSENT	SITE DETAILS
Floodplain characteristics: flat/undulating		
Terraces		
Palaeochannels: vegetated		
unvegetated		
Backwaters		
Abandoned channels: vegetated		
Unvegetated		
Channel avulsion		
Active bank erosion		
Active deposition		
Overbank vertical accretion		
Abandoned channel accretion		
Lateral accretion		
Channel migration		
Islands		
Gravel bars		
Bare gravel		
Unvegetated gravel bars		
Vegetated gravel bars		
Riffles (shallows)		
Pools (deeps)		

Appendix 3.
Floristic tables of species data from Tomdachoille Island SSSI.

Table 3.1: TWINSPAN end group 1, SHhr community

Code	Environmental variables	D5	J8	K6	K7	L6	M5	M6	L7	I4	I8	I9	J7	J9	0
4	Elevation, (m)	2.94	3.24	2.90	3.12	0.78	2.07	3.52	3.25	0.56	2.68	2.71	2.72	3.82	
7	Soil depth, (cm)	0	0	0	0	0	0	28	20	0	20	15	25	25	
9	Tree height, (m)	7.1	5.8	6.1	5.4	2.6	3.3	3.1	2.9	0.0	6.0	3.3	5.0	5.5	
10	Shrub height, (m)	1	1	1	1	1	1	1	2	1	2	1	1	1	
11	Herb height, (cm)	0	5	10	5	5	5	15	5	10	10	5	5	10	
12	Moss height, (mm)	0	3	3	3	4	4	3	3	3	4	3	3	2	
13	Tree cover (%)	25	5	5	10	5	5	10	5	0	10	15	5	5	
14	Shrub cover (%)	5	5	5	5	5	5	5	80	5	5	5	20	5	
15	Herb cover (%)	0	33	50	10	60	65	75	80	50	75	90	80	80	
16	Moss cover (%)	0	15	20	30	70	25	30	30	30	20	20	20	30	
17	soil pH	*	*	*	*	*	*	5.0	5.1	*	5.2	5.0	5.2	5.6	
21	Bare rock (shingle)	0	80	0	75	45	35	0	0	50	10	0	10	0	
22	Bare soil (including sand)	0	0	60	0	0	0	15	10	0	0	10	10	5	
23	Open water (%)	100	0	0	0	0	0	0	0	10	0	0	0	0	
34	SMC % dry weight	0.00	0.00	0.00	0.00	0.00	0.00	5.78	7.10	0.00	17.04	11.67	8.46	4.49	
35	SOMC % dry weight	0.00	0.00	0.00	0.00	0.00	0.00	3.12	4.48	0.00	5.31	4.69	5.35	3.22	
42	MEAN		-2		-3	-3	-4	-4	-2	-3	-6	-1	-4	-2	
43	MINDOM		-2		-4	-1	-4	5	5	-4	5	5	5	5	
44	MAXDOM		-8		-7	-8	-8	-7	-4	-7	-8	-4	-7	-4	
45	MODOM		-6		-7	-7	-7	-7	-4	-7	-8	3	-7	3	
46	MEDOM		-2		-3	-2	-4	-4	1	-3	-6	2	-4	1	
47	Range	0.0	248.0	0.0	158.6	253.0	224.5	179.9	15.9	106.6	15.9	15.9	15.9	15.9	
48	Heterogenity	0	11	0	7	14	7	12	10	6	10	10	10	10	
66	Tall herb height, (cm)	0	0	0	0	0	0	0	0	0	70	50	80	60	
67	Tall herb cover (%)	0	0	0	0	0	0	0	0	0	50	25	20	60	
68	Litter (%)	0	0	50	10	25	5	10	20	5	10	2	20	5	
	Species name														
371	<i>Centaurea nigra</i>		3	4	2	3	4	4	5	4	4	4	4	4	V
171	<i>Anthoxanthum odoratum</i>		3	3	3	2	3	5	5		4	4	3	5	V
237	<i>Betula pendula (c)</i>	4	2	2	1	1	1	2	2			2	2	2	V
1333	<i>Thymus drucei</i>		3	5	3	5	4	4	6	3	4	8	5	5	V
965	<i>Pilosella officinarum agg</i>		4	6	5	5	5	5	6	2	5	3	5	5	V
1928	<i>Racomitrium canescens</i>		4	3	5	7	5			4	4		1	1	IV
1363	<i>Ulex europaeus (s)</i>		2	2	1	1	1	2				2	2	2	IV
576	<i>Festuca rubra</i>			1	2		1	5	6	4	6	6	5	6	IV
2601	<i>Acer pseudoplatanus (g)</i>	1	2	2	1	1	2	2				1	2	2	IV
1193	<i>S. scoparius (s)</i>		2	3	3	2	2	3	9			3	3	4	IV
701	<i>Hypericum perforatum</i>		3	2	2	2	1	1			4	2	4	2	IV
2628	<i>Quercus robur (g)</i>		1	1	1	1	1	1				1	1	1	IV
1638	<i>Dicranum scoparium</i>		4	4	5	5	5	5		5			4	3	IV
1270	<i>Solidago virgaurea</i>		2	4	3	4	3	1	5		2	2		2	IV
1761	<i>Hylocomium splendens</i>			4				5	5		4	5	5	5	III
2802	<i>Betula seedling/sp</i>		2	2	1					1		2		1	III
914	<i>Ononis repens</i>		2	3	3		3	2		1	2				III
773	<i>Lepidium heterophyllum</i>		2		1		1	2			3			4	III
2602	<i>Alnus glutinosa (s)</i>		1				1	1		3		1	1	1	III
278	<i>Calluna vulgaris</i>			2	2	2	4	2			2				III
1914	<i>P. purum</i>		2	2	1	2	2	2		2					III
197	<i>Arrhenatherum elatius</i>		2		3										III
613	<i>Galium verum</i>									4	4	3		3	II
153	<i>Alnus glutinosa (c)</i>										2	1	1		II
1940	<i>R. squarrosus</i>							3	5					4	II
680	<i>Holcus lanatus</i>		2						5	4	2			3	II
988	<i>Poa pratensis</i>		1					2	4					5	II
1296	<i>Stellaria graminea</i>									1	5	4	3	2	II
973	<i>Plantago lanceolata</i>									4	4	4	4		II
1175	<i>Salix myrsinifolia</i>			1						2	1	1			II
127	<i>Ajuga reptans</i>										1	1	3		II
403	<i>C. leucanthemum</i>		1				1	1			2			1	II
2607	<i>Betula pendula (g)</i>					1	2	1					2		II

Code	Species name	D5	J8	K6	K7	L6	M5	M6	L7	I4	I8	I9	J7	J9	0
804	<i>Lupinus polyphyllus</i>		1								6	6	5		II
445	<i>Crataegus monogyna (s)</i>		1	1				1					1	1	II
1064	<i>Prunus padus (s)</i>		1	1								1	1	1	II
1140	<i>Rumex acetosella</i>		1							4	1			2	II
2612	<i>Fagus sylvatica (s)</i>					1	1	1				1			II
2776	<i>Euphrasia nemorosa</i>									1	2	3	2	1	II
174	<i>Anthyllis vulneraria</i>										1	2	2		II
2613	<i>Fagus sylvatica (g)</i>		1										1	1	II
1401	<i>Veronica officinalis</i>										1	1			I
574	<i>Festuca ovina</i>							3							I
812	<i>Luzula sylvatica</i>								4						I
800	<i>Lotus corniculatus</i>									3		2			I
889	<i>Myosotis scorpioides</i>									2					I
419	<i>Cirsium vulgare</i>									1					I
1350	<i>Trifolium repens</i>									2	3				I
1106	<i>Rhinanthus minor</i>													1	I
1239	<i>Senecio jacobaea</i>									1					I
1807	<i>Plagiomnium undulatum</i>										3		3		I
654	<i>H. chamaecistus</i>											2			I
2605	<i>Betula pubescens (g)</i>										3				I
990	<i>Poa trivialis</i>										3				I
1136	<i>Rubus fruticosus agg.</i>									3	1				I
1256	<i>Silene maritima</i>						2	2							I
1308	<i>Symphytum officinale</i>									1					I
1429	<i>Viola riviniana</i>									2				2	I
1396	<i>Veronica chamaedrys</i>										3				I
1051	<i>Potentilla sterilis</i>									1					I
2764	<i>Rubus idaeus (g)</i>									3					I
236	<i>Betula pubescens (c)</i>										2				I
583	<i>Filipendula ulmaria</i>									2					I
708	<i>Impatiens glandulifera</i>									2					I
477	<i>Deschampsia cespitosa</i>					3									I
455	<i>Galium cruciata</i>								4						I
465	<i>Dactylis glomerata</i>											3			I
103	<i>Acer pseudoplatanus (c)</i>								1						I
681	<i>Holcus mollis</i>			2											I
104	<i>Achillea millefolium</i>								4			3			I
1056	<i>Primula veris</i>									1					I
1321	<i>Teucrium scorodonia</i>			4						5					I
167	<i>Angelica sylvestris</i>									1					I
955	<i>Phalaris arundinacea</i>										2				I
3127	<i>Hieracium perpropinquum</i>							1							I
1432	<i>Viola tricolor</i>										2				I
251	<i>Briza media</i>				1										I
2603	<i>Alnus glutinosa (g)</i>										1				I
1169	<i>Salix cinerea (s)</i>										1		2		I
288	<i>Campanula rotundifolia</i>		1									1			I
482	<i>Digitalis purpurea</i>			1						1					I
782	<i>Linaria repens</i>										2				I
1259	<i>Silene vulgaris</i>									4					I
1349	<i>Trifolium pratense</i>										2				I
1888	<i>Polystichum aculeatum</i>				1	1									I
2023	<i>T. ruralis ssp ruraliformis</i>			1		1									I
2614	<i>Fraxinus excelsior (s)</i>			1	1										I
2639	<i>Ulex europaeus (g)</i>									1					I
3042	<i>S. scoparius (g)</i>									1			2		I
481	<i>Dianthus deltoides</i>										1				I
968	<i>Pimpinella saxifraga</i>									1					I
971	<i>Pinus sylvestris (c)</i>												1		I
1137	<i>Rubus idaeus</i>										2				I
2620	<i>Pinus sylvestris (g)</i>					1									I
Number of species per sample		2	28	27	23	22	23	28	16	37	41	34	30	32	
Mean number of species per sample is		26.38													
The standard error of the mean is		2.749													

Table 3.2: TWINSPAN end group 2, W23a community

Code	Environmental variable	D12	E9	J10	K8	K9	L8	L9	M8
4	Elevation, (m)	2.40	2.22	3.24	3.97	3.82	1.81	3.27	3.19
7	Soil depth, (cm)	0	20	25	50	30	90	70	95
9	Tree height, (m)	0.0	10.6	13.9	11.2	13.9	9.6	10.9	0.0
10	Shrub height, (m)	1	1	1	1	1	2	2	2
11	Herb height, (cm)	5	15	10	10	15	5	5	5
12	Moss height, (mm)	0	3	2	1	3	3	3	3
13	Tree cover (%)	0	10	5	5	5	5	5	0
14	Shrub cover (%)	5	25	75	50	50	75	75	75
15	Herb cover (%)	10	50	50	90	75	80	60	95
16	Moss cover (%)	0	30	20	40	10	30	15	30
17	Soil pH	*	5.6	4.8	4.6	5.0	4.3	4.2	4.3
21	Bare rock (shingle)	90	0	0	0	0	0	0	0
22	Bare soil (including sand)	0	50	5	5	2	0	0	5
34	SMC % dry weight	0.00	29.04	12.80	5.35	4.72	8.86	3.83	14.55
35	SOMC % dry weight	0.00	5.84	6.88	3.07	3.13	3.25	3.28	3.02
42	MEAN	8	0	1	2	-2	3	-2	0
43	MINDOM	-2	5	5	5	5	5	5	5
44	MAXDOM	-8	-3	-4	-1	-4	-2	-4	-3
45	MODOM	-7	1	3	2	-4	3	2	2
46	MEDOM	-3	1	2	2	-1	3	2	3
47	Range	250.40	7.94	15.94	1.94	15.94	3.94	15.94	7.94
48	Heterogeneity	12	9	10	7	10	8	10	9
66	Tall herb height, (cm)	70	60	60	80	100	100	100	90
67	Tall herb cover %	15	50	50	90	85	85	95	75
68	Litter %	10	20	5	25	5	5	5	75
	Species name								
197	<i>Arrhenatherum elatius</i>	3	6	7	6	7	5	6	8
1193	<i>Sarothamnus scoparius (s)</i>	6	6	8	8	7	8	8	8
576	<i>Festuca rubra</i>		6	7	1	8			5
371	<i>Centaurea nigra</i>	5	3	2	5			2	
1396	<i>Veronica chamaedrys</i>	4		4	1	3		3	
1296	<i>Stellaria graminea</i>			5	2	4	1	2	
1940	<i>Rhynchospora squarrosus</i>		4	4	5		6	4	6
1761	<i>Hylocomium splendens</i>		5	4	6	4	4	4	
988	<i>Poa pratensis</i>		5	4	5	5	5		3
237	<i>Betula pendula (c)</i>			2	1	2	1	2	
1139	<i>Rumex acetosa</i>		1	1	4		2		2
680	<i>Holcus lanatus</i>			3		4		7	5
1051	<i>Potentilla sterilis</i>		2				1	1	3
2954	<i>Rosa rubiginosa</i>	2	2					1	1
103	<i>Acer pseudoplatanus (c)</i>			1	1	1			
681	<i>Holcus mollis</i>		7		5		7		
701	<i>Hypericum perforatum</i>			1		1			
104	<i>Achillea millefolium</i>				4			2	
630	<i>Geranium robertianum</i>		5	4		5			
1056	<i>Primula veris</i>				5	5			
1321	<i>Teucrium scorodonia</i>		3	2					
973	<i>Plantago lanceolata</i>	4		4	4				
2764	<i>Rubus idaeus (g)</i>	2	1						
613	<i>Galium verum</i>				4	2			2
477	<i>Deschampsia cespitosa</i>			4	4	4			
1254	<i>Silene dioica</i>		2					1	
482	<i>Digitalis purpurea</i>			1	1	1			
1363	<i>Ulex europaeus (s)</i>		1		2			2	
1368	<i>Urtica dioica</i>		7					1	
522	<i>Epilobium montanum</i>			2		2			
884	<i>Myosotis arvensis</i>				2	2		1	
1432	<i>Viola tricolor</i>					1		2	
1429	<i>Viola riviniana</i>						5		5
1136	<i>Rubus fruticosus agg.</i>	2	3	3					

Code	Species name	D12	E9	J10	K8	K9	L8	L9	M8
167	<i>Angelica sylvestris</i>		3						
127	<i>Ajuga reptans</i>								1
1293	<i>Stachys sylvatica</i>		5						
288	<i>Campanula rotundifolia</i>					1			
2003	<i>Thuidium tamariscinum</i>			4					
914	<i>Ononis repens</i>	3							
773	<i>Lepidium heterophyllum</i>	2							
2607	<i>Betula pendula (g)</i>		1						
1239	<i>Senecio jacobaea</i>			1					
414	<i>Circaea lutetiana</i>		6						
1807	<i>Plagiomnium undulatum</i>			3					
1297	<i>Stellaria holostea</i>	4							
295	<i>Cardamine pratensis</i>				1				
990	<i>Poa trivialis</i>			4					
574	<i>Festuca ovina</i>						2		
891	<i>Myosotis sylvatica</i>			2					
834	<i>Malus sylvestris (s)</i>			1					
981	<i>Poa annua</i>		1						
1337	<i>Torilis japonica</i>				2				
153	<i>Alnus glutinosa (c)</i>		4						
171	<i>Anthoxanthum odoratum</i>						4		
1175	<i>Salix myrsinifolia</i>	1							
583	<i>Filipendula ulmaria</i>								4
465	<i>Dactylis glomerata</i>					1			
1305	<i>Succisa pratensis</i>							1	
605	<i>Galium aparine</i>		4						
Number of species per sample		12	25	27	23	21	13	18	13
Mean number of species per sample is		19.00							
The standard error of the mean is		2.079							

Table 3.3: TWINSPAN end group 3, W23 community

Code	Environmental variable	E12	F9	F11	H9	H11	H12	I10	0
4	Elevation, (m)	2.60	1.61	2.94	2.99	2.08	3.05	2.73	
7	Soil depth, (cm)	0	25	25	12	20	17.5	15	
9	Tree height, (m)	2.43	2.93	2.62	3.64	4.68	4.58	3.53	
10	Shrub height, (m)	1	1	1	1	1	1	1	
11	Herb height, (cm)	15	15	5	10	5	10	10	
12	Moss height, (mm)	2	3	0	2	3	3	2	
13	Tree cover (%)	10	25	20	95	80	50	50	
14	Shrub cover (%)	25	5	5	5	5	5	5	
15	Herb cover (%)	90	50	25	40	33	75	75	
16	Moss cover (%)	2	15	0	2	30	10	50	
17	Soil pH	*	5.5	5.0	5.5	5.5	5.1	5.0	
22	Bare soil (including sand)	5	5	50	20	0	5	20	
34	SMC % dry weight	0.00	24.83	35.67	15.06	7.15	3.48	10.99	
35	SOMC % dry weight	0.00	3.66	4.32	5.19	5.77	3.95	6.64	
42	MEAN	0	2	-2	2	-2	3	1	
43	MINDOM	0	5	5	5	5	5	5	
44	MAXDOM	0	-4	-4	-2	-4	-2	-2	
45	MODOM	0	2	3	3	-4	3	2	
46	MEDOM	0	2	2	2	-1	3	2	
47	Range	0.00	15.94	15.94	3.94	15.94	3.94	3.94	
48	Heterogeneity	0	9	10	8	10	8	8	
66	Tall herb height, (cm)	100	75	80	100	60	75	100	
67	Tall herb cover %	90	95	50	60	75	90	30	
68	Litter %	10	10	25	5	2	5	25	
	Species name								
680	<i>Holcus lanatus</i>	4	5	4		5	4	5	V
1429	<i>Viola riviniana</i>		4	3	3	1	3	3	V
576	<i>Festuca rubra</i>	7	7	4	5	6	4	7	V
153	<i>Alnus glutinosa (c)</i>	2	4	3	3	3	2	1	V
371	<i>Centaurea nigra</i>	6	7	5	5	4	6	6	V
1136	<i>Rubus fruticosus agg.</i>	3	3	2	3	3	2		V
104	<i>Achillea millefolium</i>	2	3	2	1	4		4	V
403	<i>Chrysanthemum leucanthemum</i>	1	2	1	3	4	1	2	V
973	<i>Plantago lanceolata</i>	4	3	3	5	5		5	V
1175	<i>Salix myrsinifolia</i>		1	1	3	2	1		IV
2764	<i>Rubus idaeus (g)</i>	2		3	2	1	1		IV
477	<i>Deschampsia cespitosa</i>			4	2	2	5	5	IV
465	<i>Dactylis glomerata</i>	4	4		2	3		2	IV
701	<i>Hypericum perforatum</i>	3	3			2	3	2	IV
804	<i>Lupinus polyphyllus</i>	3		7	6	8		7	IV
197	<i>Arrhenatherum elatius</i>	6			5			5	III
1396	<i>Veronica chamaedrys</i>		3	2		1			III
1296	<i>Stellaria graminea</i>	4	4	2		3			III
171	<i>Anthoxanthum odoratum</i>					3	4	5	III
1940	<i>Rhytidadelphus squarrosus</i>	3	4			6		4	III
1761	<i>Hylocomium splendens</i>		4		3		4	7	III
988	<i>Poa pratensis</i>			4		5		4	III
1081	<i>Ranunculus acris</i>		3		4		2	1	III
237	<i>Betula pendula (c)</i>				7	8	5	2	III
1193	<i>Sarothamnus scoparius (s)</i>	4		3				3	III
613	<i>Galium verum</i>	3				3		2	III

Code	Species name	E12	F9	F11	H9	H11	H12	I10	0
455	<i>Galium cruciata</i>	4	4	3			2		III
605	<i>Galium aparine</i>	4		4	1				III
630	<i>Geranium robertianum</i>		4	2	1		1		III
1139	<i>Rumex acetosa</i>	2	3			1	4		III
889	<i>Myosotis scorpioides</i>				2	2	3		III
127	<i>Ajuga reptans</i>	4	4				3		III
955	<i>Phalaris arundinacea</i>	5	3		4				III
1169	<i>Salix cinerea (s)</i>	2			1	2	1		III
1270	<i>Solidago virgaurea</i>				1	2	1	1	III
1305	<i>Succisa pratensis</i>			4			3		II
583	<i>Filipendula ulmaria</i>				3	2			II
681	<i>Holcus mollis</i>				3	3			II
2954	<i>Rosa rubiginosa</i>				1	1			II
1056	<i>Primula veris</i>						1	3	II
1321	<i>Teucrium scorodonia</i>			3		2			II
123	<i>Agrostis capillaris</i>						8	2	II
1254	<i>Silene dioica</i>				1		2		II
1360	<i>Tussilago farfara</i>		5				2		II
288	<i>Campanula rotundifolia</i>	3						2	II
965	<i>Pilosella officinarum agg</i>		3					3	II
606	<i>Galium boreale</i>			3			2		II
914	<i>Ononis repens</i>		4					4	II
2633	<i>Sambucus nigra (g)</i>				1	1			II
1239	<i>Senecio jacobaea</i>	2						2	II
730	<i>Juncus effusus</i>			3		3			II
2622	<i>Prunus avium (g)</i>				1	1			II
2950	<i>Rosa canina (s)</i>				1	1			II
729	<i>Juncus conglomeratus</i>					2			I
1043	<i>Potentilla anserina</i>				1				I
698	<i>Hypericum humifusum</i>				3				I
699	<i>Hypericum maculatum</i>			3					I
1059	<i>Prunella vulgaris</i>				4				I
1293	<i>Stachys sylvatica</i>		4						I
633	<i>Geum rivale</i>			4					I
431	<i>Conopodium majus</i>					1			I
800	<i>Lotus corniculatus</i>						3		I
2628	<i>Quercus robur (g)</i>							1	I
1363	<i>Ulex europaeus (s)</i>							2	I
2003	<i>Thuidium tamariscinum</i>						3		I
1333	<i>Thymus drucei</i>							2	I
414	<i>Circaea lutetiana</i>	1							I
1140	<i>Rumex acetosella</i>							1	I
2612	<i>Fagus sylvatica (s)</i>							1	I
2707	<i>Vicia sativa</i>		3						I
278	<i>Calluna vulgaris</i>			1					I
295	<i>Cardamine pratensis</i>			3					I
990	<i>Poa trivialis</i>				5				I
1308	<i>Symphytum officinale</i>		5						I
868	<i>Mimulus guttatus</i>						1		I
1147	<i>Rumex obtusifolius</i>			1					I
1095	<i>Ranunculus repens</i>			3					I
1051	<i>Potentilla sterilis</i>						2		I
419	<i>Cirsium vulgare</i>		2						I
986	<i>Poa nemoralis</i>					5			I
708	<i>Impatiens glandulifera</i>			3					I
2802	<i>Betula seedling/sp</i>							2	I
1350	<i>Trifolium repens</i>	3							I
	Number of species per sample	27	29	31	34	37	32	34	
	Mean number of species per sample is	32.00							
	The standard error of the mean is	1.272							

Table 3.4: TWINSpan end group 4, MG1e community

Code	Environmental variable	G3	I11	I12	J11	J12	K10	K11	K12	L10	L11	L12	M7	M9	M10	M11	M12	0
4	Elevation, (m)	2.85	4.06	3.35	3.26	3.29	3.22	2.84	3.27	3.24	2.80	3.21	3.49	3.17	3.24	2.50	3.03	
7	Soil depth, (cm)	110	77	50	73	60	25	80	62	73	25	60	27	50	60	82	83	
9	Tree height, (m)	20.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.0	
10	Shrub height, (m)	0	1	1	1	0	1	1	0	1	0	1	1	1	1	0	0	
11	Herb height, (cm)	15	15	20	10	10	10	10	30	10	15	20	20	15	10	10	30	
12	Moss height, (mm)	3	2	2	2	2	3	3	2	2	3	3	3	3	3	3	2	
13	Tree cover (%)	50	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	
14	Shrub cover (%)	0	2	2	2	0	2	1	0	5	0	0	33	5	2	0	0	
15	Herb cover (%)	95	75	80	85	80	40	80	85	65	80	60	80	6	50	90	60	
16	Moss cover (%)	40	10	10	10	5	60	20	5	60	10	2	60	65	50	60	10	
17	Soil pH	4.9	5.1	5.2	5.0	5.2	5.2	5.1	4.9	5.0	5.2	4.9	5.1	5.2	4.8	4.8	4.8	
22	Bare soil	0	0	0	5	5	0	5	0	0	0	0	0	0	0	0	2	
34	SMC % dry weight	13.7	12.2	10.2	7.3	17.3	8.2	10.4	15.7	12.1	11.2	12.4	16.4	13.2	10.5	16.4	6.5	
35	SOMC % dry weight	4.0	3.1	3.7	3.1	4.4	5.7	3.8	4.3	3.2	8.6	4.5	3.3	2.9	4.2	2.9	3.2	
42	MEAN	3	2	2	1	2	-1	2	2	1	-2	1	-3	2	2	-1	3	
43	MINDOM	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
44	MAXDOM	-1	-2	-2	-4	-3	-4	-3	-3	-3	-4	-3	-4	-3	-3	-4	0	
45	MODOM	3	3	2	2	3	3	3	3	2	-4	3	-4	3	3	2	3	
46	MEDOM	3	3	2	2	3	0	2	2	2	-2	2	-3	3	3	2	3	
47	Range	1.9	3.9	3.9	15.9	7.9	15.9	7.9	7.9	7.9	15.9	7.9	15.9	7.9	7.9	15.9	0.9	
48	Heterogeneity	7	8	8	10	9	10	9	9	9	10	9	10	9	9	9	6	
66	Tall herb height, (cm)	100	150	200	80	150	150	50	200	150	0	100	90	80	100	150	150	
67	Tall herb cover %	95	90	95	95	95	80	65	95	90	0	90	90	80	100	85	90	
68	Litter %	0	4	2	2	5	0	2	0	0	0	0	2	2	2	2	0	
	Species name																	
197	<i>A. elatius</i>	8	9	10	8	10	8	7	10	9	3	9	4	8	9	10	9	V
1429	<i>Viola riviniana</i>	5	4	4	3		2	3	3	4		4	1	5		2	4	V
576	<i>Festuca rubra</i>		6	8	8		7	7	8	4	7	8	9	7	8	5	7	V
371	<i>Centaurea nigra</i>	5	3	4	3	4	4	4	5	3	4	4	5	4	6	4	4	V
1396	<i>P. chamaedrys</i>	5	5	4	4	4	3	4	4	2			5	5	4	5	4	V
1296	<i>Stellaria graminea</i>	3	3	3	2	1	4	3		4	3	3	5	4	3	3	3	V
613	<i>Galium verum</i>	4	3	4	3		4	3	4	4	5	3	5	5	4	5	3	V
1940	<i>H. squarrosus</i>	5	4	4	4	3	7	4	3	8	4	3	8	6		8	4	V
680	<i>Holcus lanatus</i>	3	4	3	4	2	3	3	3	2	2		4	3	3	3	4	V
1056	<i>Primula veris</i>	4			3	1	1	2	1	1	1	1	4	3	1	1	1	V
104	<i>Achillea millefolium</i>		1	2	3		3	4	3	4	4		5	4	3	3		IV
167	<i>Angelica sylvestris</i>	2		1	2	2		1	3	2	2	4						IV
701	<i>Hypericum perforatum</i>		1	2	1	1	1		4	2		1		5	1		2	IV
419	<i>Cirsium vulgare</i>		3	2	1	4	1				2	4			1	3	3	IV
171	<i>A. odoratum</i>	3	2		3		5	4						3	4	2		III
1761	<i>H. splendens</i>	6		3		2	5	4	3	4				7			3	III
988	<i>Poa pratensis</i>	3	3				2	4		2			4		4	2		III
973	<i>Plantago lanceolata</i>	2	3		2		4	2		1			4		5	4		III
1193	<i>S. scaparius (s)</i>		2	2	1		1	1		2			6	2	1			III
800	<i>Lotus corniculatus</i>	4	3		3						4			3	2	2		III
986	<i>Poa nemoralis</i>		3		2		3		2			3		3		3		III
455	<i>Galium cruciatum</i>						2	2		4					3	3		II
2954	<i>Rosa rubiginosa</i>	1	1				1			1				1		3		II
1305	<i>Succisa pratensis</i>	4	3	2								3						II
1139	<i>Rumex acetosa</i>				1		2						4		2			II
123	<i>Agrostis capillaris</i>	2					3	4						3				II
1239	<i>Senecio jacobaea</i>	2	1	1						1					1			II
758	<i>Lathyrus pratensis</i>	2		1	2		2					1						II
1297	<i>Stellaria holostea</i>						4		3		4			3				II
1081	<i>Ranunculus acris</i>				1	1	1	4		1			1					II
1051	<i>Potentilla sterilis</i>			2	3	2					4			4				II
403	<i>C. leucanthemum</i>	1					1											I
431	<i>Conopodium majus</i>													1				I
288	<i>Campanula rotundifolia</i>											1					2	I
482	<i>Digitalis purpurea</i>							1										I
1046	<i>Potentilla erecta</i>					2			2									I
965	<i>Pilosella officinarum agg</i>									1								I
1363	<i>Ulex europaeus (s)</i>												3					I
914	<i>Ononis repens</i>												5					I
681	<i>Holcus mollis</i>	5	2				4											I
477	<i>Deschampsia cespitosa</i>	5												4		1		I
465	<i>Dactylis glomerata</i>	2											5					I
103	<i>Acer pseudoplatanus (c)</i>												1					I
2802	<i>Betula seedling/sp</i>	3																I
2707	<i>Vicia sativa</i>		3				1											I
574	<i>Festuca ovina</i>	7						5			6							I
1432	<i>Viola tricolor</i>			1								1						I
587	<i>Fragaria vesca</i>	1																I
1218	<i>Scleranthus annuus</i>												5					I
1095	<i>Ranunculus repens</i>										1				1			I
445	<i>Crataegus monogyna (s)</i>		1							1								I
237	<i>Betula pendula (c)</i>		5										1					I
236	<i>Betula pubescens (c)</i>	2																I
	Number of species per sample	25	27	19	24	15	26	24	17	22	19	16	22	23	20	18	20	
	Mean number of species per sample is 21.06																	
	The standard error of the mean is 0.906																	

Table 3.5: TWINSPAN end group 5, U4b community

Code	Environmental variable	B4	B5	B6	C4	C5	D4	E4	F3	0
4	Elevation, (m)	2.99	3.26	2.13	3.20	1.59	3.09	2.72	3.01	
7	Soil depth, (cm)	25	97	55	121	59	123	121	120	
9	Tree height, (m)	0	0	0	0	0	0	0	0	
10	Shrub height, (m)	0	0	0	0	0	0	0	0	
11	Herb height, (cm)	20	20	30	30	20	6	5	5	
12	Moss height, (mm)	2	3	2	2	2	3	3	3	
13	Tree cover (%)	0	0	0	0	0	0	0	0	
14	Shrub cover (%)	0	0	0	0	0	0	0	0	
15	Herb cover (%)	50	70	30	75	60	60	50	75	
16	Moss cover (%)	75	40	20	75	75	40	2	15	
17	Soil pH	4.7	5.2	4.8	4.8	4.9	4.8	4.6	4.8	
22	Bare soil (including sand)	0	2	5	4	4	0	20	5	
34	SMC % dry weight	25.23	12.53	8.99	8.01	15.98	7.67	14.44	9.77	
35	SOMC % dry weight	5.94	3.61	2.87	4.16	5.15	2.41	3.99	3.52	
42	MEAN	1	2	1	2	1	3	1	3	
43	MINDOM	5	5	5	5	5	5	5	5	
44	MAXDOM	-3	-2	0	-1	-2	0	-2	-2	
45	MODOM	2	3	2	2	3	3	3	3	
46	MEDOM	1	3	2	2	2	3	3	3	
47	Range	7.937	3.937	0.937	1.937	3.937	0.937	3.937	3.937	
48	Heterogeneity	9	8	6	7	8	6	8	8	
66	Tall herb height, (cm)	0	0	0	0	0	50	40	30	
67	Tall herb cover, %	0	0	0	0	0	60	10	60	
68	Litter %	10	2	4	3	3	4	2	2	
	Species name									
973	<i>Plantago lanceolata</i>	2	6	5	5	5	2	5	6	V
1429	<i>Viola riviniana</i>	4	4	4	5	4	5	3	4	V
576	<i>Festuca rubra</i>	9	7	7	7	8	8	6	7	V
1396	<i>Veronica chamaedrys</i>	3		3	4	3	3	4	4	V
1296	<i>Stellaria graminea</i>	3	2	3	3	3	2	3		V
171	<i>Anthoxanthum odoratum</i>	3		4	7	5	4	4	4	V
1940	<i>Rhytidadelphus squarrosus</i>	7	7	4	8	8	7	2	4	V
613	<i>Galium verum</i>	4	3	3	4	3	3	3	5	V
1305	<i>Succisa pratensis</i>	3	6	4	5	4	4			V
104	<i>Achillea millefolium</i>		4	3	1	3	3	3	3	V
1106	<i>Rhinanthus minor</i>	1			4	1		3	2	IV
197	<i>Arrhenatherum elatius</i>			4	3	3		3	2	IV
680	<i>Holcus lanatus</i>	6			5	4	4	4	4	IV
1761	<i>Hylocomium splendens</i>	6		4	3		3		4	IV
1051	<i>Potentilla sterilis</i>	3			4	3	5	4		IV
800	<i>Lotus corniculatus</i>	4	4			4	5	4	5	IV
986	<i>Poa nemoralis</i>	2	2		3	4	5			IV
1350	<i>Trifolium repens</i>	1	6	4		5		5	5	IV
1095	<i>Ranunculus repens</i>	3	4			4		2		III
288	<i>Campanula rotundifolia</i>	3	3				3	3		III
1046	<i>Potentilla erecta</i>	2	2			3			1	III
251	<i>Briza media</i>	3	4			2			1	III
384	<i>Cerastium fontanum</i>	2	3	3		3				III
371	<i>Centaurea nigra</i>		2				3	2	4	III
2601	<i>Acer pseudoplatanus (g)</i>			1					2	II
988	<i>Poa pratensis</i>			4				2		II
1081	<i>Ranunculus acris</i>				2			1	2	II
237	<i>Betula pendula (c)</i>			1					5	II
1139	<i>Rumex acetosa</i>							1	1	II
123	<i>Agrostis capillaris</i>		4	4	4					II
1056	<i>Primula veris</i>				1			3	1	II
167	<i>Angelica sylvestris</i>					1	1		1	II
583	<i>Filipendula ulmaria</i>				3				1	II
2802	<i>Betula seedling/sp</i>	2							3	II
2954	<i>Rosa rubiginosa</i>						4		1	II
965	<i>Pilosella officinarum agg</i>	2							1	II
654	<i>Helianthemum chamaecistus</i>						2	4		II
252	<i>Bromus arvensis</i>		4				4			II
2785	<i>Achemilla vulgaris agg.</i>	1			1					II
1638	<i>Dicranum scoparium</i>			3						I
914	<i>Ononis repens</i>			6						I
2633	<i>Sambucus nigra (g)</i>								2	I
1321	<i>Teucrium scorodonia</i>							4		I
633	<i>Geum rivale</i>				5					I
2628	<i>Quercus robur (g)</i>						1			I
445	<i>Crataegus monogyna (s)</i>								1	I
278	<i>Calluna vulgaris</i>	3								I
758	<i>Lathyrus pratensis</i>	2								I
1941	<i>Rhytidadelphus triquetrus</i>					1				I
323	<i>Carex flacca</i>	4								I
587	<i>Fragaria vesca</i>								4	I
1298	<i>Stellaria media</i>							2		I
2982	<i>Taraxacum seedling/sp</i>				1					I
807	<i>Luzula campestris</i>					1				I
450	<i>Crepis vesicaria</i>			2						I
570	<i>Fagus sylvatica (c)</i>			1						I
339	<i>Carex panicea</i>		4							I
900	<i>Nardus stricta</i>					4				I
1411	<i>Piceta cracca</i>	2								I
236	<i>Betula pubescens (c)</i>									I
1136	<i>Rubus fruticosus agg.</i>								3	I
477	<i>Deschampsia cespitosa</i>								1	I
455	<i>Gallium cruciata</i>								2	I
465	<i>Dactylis glomerata</i>							1		I
103	<i>Acer pseudoplatanus (c)</i>							3		I
681	<i>Holcus mollis</i>			5					2	I
	Number of species per sample	28	21	23	23	25	22	27	34	
	Mean number of species per sample is 25.38									
	The standard error of the mean is 1.499									

Table 3.6: TWINSPLAN end group 6, W11d community

Code	Environmental variable	E1	E2	E3	F1	F2	G1	G2	H1	H2	H3	I1	I2	I3	J2	K2	B1	B2	B3	C1	C2	C3	D1	D2	D3	J1	K1	0	
4	Elevation, (m)	3.25	2.85	2.58	3.23	3.09	2.38	2.91	3.00	2.95	2.31	3.17	3.05	2.37	2.93	2.70	3.21	3.45	2.79	3.24	3.34	2.80	3.19	3.16	3.08	2.98	2.40		
7	Soil depth, (cm)	100	119	116	110	128	120	118	60	89	97	75	70	89	64	72	75	122	127	150	125	117	100	125	115	91	102		
9	Tree height, (m)	28.4	14.6	19.6	17.2	19.3	21.0	19.8	13.7	14.9	13.2	26.7	18.7	18.0	23.1	10.0	20.5	18.9	15.9	15.8	15.2	20.1	16.7	18.8	16.7	25.0	8.5		
10	Shrub height, (cm)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
11	Herb height, (cm)	4	5	15	5	15	5	5	5	5	15	10	5	10	5	15	5	6	10	10	7	5	5	5	5	10	10		
12	Moss height, (mm)	2	0	0	3	0	4	3	3	3	2	0	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3		
13	Tree cover (%)	25	25	25	50	25	25	50	50	50	75	75	50	75	50	75	100	60	60	20	50	33	25	50	50	90	90		
14	Shrub cover (%)	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5		
15	Herb cover (%)	70	70	50	95	75	80	75	90	80	95	80	60	95	80	60	80	85	65	80	75	80	90	90	90	85	80		
16	Moss cover (%)	30	0	0	0	0	75	5	50	60	50	0	30	30	10	10	5	10	60	10	25	5	30	5	50	10	60		
17	Soil pH	5.1	4.9	5.2	4.9	5.0	4.9	5.0	4.6	4.8	4.9	4.8	4.7	4.7	4.9	5.1	4.8	5.1	4.9	4.5	4.8	5.1	5.1	5.2	4.7	5.2	5.0		
22	Bare soil (including sand)	0	0	0	0	0	0	10	0	5	0	0	20	0	10	5	0	2	2	0	3	0	2	3	0	2	0		
34	SMC % dry weight	15	19	10	15	5	16	12	14	17	11	6	8	10	15	17	9	11	19	10	17	12	12	7	11	8	12		
35	SOMC % dry weight	3	3	4	3	4	4	3	4	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4		
42	MEAN	2	2	2	1	2	2	3	3	3	2	3	3	2	3	2	3	3	3	1	1	2	1	0	3	3	3		
43	MINDOM	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5		
44	MAXDOM	-2	-2	-2	-1	-2	-2	-2	-2	-2	-2	-1	-2	-2	-2	-2	-2	-2	-2	-2	-2	-1	-2	-2	-2	-2	-2		
45	MODOM	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3		
46	MEDOM	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3		
47	Range	3.94	3.94	3.94	1.94	3.94	3.94	3.94	3.94	3.94	3.94	1.94	3.94	3.94	7.94	3.94	0.94	1.94	1.94	0.94	3.94	1.94	3.94	3.94	3.94	3.94	3.94	0.94	
48	Heterogeneity	8	8	7	8	8	8	8	8	8	8	7	8	8	8	9	8	6	8	8	8	7	8	8	8	8	6		
66	Tall herb height, (cm)	45	40	50	45	100	30	100	50	75	100	50	50	90	70	70	95	80	50	75	50	50	50	60	40	90	50		
67	Tall herb cover %	80	80	85	75	80	80	80	75	90	90	90	75	85	75	95	95	90	50	95	90	80	90	90	95	80	85		
68	Litter %	10	20	20	3	0	5	2	5	5	0	3	5	0	2	0	10	33	50	10	33	15	2	10	20	0	25		
	Species name																												
197	<i>Arrhenatherum elatius</i>	3	8	8	6	8	6	6	7	6	8	8																	
1429	<i>Viola riviniana</i>	4	5	4	4	4	4	5	5	5	5	5	5	6	5	5	4	4	6	5	5	6	5	4	6	6	7	V	
681	<i>Holcus mollis</i>	4	4	5	4	4	2	3	5	8	2	6	4	4	5	4	5	8	9	7	8	8	8	8	8	8	8	6	V
1396	<i>Veronica chamaedrys</i>	5	3	3	4	4	5	3	4	4	2	4	2	5	4	4	3	2	3	3	2	4	3	4	3	3	2	V	
1296	<i>Stellaria graminea</i>	3	2	2	2	1	1	2	1	1	1	1	2	3	1	2	3	2	3	1	4	2	1	4	1	4	1	3	V
171	<i>Anthoxanthum odoratum</i>	4	4	3	4	4	4	4	7	4	6	5	5	6	5	5	3	5	6	6	5	6	4	4	4	4	5	5	V
237	<i>Betula pendula (c)</i>	4	4	4	6	4	5	6	7	5	7	6	4	6	4	5	6	6	4	5	4	4	4	4	5	6	6	V	

Code	Species name	E1	E2	E3	F1	F2	G1	G2	H1	H2	H3	I1	I2	I3	J2	K2	B1	B2	B3	C1	C2	C3	D1	D2	D3	J1	K1	0	
1051	<i>Potentilla sterilis</i>	5	2	2	4	4	3		5		4		5	3	2	3			3	4	3	3	4	2		3	3	V	
2601	<i>Acer pseudoplatanus (g)</i>	2			2	2	2	2	1	2	1	1	1	1	1	1	1	3	2	3	3	3	3	3	3	3	1	V	
988	<i>Poa pratensis</i>	6		2	5	4	5	4		4	5	5	4		5	4	3	4	3	3	4	4	4	5	4	5	3	V	
455	<i>Galium cruciata</i>	3	4	3	4	3	3	3	4	3	3	3	1	3	3		4	4	4	3	4	2	4	4	4	4	4	V	
465	<i>Dactylis glomerata</i>	8	2	3	4	4	6	7	5	8	8	2	6				4	7		6			3	3	4	2	6	V	
103	<i>Acer pseudoplatanus (c)</i>	3	2	3	3	2	2	3	4	2	2	2	1	3	1	3	1	4	3	1	4	1	1	4	3	2	4	V	
2802	<i>Betula seedling/sp</i>	3	2	3	3	2	3	2	1	1	1	1	1	1	1	1	3	3	3	3	3	3	3	3	3	1	V		
576	<i>Festuca rubra</i>	5		6	4		7	7	9	7	8	8	7	8	8	7	8	5	8	7	8	7	5	7	8		7	IV	
1305	<i>Succisa pratensis</i>	5	2		4		1		4			4	2	4	2	3	1		4	3			1	2	1		7	IV	
633	<i>Geum rivale</i>	5	3			1	5	2	4	2	4	4			2	2	2	2	3	2	4	4	3	3	3	5	4	IV	
932	<i>Oxalis acetosella</i>	3	2		2		3	4	3	5						3	4	4	6	5	3	3	4	6	3	4	4	IV	
2603	<i>Alnus glutinosa (g)</i>	2	2	2	1		1		2	3	2	2	1	2			2	2	2	2	3	2	2	3	2			IV	
1940	<i>Rhytidadelphus squarrosus</i>	3	2	2	3	2	1	1	2	3	2					3		2	3	3	1	3	4	3	2	2		IV	
680	<i>Holcus lanatus</i>	6		3	4	5	3	4	4	4	7		5	6	4	4	3	2	6	2	3	2	4	2	5		4	IV	
1761	<i>Hylocomium splendens</i>	4	3	4			5	3	6	7	4		2	4		3	3	4	5	4	5		5	3	5	3	6	IV	
1081	<i>Ranunculus acris</i>	2																											IV
236	<i>Betula pubescens (c)</i>	3	1	3	2	1	3	3	2	2		2	2	3	3	1	3	3	3	2	2	2	2	2	1	2		IV	
583	<i>Filipendula ulmaria</i>	3	1	3	1		1	2								4	5	3	4	3	2	2	2		4			IV	
471	<i>Deschampsia cespitosa</i>	2	3	3			3		3	3		3		4	1	3	4	3	4	2	1	3	3	3	3		2	IV	
153	<i>Alnus glutinosa (c)</i>	4	4	4	5	4	4	4	3	4	7				3	4	3	4		6		3	3	5	5	2	3	IV	
2954	<i>Rosa rubiginosa</i>	2			1		1		1	2	1	2	1	1	4	1	4						3	3	2		1	III	
1056	<i>Primula veris</i>	1	1														2		3		3	2		2	1			III	
1321	<i>Tenacium scorodonia</i>	3		1	2		2	2	1	1	2		3	3	3									1	2	2		III	
167	<i>Angelica sylvestris</i>	3	5	4			7	4			2		3	5	5									7	7	2		III	
800	<i>Lotus corniculatus</i>	2	3	3	4	4	2		2	2		3	6	5	4		1	4		6	6	6	6	6	1	4		III	
127	<i>Ajuga reptans</i>	2		3	3		1		2				1	1	1	2				1	2							III	
632	<i>Geranium sylvaticum</i>	5		1	3		1		2								2			2	2	2	2	1	1			III	
1187	<i>Sambucus nigra (s)</i>	2					2										2	3	2	1	3	1	3	1	2			III	
371	<i>Centaurea nigra</i>	4	1	4	1		1	4	1	2		3	2	4	4							3		2				III	
1136	<i>Rubus fruticosus agg.</i>	1			1		1		2	1	1	1	2	2	1	2												III	
973	<i>Plantago lanceolata</i>	7		2	4	4	3		3	3		1	6	5	5						3							III	
613	<i>Galium verum</i>	3	2	2	5	3		3	3	4	3	2	4	4	3													III	
2764	<i>Rubus idaeus (g)</i>	3	3	1	1	3	3	3	3	2	2	3	3	3	1											2	1	III	
1139	<i>Rumex acetosa</i>	4	1				2	1	1			2		2		1				1								III	
123	<i>Agrostis capillaris</i>						3									3			3							6	2	3	II
1254	<i>Silene dioica</i>						1		1							2			1	3				1	1				II

Code	Species name	E1	E2	E3	F1	F2	G1	G2	H1	H2	H3	I1	I2	I3	J2	K2	B1	B2	B3	C1	C2	C3	D1	D2	D3	J1	K1	0	
2003	<i>Thuidium tamariscinum</i>						1		2		3								4					3		4		0	
1293	<i>Stachys sylvatica</i>								2											2					3		4	5	II
1175	<i>Salix myrsinifolia</i>				1				1		1	1	1	1			3		2						4			II	
2628	<i>Quercus robur (g)</i>															1												II	
288	<i>Campanula rotundifolia</i>	3	3																									II	
1046	<i>Potentilla erecta</i>		1	1	4	2		2	4	1		2	1	2	3						1	3	3	1	2	3		II	
812	<i>Luzula sylvatica</i>				1		4		3	1		1			2													II	
606	<i>Galium boreale</i>		3		2	3	3		4	3		1			3	6					3							II	
1106	<i>Rhinanthus minor</i>		1		4		5	1	4	3	2	2			2					3	4	4	5	2			II		
610	<i>Galium saxatile</i>	3			4				4			3												4				II	
864	<i>Mercurialis perennis</i>		4			3					6													2	5	3	3	2	II
2472	<i>Parmelia sinuosa</i>								3	3	3	3	2	3		3					2	4						II	
445	<i>Crataegus monogyna (s)</i>	1	1	1																								3	II
1807	<i>Plagiomnium undulatum</i>																												II
589	<i>Fraxinus excelsior (C)</i>																												II
634	<i>Helianthemum chamaecistus</i>	1	2			1	1							3										1				II	
1297	<i>Stellaria holostea</i>		1		2		5															2						II	
2707	<i>Vicia sativa</i>										1																	II	
990	<i>Poa trivialis</i>				4																							II	
1401	<i>Veronica officinalis</i>				3	2	5					2		7			1						4					II	
417	<i>Cirsium heterophyllum</i>		3				4				5														3	4		II	
574	<i>Festuca ovina</i>																											II	
634	<i>Geum urbanum</i>		1		4												3	4			5			3				II	
110	<i>Aegopodium podagraria</i>																											II	
384	<i>Cerastium fontanum</i>																										2	II	
1941	<i>Rhytidadelphus triquetrus</i>												2															II	
122	<i>Agrostis stolonifera</i>	2																	4									II	
323	<i>Carex flacca</i>							2	4			4																II	
587	<i>Fragaria vesca</i>									4		1												1				II	
1058	<i>Primula vulgaris</i>																											II	
1298	<i>Stellaria media</i>	2			1							1																II	
2982	<i>Taraxacum seedling/sp</i>		2																									II	
252	<i>Bromus arvensis</i>																											II	
359	<i>Carex sylvatica</i>																											II	
807	<i>Luzula campestris</i>											1																II	
2785	<i>Alchemilla vulgaris</i> agg.																											II	
661	<i>Heracleum sphondylium</i>																											II	

Code	Species name	E1	E2	E3	F1	F2	G1	G2	H1	H2	H3	I1	I2	I3	J2	K2	B1	B2	B3	C1	C2	C3	D1	D2	D3	J1	K1	0
702	<i>Hypericum pulchrum</i>										1																	1
891	<i>Myosotis sylvatica</i>								3											1								1
1188	<i>Sambucus racemosa</i>																			1								1
1795	<i>Plagionium rostratum</i>								2																			1
1934	<i>Rhodobryum roseum</i>																		3			2						1
2471	<i>Parmelia saxatilis</i>												2													3		1
446	<i>Crepis biennis</i>																								2			1
1078	<i>Quercus robur (c)</i>																1								2			1
1148	<i>Rumex sanguineus</i>	5																										1
1381	<i>Valeriana officinalis</i>		1																									1
1939	<i>Rhytidadelphus loreus</i>																											1
403	<i>Chrysanthemum leucanthemum</i>			1		1							1		1												4	1
482	<i>Digitalis purpurea</i>																											1
605	<i>Galium aparine</i>																	1										1
104	<i>Achillea millefolium</i>			2			1				2			2													2	1
1638	<i>Dicranum scoparium</i>																		5									1
914	<i>Ononis repens</i>																											1
2602	<i>Alnus glutinosa (s)</i>							1									2	4										1
2633	<i>Sambucus nigra (p)</i>					1																						1
986	<i>Foa nemoralis</i>																											1
1350	<i>Trifolium repens</i>			3									6		5							3			3			1
1095	<i>Ranunculus repens</i>											1					2											1
	Number of species per sample	43	39	42	34	36	45	36	39	38	37	39	35	38	36	31	35	28	30	34	33	39	39	38	43	31		
	Mean number of species per sample is	36.69																										
	The standard error of the mean is	0.813																										

Table 3.7: TWINSPAN end group 7, W7c community

Code	Environmental variable	J3	L1	L2	M1	G10	J6	0
4	Elevation, (m)	2.17	2.81	2.63	2.74	1.40	0.19	
7	Soil depth, (cm)	44	120	100	103	15	20	
9	Tree height, (m)	14.2	21.7	13.7	12.9	12.5	7.1	
10	Shrub height, (m)	1	2	2	2	1	1	
11	Herb height, (cm)	10	5	10	5	10	10	
12	Moss height, (mm)	3	0	2	3	0	2	
13	Tree cover (%)	50	95	75	75	75	50	
14	Shrub cover (%)	20	20	20	20	5	5	
15	Herb cover (%)	85	75	70	75	35	50	
16	Moss cover (%)	30	0	50	50	0	10	
17	Soil pH	4.8	5.2	4.8	5	4.9	5.2	
22	Bare soil (including sand)	33	0	20	0	0	10	
23	Open water (%)	0	0	0	0	0	5	
34	SMC % dry weight	13.20	14.04	18.34	21.20	42.54	21.40	
35	SOMC % dry weight	3.42	4.04	3.53	4.04	5.39	4.53	
42	MEAN	3	2	1	1	-2	-1	
43	MINDOM	5	5	5	5	5	5	
44	MAXDOM	-1	-1	-3	-2	-4	-4	
45	MODOM	3	2	3	2	-4	3	
46	MEDOM	3	2	3	2	-1	2	
47	Range	1.94	1.94	7.94	3.94	15.94	15.94	
48	Heterogeneity	7	7	9	8	10	10	
66	Tall herb height, (cm)	90	50	40	30	100	100	
67	Tall herb cover, %	75	90	90	75	75	75	
68	Litter, %	15	75	33	5	15	50	
	Species name							
1175	<i>Salix myrsinifolia</i>	1	1	1		2	1	V
1051	<i>Potentilla sterilis</i>		3	5	4	2	2	V
1429	<i>Viola riviniana</i>	5	5	5	5	3	4	V
153	<i>Alnus glutinosa (c)</i>	6	7	6	7	7	6	V
371	<i>Centaurea nigra</i>	5	3		2	4	3	V
1136	<i>Rubus fruticosus agg.</i>	3	3	2	2	2	1	V
236	<i>Betula pubescens (c)</i>	3	5	4	3	2	2	V
1193	<i>Sarothamnus scoparius (s)</i>	1	1	1	1	1		V
633	<i>Geum rivale</i>		2	5	3	3	4	V
1940	<i>Rhytiadelphus squarrosus</i>	6		7	5		4	IV
2764	<i>Rubus idaeus (g)</i>	3	1	2	1			IV
1396	<i>Veronica chamaedrys</i>		3	4		3	4	IV
583	<i>Filipendula ulmaria</i>	3		4	2	2		IV
477	<i>Deschampsia cespitosa</i>	4	2		2	4		IV
465	<i>Dactylis glomerata</i>	3	3		2	3		IV
1305	<i>Succisa pratensis</i>	1	2	1	1			IV
123	<i>Agrostis capillaris</i>			6	6	4	7	IV
2612	<i>Fagus sylvatica (s)</i>	3	1	1	2			IV
441	<i>Corylus avellana (s)</i>	2	2	1	2			IV
197	<i>Arrhenatherum elatius</i>	4	5		5		8	IV
455	<i>Galium cruciata</i>	4	4				1	III
103	<i>Acer pseudoplatanus (c)</i>	3	4	3				III
681	<i>Holcus mollis</i>		8	9	8			III

Code	Species name	J3	L1	L2	M1	G10	J6	0
630	<i>Geranium robertianum</i>			4		1	4	III
167	<i>Angelica sylvestris</i>		3		2		2	III
932	<i>Oxalis acetosella</i>		7			2	4	III
1095	<i>Ranunculus repens</i>		2		1	2		III
589	<i>Fraxinus excelsior (c)</i>	1	1		1			III
2707	<i>Vicia sativa</i>	4	5		4			III
1081	<i>Ranunculus acris</i>	1		4		2		III
576	<i>Festuca rubra</i>	7			5	5		III
171	<i>Anthoxanthum odoratum</i>	4	6			3		III
680	<i>Holcus lanatus</i>	3			4	3		III
1761	<i>Hylocomium splendens</i>				4		4	II
988	<i>Poa pratensis</i>	5	5					II
973	<i>Plantago lanceolata</i>	3				2		II
613	<i>Galium verum</i>	3		3				II
864	<i>Mercurialis perennis</i>				3	3		II
127	<i>Ajuga reptans</i>				3		4	II
605	<i>Galium aparine</i>					3	4	II
1056	<i>Primula veris</i>	1			1			II
955	<i>Phalaris arundinacea</i>					3	3	II
1254	<i>Silene dioica</i>			1		1		II
1293	<i>Stachys sylvatica</i>		2		2			II
812	<i>Luzula sylvatica</i>					1	5	II
2003	<i>Thuidium tamariscinum</i>				5		3	II
606	<i>Galium boreale</i>			1		2		II
884	<i>Myosotis arvensis</i>	4				3		II
2603	<i>Alnus glutinosa (g)</i>						2	I
1169	<i>Salix cinerea (s)</i>						1	I
288	<i>Campanula rotundifolia</i>	2						I
1046	<i>Potentilla erecta</i>	2						I
1321	<i>Teucrium scorodonia</i>						3	I
800	<i>Lotus corniculatus</i>	3						I
889	<i>Myosotis scorpioides</i>					3		I
804	<i>Lupinus polyphyllus</i>					8		I
610	<i>Galium saxatile</i>				1			I
1807	<i>Plagiomnium undulatum</i>				3			I
654	<i>Helianthemum chamaecistus</i>	1						I
2605	<i>Betula pubescens (g)</i>						1	I
990	<i>Poa trivialis</i>		4					I
151	<i>Allium ursinum</i>						2	I
417	<i>Cirsium heterophyllum</i>				6			I
1147	<i>Rumex obtusifolius</i>		1					I
110	<i>Aegopodium podagraria</i>		2					I
730	<i>Juncus effusus</i>					3		I
1168	<i>Salix caprea (s)</i>					1		I
2982	<i>Taraxacum seedling/sp</i>	4						I
359	<i>Carex sylvatica</i>					3		I
640	<i>Glyceria maxima</i>					2		I
699	<i>Hypericum maculatum</i>					1		I
1296	<i>Stellaria graminea</i>					2		I
2601	<i>Acer pseudoplatanus (g)</i>				4			I
708	<i>Impatiens glandulifera</i>					2		I
Number of species per sample		34	31	23	35	38	27	
Mean number of species per sample is		31.33						
The standard error of the mean is		2.261						

Table 3.8: TWINSpan end group 8, W6 community

Code	Environmental variable	D6	E5	F4	D7	E6	F5	G4	G5	H4	0
4	Elevation, (m)	2.02	1.74	3.08	2.21	1.63	0.97	1.22	1.17	2.07	
7	Soil depth, (cm)	0	0	0	0	0	0	0	0	0	
9	Tree height, (m)	17.4	14.4	16.1	20.9	15.5	16.1	20.4	16.7	18.1	
10	Shrub height, (m)	1	1	1	1	1	1	1	1	1	
11	Herb height, (cm)	5	0	0	5	5	0	10	5	2	
12	Moss height, (mm)	0	0	0	0	0	0	3	2	0	
13	Tree cover (%)	75	95	50	75	95	75	75	95	75	
14	Shrub cover (%)	5	5	5	5	5	5	5	5	5	
15	Herb cover (%)	2	0	0	2	2	0	33	33	2	
16	Moss cover (%)	0	0	0	0	0	0	2	10	0	
17	Soil pH	*	*	*	*	*	*	*	5.4	*	
21	Bare rock (shingle)	100	0	100	95	95	100	33	85	100	
23	Open water (%)	0	50	30	0	0	0	20	0	30	
42	MEAN	-1		-4	-2	-1	-1	-2	-3	-3	
43	MINDOM	-1		-2	-1	-1	-1	-2	-1	-1	
44	MAXDOM	-8		-8	-8	-7	-7	-7	-8	-8	
45	MODOM	-4		-8	-5	-6	-4	-7	-6	-7	
46	MEDOM	0		-3	-1	-1	-1	-1	-2	-2	
47	Range	253	0	248	253	125	125	174	256	253	
48	Heterogeneity	14	0	11	14	12	12	11	20	14	
66	Tall herb height, (cm)	60	25	20	0	30	25	60	60	30	
67	Tall herb cover, %	2	3	3	0	2	3	25	5	3	
68	Litter, %	5	10	10	2	10	10	33	33	2	
	Species name										
153	<i>Alnus glutinosa (c)</i>	5	6	3	8	9	8	4	8	5	V
1182	<i>Salix viminalis (c)</i>			1		2	2	1	2	1	IV
708	<i>Impatiens glandulifera</i>				1	1	2	1	3	3	IV
1136	<i>Rubus fruticosus agg.</i>	2			2	2	2	2	2	2	IV
2601	<i>Acer pseudoplatanus (g)</i>				2	1	1	1	1	1	IV
237	<i>Betula pendula (c)</i>	1	4	4				3			III
1175	<i>Salix myrsinifolia</i>						3	1	1	2	III
2764	<i>Rubus idaeus (g)</i>				1	2	2		2	2	III
605	<i>Galium aparine</i>				1	2		3	2		III
630	<i>Geranium robertianum</i>	2			2	1		3	2		III
1360	<i>Tussilago farfara</i>					2		3	2	1	III
197	<i>Arrhenatherum elatius</i>	2			2			3	4		III
1254	<i>Silene dioica</i>				1	2					II
1368	<i>Urtica dioica</i>	3				1					II
1638	<i>Dicranum scoparium</i>							1	4		II
414	<i>Circaea lutetiana</i>							6	6		II
1178	<i>Salix purpurea (s)</i>						1		1	1	II
407	<i>Chrysosplenium alternifolium</i>					1			2		II
889	<i>Myosotis scorpioides</i>								2	2	II
236	<i>Betula pubescens (c)</i>						2		1	2	II
171	<i>Anthoxanthum odoratum</i>				2			2			II
1429	<i>Viola riviniana</i>							2		1	II
576	<i>Festuca rubra</i>								4		I
680	<i>Holcus lanatus</i>							2			I
482	<i>Digitalis purpurea</i>							1			I
127	<i>Ajuga reptans</i>					1					I
955	<i>Phalaris arundinacea</i>	2									I
2607	<i>Betula pendula (g)</i>				2						I
2603	<i>Alnus glutinosa (g)</i>			1							I
662	<i>Hesperis matronalis</i>				1						I
1140	<i>Rumex acetosella</i>	1									I
1256	<i>Silene uniflora</i>				1						I
536	<i>Equisetum pratense</i>				1						I
477	<i>Deschampsia cespitosa</i>					2					I
465	<i>Dactylis glomerata</i>				1						I
681	<i>Holcus mollis</i>							5			I
	Number of species per sample	8	2	4	15	14	9	18	18	12	
	Mean number of species per sample is	11.11									
	The standard error of the mean is	1.925									

Table 3.9: TWINSPAN end group 9, W7a community

Code	Environmental variable	F6	F7	F8	F6	F7	F8	G6	G7	G8	G9	G11	G12	H5	H6	H7	H8	H10	I5	I6	I5	J5	K4	L4	C7	E7	E8	E11	F10	F12	I7	K5	L5	M4		
4	Elevation, (m)	-0.2	1.2	1.3	1.2	3.0	-0.2	0.0	3.1	3.0	0.9	-0.5	3.0	0.5	2.6	0.4	0.2	0.2	2.1	2.2	1.9	2.5	1.7	1.7	2.6	2.6	2.6	1.3	1.5							
7	Soil depth, (cm)	22	30	20	40	25	20	10	20	20	53	30	14	5	25	21	15	25	30	20	0	22	35	0	0	10	18	25	30	25						
9	Tree height, (m)	3.7	9.5	9.5	5.6	8.2	6.4	6.7	6.7	12.9	8.4	2.3	6.2	13.3	8.4	6.7	3.6	9.6	13.7	17.4	6.3	13.5	7.4	3.9	5.7	4.2	6.6	15.8	15.6	12.3						
10	Shrub height, (m)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
11	Herb height, (cm)	5	5	5	10	10	10	5	10	10	25	5	5	10	15	10	3	20	30	10	20	20	10	10	5	5	10	20	10							
12	Moss height, (mm)	0	0	2	0	0	2	2	0	3	0	2	3	2	2	0	2	3	4	0	0	0	0	0	2	2	3	0	1							
13	Tree cover (%)	95	80	95	95	95	95	50	95	80	95	95	80	95	80	95	80	95	75	95	20	15	50	20	10	25	80	25	95	75						
14	Shrub cover (%)	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5		
15	Herb cover (%)	4	5	25	25	25	25	25	15	5	60	20	20	75	5	40	30	50	40	5	75	10	30	25	10	95	75	75	50							
16	Moss cover (%)	0	0	5	0	0	10	2	0	2	0	5	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
17	Soil pH	5.0	5.2	5.4	5.4	5.4	4.9	4.7	5.0	4.7	4.8	4.5	4.6	4.9	5.1	5.3	4.6	4.9	5.0	5.0	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	5.6	
21	Bare rock (shingle)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	95	0	0	60	20	0	0	0	0	0	0	
22	Bare soil (including sand)	95	90	75	75	75	95	90	90	90	85	80	33	10	100	90	75	50	60	0	25	90	0	55	90	5	33	50	25							
23	Open water (%)	30	30	0	40	0	0	0	0	0	0	50	20	0	0	30	0	20	0	50	0	0	0	50	0	0	10	0	0	0	0	0	0	0	0	0
34	SMC % dry weight	38.6	37.7	48.3	29.7	42.0	30.7	36.4	18.3	55.7	38.1	36.2	32.4	11.2	22.2	70.6	51.0	20.1	98.8	63.4	0.0	18.7	0.0	0.0	0.0	24.6	25.9	8.0	2.7	4.3						
35	SOMC % dry weight	3.1	4.5	6.1	1.9	3.3	3.0	3.3	3.9	6.5	3.1	3.0	1.8	4.0	6.4	25.1	5.7	4.3	9.1	5.9	0.0	3.0	0.0	0.0	0.0	5.8	5.3	4.5	2.8	5.1						
42	MEAN	2	2	1	2	2	1	-1	2	3	1	2	2	2	1	2	1	2	-1	0	-1	0	2	-3	1	3	-3	-3	0	0	-2	-3	-1			
43	MINDOM	5	5	5	4	5	5	5	5	5	5	5	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
44	MAXDOM	-2	-3	-2	-3	-1	-2	-4	-2	-1	-2	-3	-3	-2	-1	-2	-4	-3	-2	-2	-2	-2	-2	-2	-8	-4	-2	-8	-7	-3	-2	-4	-4			
45	MODOM	2	2	3	2	2	1	2	3	3	1	2	2	2	1	3	0	2	0	3	-6	2	3	-6	2	3	-6	-6	2	3	-4	-4	3			
46	MEDOM	2	2	2	2	2	2	2	2	3	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
47	Range	4	8	4	8	2	4	16	4	2	4	8	8	4	2	4	16	8	4	4	256	16	4	240	65	8	4	16	16	16						
48	Heterogeneity	8	9	8	8	7	8	9	8	7	8	8	8	8	7	10	9	8	8	8	20	10	8	9	3	9	8	10	10							
66	Tall herb height, (cm)	50	0	0	100	100	80	50	0	0	100	100	90	0	0	80	100	150	125	60	0	80	90	0	80	0	80	0	150							
67	Tall herb cover, %	5	0	0	3	10	5	5	0	0	20	3	10	0	0	10	25	30	90	40	0	25	10	0	20	0	20	0	0	2	0	3				
68	Litter, %	90	33	33	30	75	50	50	10	0	90	60	20	33	50	20	50	20	30	90	5	10	33	10	75	100	10	5	50	5						

Code	Species name	F6	F7	F8	F6	F7	G8	G9	G11	G12	H5	H6	H7	H8	H10	I5	I6	J5	K4	L4	C7	E7	E8	E11	F10	F12	I7	K5	L5	M4	0		
708	<i>Impatiens glandulifera</i>	3	1	1	3	1	1				2	2	2	2	1	2	3	2	1	1	2	1			1	1	1	1	1	V			
153	<i>Alnus glutinosa (c)</i>	9	9	10	10	10	10	3	9	10	9	9	8	8	9	9	9	7	9	7	9	2	4	7	5	3	7	5	7	4	7	V	
1136	<i>Rubus fruticosus agg.</i>	2	2	2	2	3	2	2	1	2	3	3	2	1	2	3	1	1	1	3	3				1	1	1	3	1	1	1	V	
605	<i>Gallium aparine</i>	3	1	3	3	3	2	5		3	4	3	2	4	2	2	2	2	1	5	5	3	4	4	3		6	3	5	2	V		
889	<i>Myosotis scorpioides</i>	2	4	4	1	2	4	3	2	2	4	3	2	3	2	2	2		4	1	2	2									IV		
1081	<i>Ranunculus acris</i>		2	4	3	2		5	2	1			3	2		4	1	4		4		2	4	3	5					4	IV		
1175	<i>Salix myrsinifolia</i>	1	1	1				2		1	2	2	1	1	1	3	1	3	3	2	2				2	1	2	1	1	1	1	IV	
236	<i>Betula pubescens (c)</i>	1	1	2	2	2	2		2	2	2	1	2	2	2	3	2	3	2	3	3						3	3	1	2	IV		
197	<i>Arrhenatherum elatius</i>			4	3					5							2	5				7	4	4			3	3	1	2	IV		
1429	<i>Viola riviniana</i>			3	2	4	2	2	2	2		3	3	3			4	2									4	4	8	2	III		
630	<i>Geranium robertianum</i>			3	2	4	2	2	2	2		3	3	3			4	2									3	5	2	3	III		
583	<i>Filipendula ulmaria</i>		3		4	5	4	3		2	3	4	4	3	2	4	5	2	2	4	4	3	5				5	5	4	3	III		
955	<i>Phalaris arundinacea</i>	4			3	5	4	3		5	5	3	4	4		4	5	6	9	7											1	III	
1293	<i>Stachys sylvatica</i>			5		2	5	3	3	4				5				4										2			2	III	
1169	<i>Salix cinerea (s)</i>										1					2	1	2	1	1	1						5	4	5	2	III		
1368	<i>Urtica dioica</i>	1	3	3			3				4		1					4	1	1	1						1	4	2	2	1	III	
812	<i>Luzula sylvatica</i>	1							1									1	4	4	4	4	3									III	
371	<i>Centaurea nigra</i>	3															3	7					2	2		5	4					II	
1396	<i>Veronica chamaedrys</i>			2			2						1	3									8	2			3	5	7	4	4	II	
1761	<i>Hylocomium splendens</i>						4							3	2						2	1					4				2	II	
988	<i>Poa pratensis</i>							3					3	7	1		4										4	5	5	2	2	II	
1051	<i>Potentilla sterilis</i>			1			1	1				1										2					8	8				II	
2764	<i>Rubus idaeus (g)</i>						1	1			2	1				2	2	1	1	1	1		1	1	2	1	1	1	1	1		II	
1193	<i>S. scoparius (s)</i>	4					2	2															2										II
1321	<i>Tenacium scorodonia</i>							2			4																3						II
477	<i>Deschampsia cespitosa</i>			4					3		4		2	4	2							2	4	1		4		4	5	4		II	
465	<i>Dactylis glomerata</i>							2						2								2						4					II
1139	<i>Rumex acetosa</i>			1					2														4					2	2	4			II
123	<i>Agrostis capillaris</i>						4	5		4											3		4			1	1	1	1	1		II	
1360	<i>Tussilago farfara</i>	3	2		2	1		2		4	4				3	5	3	3		3	3					4	3		5	7	II		
1254	<i>Silene dioica</i>							1			4	4				5							5	4									II
2603	<i>Alnus glutinosa (g)</i>										3	2	2	2	2	3	2	3				1							2	4	1	II	

Code	Species name	F6	F7	F8	G6	G7	G8	G9	G11	G12	H5	H6	H7	H8	H10	I5	I6	J5	K4	L4	C7	E7	E8	E11	F10	F12	I7	K5	L5	M4	0	
2633	<i>Sambucus nigra</i> (g)																															
414	<i>Circaea luteitana</i>		2	2	2					2									1	1							1			1	II	
1807	<i>P. undulatum</i>									3		4							4	4											II	
522	<i>Epilobium montanum</i>				1															5							3				II	
2605	<i>Betula pubescens</i> (g)											2						1								4		2			II	
295	<i>Cardamine pratensis</i>	1					2			1										2			3			2					II	
151	<i>Allium ursinum</i>																									1	1				II	
1445	<i>Callitregon cuspidatum</i>	2					1										2	2		1							1	1	2		II	
1777	<i>Isotrichum myurum</i>	2													2	2		1	2	1					1		1				II	
403	<i>C. leucanthemum</i>													2						1											II	
127	<i>Ajuga reptans</i>															4										2					I	
932	<i>Oxalis acetosella</i>	1					3															2				3					I	
482	<i>Digitalis purpurea</i>							1						2				4									3				I	
589	<i>Fraxinus excelsior</i> (c)																					1	2	2							I	
1363	<i>Ulex europaeus</i> (s)																															I
701	<i>Hypericum perforatum</i>																									1						I
1638	<i>Dicranum scoparium</i>			4																						3						I
2003	<i>Thuidium tamariscinum</i>									2																						I
606	<i>Galium boreale</i>						4					4	2	1																		I
2602	<i>Alnus glutinosa</i> (s)													2																		I
2707	<i>Vicia sativa</i>																															I
419	<i>Cirsium vulgare</i>																															I
1270	<i>Solidago virgaurea</i>																				1											I
1350	<i>Trifolium repens</i>																									1						I
1095	<i>Ranunculus repens</i>																															I
1106	<i>Rhinanthus minor</i>																															I
1928	<i>Racomitrium canescens</i>																															I
2607	<i>Betula pendula</i> (g)																															I
804	<i>Lupinus polyphyllus</i>								4						2								2									I
1239	<i>Senecio jacobaea</i>														1																	I
639	<i>Glyceria fluitans</i>						4																									I
632	<i>Geranium sylvaticum</i>																															I

Code	Species name	F6	F7	F8	F6	G6	G7	G8	G9	G11	G12	H5	H6	H7	H8	H10	I5	I6	J5	K4	L4	C7	E7	E8	E11	F10	F12	I7	K5	L5	M4	0					
864	<i>Mercurialis perennis</i>									1							3		3																		
662	<i>Hesperis matronalis</i>									2															3	1											
1182	<i>Salix viminalis (c)</i>	2				2									1								1	3													
884	<i>Myosotis arvensis</i>																																				
1256	<i>Silene uniflora</i>															2																					
1308	<i>Symphytum officinale</i>							1					1	2			2			4		1															
634	<i>Geum urbanum</i>													3																							
868	<i>Mimulus guttatus</i>					1			2																												
1147	<i>Rumex obtusifolius</i>	1				1																															
1178	<i>Salix purpurea (s)</i>	2				1	2													1																	
110	<i>A. podagraria</i>														1																						
730	<i>Juncus effusus</i>																																				
1168	<i>Salix caprea (s)</i>	1	1					1				3																									
338	<i>Carex pallescens</i>							3	4	4																											
536	<i>Equisetum pratense</i>																										1										
587	<i>Fragaria vesca</i>	1																						1													
532	<i>Equisetum arvense</i>	1					1		1																		2										
729	<i>Juncus conglomeratus</i>																																				
1593	<i>Climacium dendroides</i>																2																				
3226	<i>Salix x tetrapla</i>																																				
319	<i>Carex echinata</i>																										1										
350	<i>Carex remota</i>																																				
450	<i>Crepis vesicaria</i>																																				
535	<i>Equisetum palustre</i>												1																								
640	<i>Glyceria maxima</i>																																				
2601	<i>Acer pseudoplatanus (g)</i>																																				
576	<i>Festuca rubra</i>																																				
973	<i>Plantago lanceolata</i>																																				
103	<i>Acer pseudoplatanus (c)</i>																																				
2802	<i>Betula seedling/sp</i>																																				
1305	<i>Succisa pratensis</i>												2	1						2																	
455	<i>Galium cruciata</i>																																				

Code	Species name	F6	F7	F8	F9	G6	G7	G8	G9	G11	G12	H5	H6	H7	H8	H10	I5	I6	J5	K4	L4	C7	E7	E8	E11	F10	F12	I7	K5	L5	M4	0					
2954	<i>Rosa rubiginosa</i>																																				
104	<i>Achillea millefolium</i>																																				
633	<i>Geum rivale</i>					2	4			1							4							3													
1296	<i>Stellaria graminea</i>																																				
171	<i>A. odoratum</i>																																				
1940	<i>R. squarrosus</i>								3								3																				
680	<i>Holcus lanatus</i>															3																					
661	<i>Heracleum sphondylium</i>																			1																	
715	<i>Iris pseudacorus</i>												5		2																						
855	<i>Mentha aquatica</i>												2																								
1259	<i>Silene vulgaris</i>																																				
1795	<i>Plagionium rostratum</i>																																				
2639	<i>Ulex europaeus (g)</i>																			2																	
293	<i>Cardamine hirsuta</i>																																				
352	<i>Carex rostrata</i>												4																								
449	<i>Crepis paludosa</i>																																				
499	<i>Dryopteris dilatata</i>																																				
733	<i>Juncus inflexus</i>								5																												
950	<i>Petasites albus</i>																																				
1098	<i>Ranunculus sceleratus</i>												2																								
1220	<i>Scrophularia nodosa</i>															1																					
1794	<i>Mnium hornum</i>																																				
	Number of species per sample	19	16	19	20	18	24	22	17	17	17	25	22	30	30	17	23	29	28	20	23	20	23	22	17	23	30	35	30	22							
	Mean number of species per sample is 22.79																																				
	The standard error of the mean is 0.925																																				

Table 3.10: TWINSPAN end group 10, M23 community

Code	Environmental variable	J4	0
4	Elevation, (m)	-0.03	
9	Tree height, (m)	4.85	
10	Shrub height, (m)	2	
11	Herb height, (cm)	8	
13	Tree cover (%)	25	
14	Shrub cover (%)	15	
15	Herb cover (%)	25	
22	Bare soil (including sand)	30	
23	Open water (%)	50	
42	MEAN	0	
43	MINDOM	0	
44	MAXDOM	0	
45	MODOM	0	
46	MEDOM	0	
47	Range	0	
48	Heterogeneity	0	
66	Tall herb height, (cm)	50	
67	Tall herb cover, %	25	
68	Litter, %	20	
	Species name		
371	<i>Centaurea nigra</i>	2	V
1136	<i>Rubus fruticosus agg.</i>	2	V
1396	<i>Veronica chamaedrys</i>	3	V
973	<i>Plantago lanceolata</i>	4	V
1175	<i>Salix myrsinifolia</i>	2	V
2764	<i>Rubus idaeus (g)</i>	2	V
583	<i>Filipendula ulmaria</i>	3	V
708	<i>Impatiens glandulifera</i>	2	V
605	<i>Galium aparine</i>	4	V
889	<i>Myosotis scorpioides</i>	5	V
955	<i>Phalaris arundinacea</i>	3	V
403	<i>Chrysanthemum leucanthemum</i>	1	V
1360	<i>Tussilago farfara</i>	3	V
1046	<i>Potentilla erecta</i>	3	V
1363	<i>Ulex europaeus (s)</i>	1	V
2602	<i>Alnus glutinosa (s)</i>	4	V
773	<i>Lepidium heterophyllum</i>	2	V
1350	<i>Trifolium repens</i>	4	V
1106	<i>Rhinanthus minor</i>	2	V
1140	<i>Rumex acetosella</i>	1	V
2605	<i>Betula pubescens (g)</i>	2	V
639	<i>Glyceria fluitans</i>	3	V
1401	<i>Veronica officinalis</i>	1	V
1777	<i>Isotheicum myurum</i>	1	V
868	<i>Mimulus guttatus</i>	4	V
1147	<i>Rumex obtusifolius</i>	1	V
730	<i>Juncus effusus</i>	3	V
122	<i>Agrostis stolonifera</i>	3	V

Code	Species name	J4	0
729	<i>Juncus conglomeratus</i>	3	V
1043	<i>Potentilla anserina</i>	4	V
1089	<i>Ranunculus flammula</i>	2	V
319	<i>Carex echinata</i>	4	V
535	<i>Equisetum palustre</i>	2	V
702	<i>Hypericum pulchrum</i>	2	V
855	<i>Mentha aquatica</i>	3	V
1059	<i>Prunella vulgaris</i>	4	V
1349	<i>Trifolium pratense</i>	3	V
183	<i>Aquilegia vulgaris</i>	2	V
269	<i>Calamagrostis canescens</i>	2	V
277	<i>Callitriche stagnalis</i>	2	V
533	<i>Equisetum fluviatile</i>	2	V
609	<i>Galium palustre</i>	3	V
722	<i>Juncus articulatus</i>	4	V
726	<i>Juncus bulbosus</i>	4	V
860	<i>Mentha x piperata</i>	3	V
1069	<i>Pulicaria dysenterica</i>	2	V
1093	<i>Ranunculus lingua</i>	3	V
1236	<i>Senecio aquaticus</i>	1	V
3248	<i>Thymus pulegioides</i>	3	V
Number of species per sample		49	
Mean number of species per sample is		49.00	
The standard error of the mean is		-1.000	

Table 3.11: TWINSPAN end group 11, SHscb community

Code	Environmental variable	B11	B12	C8	C10	C11	C12	D8	D9	E10	B7	C6	D11	0
4	Elevation, (m)	3.13	2.63	1.97	2.87	2.90	2.66	1.89	2.63	2.46	1.88	2.49	2.64	
9	Tree height, (m)	0.0	9.3	5.8	0.0	0.0	8.2	10.3	9.9	10.7	9.5	12.3	0.0	
10	Shrub height, (m)	1	1	1	1	1	1	1	1	1	1	1	1	
11	Herb height, (cm)	10	15	10	5	4	15	10	40	2	70	0	0	
12	Moss height, (mm)	0	0	2	2	2	0	2	0	3	0	0	0	
13	Tree cover (%)	5	5	5	5	5	5	5	95	10	5	5	5	
14	Shrub cover (%)	5	5	2	5	5	5	2	5	25	2	2	5	
15	Herb cover (%)	55	1	5	10	5	25	10	25	2	20	0	0	
16	Moss cover (%)	0	0	2	5	2	0	2	0	2	0	0	0	
21	Bare rock (shingle)	90	100	95	90	100	85	95	95	100	95	100	100	
42	MEAN	-3	-3	-2	-3	-3	-3	-2	-3	-3	-3	-3	-3	
43	MINDOM	-3	-1	-1	-1	-3	-2	-1	-3	-1	-1	-1	-3	
44	MAXDOM	-8	-8	-8	-8	-8	-8	-7	-8	-8	-8	-8	-8	
45	MODOM	-6	-6	-6	-8	-6	-7	-6	-6	-6	-6	-7	-5	
46	MEDOM	-2	-2	-1	-2	-2	-2	-1	-2	-1	-1	-2	-1	
47	Range	140	253	253	253	245	250	177	245	253	253	253	245	
48	Heterogeneity	9	14	14	14	10	12	13	10	14	14	14	10	
68	Litter, %	10	0	50	0	0	10	5	10	0	5	2	0	
	Species name													
708	<i>Impatiens glandulifera</i>	2		1	2		1	1	1	1		2	2	IV
1136	<i>Rubus fruticosus</i> agg.	2	1	2	2	2	2			1	1		3	IV
2601	<i>Acer pseudoplatanus</i> (g)	2		3	2			2	1	2				III
1321	<i>Teucrium scorodonia</i>	2			1		5	3	4					III
973	<i>Plantago lanceolata</i>	1	1			1				2	1			III
1175	<i>Salix myrsinifolia</i>		1		2	1	2	2						III
2764	<i>Rubus idaeus</i> (g)	1	1	1	2								2	III
1193	<i>Sarothamnus scoparius</i> (s)	3	3		2	3	4	2	2					III
2954	<i>Rosa rubiginosa</i>				2	1	1	1		2	1		2	III
482	<i>Digitalis purpurea</i>	1	1	1	1			2	1	1				III
153	<i>Alnus glutinosa</i> (c)		1		1			1	7	4		1	1	III
197	<i>Arrhenatherum elatius</i>	1	1	2		2								III
576	<i>Festuca rubra</i>	2			2	1		1						II
773	<i>Lepidium heterophyllum</i>				2	2		2		2				II
1928	<i>Racomitrium canescens</i>			2	4	1		3						II
914	<i>Ononis repens</i>	3		3				1						II
630	<i>Geranium robertianum</i>	2		2	1				3					II
662	<i>Hesperis matronalis</i>	2	2	1										II
1064	<i>Prunus padus</i> (s)		1		1							1		II
1242	<i>Senecio viscosus</i>				2	1		3		2				II
1256	<i>Silene maritima</i>	1					5				1			II
371	<i>Centaurea nigra</i>		1											I
1396	<i>Veronica chamaedrys</i>							3						I
1296	<i>Stellaria graminea</i>								2					I
1081	<i>Ranunculus acris</i>				1		4							I
237	<i>Betula pendula</i> (c)				2							1		I
103	<i>Acer pseudoplatanus</i> (c)			1				1						I
104	<i>Achillea millefolium</i>								1					I
1139	<i>Rumex acetosa</i>												4	I
889	<i>Myosotis scorpioides</i>										2			I
955	<i>Phalaris arundinacea</i>		3											I
1368	<i>Urtica dioica</i>			2										I
1333	<i>Thymus polytrichus</i>				3									I
2633	<i>Sambucus nigra</i> (g)		1						1					I
1638	<i>Dicranum scoparium</i>									1				I
2003	<i>Thuidium tamariscinum</i>					1								I
2607	<i>Betula pendula</i> (g)	1			2									I
610	<i>Galium saxatile</i>			2										I
589	<i>Fraxinus excelsior</i> (c)				1					1				I
1140	<i>Rumex acetosella</i>							1						I

Code	Species name	B11	B12	C8	C10	C11	C12	D8	D9	E10	B7	C6	D11	0
1914	<i>Pseudoscleropodium purum</i>									1				I
884	<i>Myosotis arvensis</i>							2						I
868	<i>Mimulus guttatus</i>										2			I
1941	<i>Rhytidadelphus triquetrus</i>					2								I
842	<i>Meconopsis cambrica</i>				2	2								I
1298	<i>Stellaria media</i>				2									I
782	<i>Linaria repens</i>					2	2							I
1043	<i>Potentilla anserina</i>		1											I
1089	<i>Ranunculus flammula</i>				1									I
3226	<i>Salix x tetrapla</i>		1		1									I
144	<i>Alliaria petiolata</i>					1			2					I
570	<i>Fagus sylvatica (c)</i>										1			I
1065	<i>Prunus spinosa (s)</i>				1	1								I
404	<i>Tanacetum parthenium</i>		1											I
1243	<i>Senecio vulgaris</i>				1									I
2373	<i>Cladonia ochrochlora</i>									4				I
2603	<i>Alnus glutinosa (g)</i>				1									I
1169	<i>Salix cinerea (s)</i>		2		2									I
1360	<i>Tussilago farfara</i>									2				I
Number of species per sample		15	17	13	29	16	10	17	12	14	8	3	5	
Mean number of species per sample is		13.25												
The standard error of the mean is		1.947												

Table 3.12: TWINSPAN end group 12, SHpc community

Code	Environmental variable	B8	B9	B10	C9	D10	0
4	Elevation, (m)	2.06	2.76	2.84	2.72	2.71	
9	Tree height, (m)	11.6	0.0	0.0	10.0	8.4	
10	Shrub height, (m)	1	1	1	1	1	
11	Herb height, (cm)	5	4	30	1	3	
12	Moss height, (mm)	0	0	2	0	0	
13	Tree cover (%)	2	0	0	5	5	
14	Shrub cover (%)	2	2	5	2	5	
15	Herb cover (%)	2	4	5	1	1	
16	Moss cover (%)	0	0	10	0	0	
21	Bare rock (shingle)	95	95	90	100	100	
42	MEAN	-2	-3	-2	-3	-2	
43	MINDOM	-1	-1	-1	-1	-2	
44	MAXDOM	-7	-8	-7	-8	-7	
45	MODOM	-6	-7	-6	-6	-6	
46	MEDOM	-1	-2	-1	-2	-1	
47	Range	177.0	253.0	177.0	253.0	250.4	
48	Heterogeneity	12	14	13	14	12	
68	Litter, %	2	5	5	0	0	
	Species name						
2607	<i>Betula pendula (g)</i>	2	1	1	2	2	V
2601	<i>Acer pseudoplatanus (g)</i>	1	1	1		1	IV
1242	<i>Senecio viscosus</i>	3	2		3		III
2764	<i>Rubus idaeus (g)</i>	1		1	1		III
773	<i>Lepidium heterophyllum</i>		2	2	1		III
708	<i>Impatiens glandulifera</i>	1	1	1			III
1320	<i>Teesdalia nudicaulis</i>	2		2		3	III
576	<i>Festuca rubra</i>			2	2		II
680	<i>Holcus lanatus</i>		2	2			II
237	<i>Betula pendula (c)</i>				2	3	II
842	<i>Meconopsis cambrica</i>				1	2	II
662	<i>Hesperis matronalis</i>		2	1			II
1064	<i>Prunus padus (s)</i>	1		1			II
1333	<i>Thymus polytrichus</i>		3	3			II
1429	<i>Viola riviniana</i>			2			I
2602	<i>Alnus glutinosa (s)</i>			1			I
419	<i>Cirsium vulgare</i>			3			I
1095	<i>Ranunculus repens</i>		2				I
1239	<i>Senecio jacobaea</i>					1	I
1761	<i>Hylocomium splendens</i>			4			I
153	<i>Alnus glutinosa (c)</i>	1					I
371	<i>Centaurea nigra</i>			2			I
1136	<i>Rubus fruticosus agg.</i>					1	I
1296	<i>Stellaria graminea</i>			2			I
973	<i>Plantago lanceolata</i>			2			I
1193	<i>Sarothamnus scoparius (s)</i>					2	I
2954	<i>Rosa rubiginosa</i>					1	I
1321	<i>Teucrium scorodonia</i>			2			I
633	<i>Geum rivale</i>			2			I
889	<i>Myosotis scorpioides</i>			2			I

Code	Species name	B8	B9	B10	C9	D10	0
1293	<i>Stachys sylvatica</i>		1				I
1360	<i>Tussilago farfara</i>		1				I
522	<i>Epilobium montanum</i>			2			I
589	<i>Fraxinus excelsior (c)</i>					1	I
2982	<i>Taraxacum seedling/sp</i>			2			I
1089	<i>Ranunculus flammula</i>				1		I
698	<i>Hypericum humifusum</i>	2					I
228	<i>Barbarea vulgaris</i>		1				I
1262	<i>Sinapis arvensis</i>			1			I
Number of species per sample		9	12	24	8	10	
Mean number of species per sample is		12.60					
The standard error of the mean is		2.926					

Table 3.13: TWINSPAN end group 13, S22a community

Code	Environmental variable	K3	L3	M2	M3	0
4	Elevation, (m)	1.30	-0.44	-0.78	-0.56	
23	Open water (%)	100	95	100	100	
42	MEAN	0	0	0	0	
43	MINDOM	0	0	0	0	
44	MAXDOM	0	0	0	0	
45	MODOM	0	0	0	0	
46	MEDOM	0	0	0	0	
47	Range	0	0	0	0	
48	Heterogeneity	0	0	0	0	
68	Litter	0	0			
52	Dead wood	10	10			
	Species name					
639	<i>Glyceria fluitans</i>	2	4	5	5	V
Number of species per sample		1	1	1	1	
Mean number of species per sample is		1.00				
The standard error of the mean is		0.000				

Appendix 4

Table 4.1: Species scores derived from CANOCO carrying a high weight ($N_2 > 65$) for interpreting the ordination diagram of axes 1 and 2.

Code	Species name	N_2
153	<i>Alnus glutinosa (c)</i>	65.80
197	<i>Arrhenatherum elatius</i>	80.45
371	<i>Centaurea nigra</i>	68.66
576	<i>Festuca rubra</i>	72.25
1136	<i>Rubus fruticosus</i>	67.70
1429	<i>Viola riviniana</i>	78.04

Appendix 5.
Soil/substrate classification, Tomdachoille.

Table 5.1: Substrate group 1 data and summary statistics.

Code	Bare gravel (%)	MEAN	MINDOM	MAXDOM	MODOM	MEDOM	Range	Heterogeneity
B7	95	-2	-1	-8	-6	-1	253	14
B9	95	-3	-1	-8	-7	-2	253	14
B12	100	-3	-1	-8	-6	-2	253	14
C6	100	-3	-1	-8	-7	-2	253	14
C7	95	-3	5	-8	-6	-2	255.94	20
C8	95	-2	-1	-8	-6	-1	253	14
C9	100	-3	-1	-8	-6	-2	253	14
C10	90	-3	-1	-8	-8	-2	253	14
C11	100	-3	-3	-8	-6	-2	244.8	10
C12	85	-3	-2	-8	-7	-2	250.4	12
D5	0	*	*	*	*	*	0	0
D6	100	-1	-1	-8	-4	0	253	14
D7	95	-2	-1	-8	-5	-1	253	14
D9	95	-3	-3	-8	-6	-2	244.8	10
D10	100	-2	-2	-7	-6	-1	250.4	12
D11	100	-3	-3	-8	-5	-1	244.8	10
D12	90	8	-2	-8	-7	-3	250.4	12
E10	100	-3	-1	-8	-6	-1	253	14
E11	60	-3	-3	-8	-6	-3	240	9
E12	0	0	0	0	0	0	0	0
F4	100	-4	-2	-8	-8	-3	248	11
G5	85	-3	-1	-8	-6	-2	255.94	20
H4	100	-3	-1	-8	-7	-2	253	14
J8	80	-2	-2	-8	-6	-2	248	11
L6	45	-3	-1	-8	-7	-2	253	14
M5	35	-4	-4	-8	-7	-4	224.5	7
Mean	82	-2	-1	-8	-6	-2	231	12
Min	0	-4	-4	-8	-8	-4	0	0
Max	100	8	5	0	0	0	256	20
Stdev	30	2	2	2	2	1	68	5

Table 5.2: Substrate group 2 data and summary statistics.

Code	Bare gravel (%)	MEAN	MINDOM	MAXDOM	MODOM	MEDOM	Range	Heterogeneity
B11	90	-3	-3	-8	-6	-2	140	9
E5	0	*	*	*	*	*	0	0
E6	95	-1	-1	-7	-6	-1	125	12
F5	100	-1	-1	-7	-4	-1	125	12
I4	50	-3	-4	-7	-7	-3	106.6	6
Mean	67	-2	-2	-7	-6	-2	99.32	8
Min	0	-3	-4	-8	-7	-3	0.00	0
Max	100	-1	-1	-7	-4	-1	140.00	12
Stdev	42	1	2	1	1	1	56.77	5

Table 5.3: Substrate group 3 data and summary statistics.

Code	Bare gravel (%)	Bare soil (%)	MEAN	MINDOM	MAXDOM	MODOM	MEDOM	Range	Heterogeneity
B8	95	0	-2	-1	-7	-6	-1	177	12
B10	90	0	-2	-1	-7	-6	-1	177	13
D8	95	0	-2	-1	-7	-6	-1	177	13
G4	33	0	-2	-2	-7	-7	-1	174.4	11
K6	0	60	*	*	*	*	*	0	0
K7	75	0	-3	-4	-7	-7	-3	158.6	7
M6	0	15	-4	5	-7	-7	-4	179.94	12
Mean	55	11	-3	-1	-7	-7	-2	149.13	10
Min	0	0	-4	-4	-7	-7	-4	0.00	0
Max	95	60	-2	5	-7	-6	-1	179.94	13
Stdev	44	22	1	3	0	1	1	66.14	5

Table 5.4: Substrate group 4 data and summary statistics.

Code	Soil depth (cm)	pH	SMC (%)	OMC (%)	Bare soil (%)	MEAN	MIN-DOM	MAX-DOM	MOD-OM	MED-OM	Range	Heterogeneity
B2	122	5.1	11.14	3.78	2	3	5	-2	3	3	1.937	8
B3	127	4.9	19.43	3.99	2	1	5	-2	1	1	1.937	8
B5	97	5.2	12.53	3.61	2	2	5	-2	3	3	3.937	8
C1	125	4.5	9.86	3.68	0	1	5	0	1	1	0.937	6
C2	125	4.8	17.29	3.72	3	2	5	-2	3	3	3.937	8
C3	117	5.1	11.89	3.12	0	1	5	-1	1	1	1.937	7
C4	121	4.8	8.01	4.16	4	2	5	-1	2	2	1.937	7
D1	100	5.1	12.35	2.57	2	0	5	-2	0	0	3.937	8
D2	125	5.2	6.81	7.08	3	3	5	-2	3	3	3.937	8
D3	115	4.7	11.15	2.92	0	3	5	-2	3	3	3.937	8
D4	123	4.8	7.67	2.41	0	3	5	0	3	3	0.937	6
E1	100	5.1	14.76	3.17	0	2	5	-2	3	3	3.937	8
E2	119	4.9	18.68	3.41	0	2	5	-2	3	3	3.937	8
E3	116	5.2	10.06	3.97	0	2	5	-2	3	3	3.937	8
E4	121	4.6	14.44	3.99	20	1	5	-2	3	3	3.937	8
F1	110	4.9	15.42	2.92	0	1	5	-1	1	1	1.937	7
F2	128	5.0	5.25	3.51	0	2	5	-2	3	3	3.937	8
F3	120	4.8	9.77	3.52	5	3	5	-2	3	3	3.937	8
G1	120	4.9	16.02	4.06	0	2	5	-2	3	3	3.937	8
G2	118	5.0	12.20	3.36	10	3	5	-2	3	3	3.937	8
G3	110	4.9	13.67	3.98	0	3	5	-1	3	3	1.937	7
H2	89	4.8	16.96	4.45	5	3	5	-2	3	3	3.937	8
H3	97	4.9	10.97	4.44	0	2	5	-2	3	3	3.937	8
I3	89	4.7	10.07	4.11	0	2	5	-2	3	3	3.937	8
J1	91	5.2	7.54	3.17	2	3	5	-2	3	3	3.937	8
K1	102	5.0	11.85	3.41	0	2	5	0	2	2	0.937	6
L1	120	5.2	14.04	4.04	0	2	5	-1	2	2	1.937	7
L2	100	4.8	18.34	3.53	20	1	5	-3	3	3	7.937	9
L8	90	4.3	8.86	3.25	0	3	5	-2	3	3	3.937	8
M1	103	5.0	21.20	4.04	0	1	5	-2	2	2	3.937	8
M8	95	4.3	14.55	3.02	5	0	5	-3	2	3	7.937	9
M12	83	4.8	6.53	3.23	0	3	5	0	3	3	0.937	6
Mean	110	4.9	12	4	3	2	5	-2	3	3	3.37	8
Min	83	4.3	5	2	0	0	5	-3	0	0	0.94	6
Max	128	5.2	21	7	20	3	5	0	3	3	7.94	9
Stdev	14	0.2	4	1	5	1	0	1	1	1	1.66	1

Table 5.5: Substrate group 5 data and summary statistics.

Code	Soil depth (cm)	pH	SMC (%)	OMC (%)	Bare soil (%)	MEAN	MIN-DOM	MAX-DOM	MOD-OM	MED-OM	Range	Heterogeneity
B1	75	4.8	9.33	2.36	0	3	5	0	3	3	0.937	6
B6	55	4.8	8.99	2.87	5	1	5	0	2	2	0.937	6
C5	59	4.9	15.98	5.15	4	1	5	-2	3	2	3.937	8
G6	40	5.4	29.66	1.91	75	2	4	-3	2	2	7.94	8
H1	60	4.6	13.73	3.75	0	3	5	-2	3	3	3.937	8
H5	53	4.8	38.14	3.11	85	1	5	-2	1	1	3.94	8
I1	75	4.8	6.33	2.63	0	3	5	-1	3	3	1.937	7
I2	70	4.7	7.85	3.54	20	3	5	-2	3	3	3.937	8
I11	77	5.1	12.19	3.11	0	2	5	-2	3	3	3.937	8
I12	50	5.2	10.22	3.68	0	2	5	-2	2	2	3.937	8
J2	64	4.9	15.12	4.02	10	2	5	-3	3	3	7.937	9
J3	44	4.8	13.20	3.42	33	3	5	-1	3	3	1.937	7
J11	73	5.0	7.26	3.07	5	1	5	-4	2	2	15.937	10
J12	60	5.2	17.33	4.40	5	2	5	-3	3	3	7.937	9
K2	72	5.1	16.99	4.15	5	2	5	-2	3	3	3.937	8
K8	50	4.6	5.35	3.07	5	2	5	-1	2	2	1.937	7
K11	80	5.1	10.41	3.83	5	2	5	-3	3	2	7.937	9
K12	62	4.9	15.72	4.26	0	2	5	-3	3	2	7.937	9
L9	70	4.2	3.83	3.28	0	-2	5	-4	2	2	15.937	10
L10	73	5.0	12.14	3.24	0	1	5	-3	2	2	7.937	9
L12	60	5.0	12.39	4.48	0	1	5	-3	3	2	7.937	9
M9	50	5.2	13.22	2.94	0	2	5	-3	3	3	7.937	9
M10	60	4.8	10.51	4.16	0	2	5	-3	3	3	7.937	9
M11	82	4.8	16.43	2.94	2	-1	5	-4	2	2	15.937	9
Mean	63	4.9	13	3	11	2	5	-2	3	2	6.44	8
Min	40	4.2	4	2	0	-2	4	-4	1	1	0.94	6
Max	82	5.4	38	5	85	3	5	0	3	3	15.94	10
Stdev	12	0.3	7	1	23	1	0	1	1	1	4.45	1

Table 5.6: Substrate group 6 data and summary statistics.

Code	Soil depth (cm)	pH	SMC (%)	OMC (%)	Bare soil (%)	MEAN	MIN-DOM	MAX-DOM	MOD-OM	MED-OM	Range	Heterogeneity
E8	35	5.6	0.00	0.00	90	3	5	-2	3	3	3.94	8
H8	5	4.9	11.23	4.02	10	1	5	-2	1	2	3.94	8
H9	12	5.5	15.06	5.19	20	2	5	-2	3	2	3.94	8
H11	20	5.5	7.15	5.77	0	-2	5	-4	-4	-1	15.94	10
H12	17.5	5.1	3.48	3.95	5	3	5	-2	3	3	3.94	8
I8	20	5.2	17.04	5.31	0	-6	5	-8	-8	-6	15.937	10
I10	15	5.0	10.99	6.64	20	1	5	-2	2	2	3.94	8
J7	25	5.2	8.46	5.35	10	-4	5	-7	-7	-4	15.937	10
J9	25	5.6	4.49	3.22	5	-2	5	-4	3	1	15.937	10
J10	25	4.8	12.80	6.88	5	1	5	-4	3	2	15.937	10
K5	25	4.7	8.00	4.54	33	-2	5	-4	-4	-1	15.94	10
K9	30	5.0	4.72	3.13	2	-2	5	-4	-4	-1	15.937	10
K10	25	5.2	8.23	5.71	0	-1	5	-4	3	0	15.937	10
L5	30	5.3	2.69	2.83	50	-3	5	-4	-4	-1	15.94	10
L7	20	5.1	7.10	4.48	10	-2	5	-4	-4	1	15.937	10
L11	25	5.2	11.20	8.63	0	-2	5	-4	-4	-2	15.937	10
M4	25	5.0	4.29	5.13	25	-1	5	-4	3	2	15.94	10
M7	27	5.1	16.35	3.28	0	-3	5	-4	-4	-3	15.937	10
Mean	23	5.2	9	5	16	-1	5	-4	-1	0	12.60	9
Min	5	4.7	0	0	0	-6	5	-8	-8	-6	3.94	8
Max	35	5.6	17	9	90	3	5	-2	3	3	15.94	10
Stdev	7	0.3	5	2	23	2	0	2	4	3	5.53	1

Table 5.7: Substrate group 7 data and summary statistics.

Code	Soil depth (cm)	pH	SMC (%)	OMC (%)	Bare soil (%)	MEAN	MIN-DOM	MAX-DOM	MOD-OM	MED-OM	Range	Heterogeneity
B4	25	4.7	25.23	5.94	0	1	5	-3	2	1	7.937	9
E7	22	5.6	18.71	3.01	25	1	5	-4	2	1	15.94	10
E9	20	5.6	29.04	5.84	50	0	5	-3	1	1	7.937	9
F6	22	5.0	38.59	3.14	95	2	5	-2	2	2	3.94	8
F7	30	5.2	37.67	4.51	90	2	5	-3	2	2	7.94	9
F9	25	5.5	25.4	3.66	5	2	5	-4	2	2	15.94	9
F11	25	5.0	35.67	4.32	50	2	5	-4	2	2	15.94	9
F12	10	5.7	24.56	5.82	90	0	5	-3	2	1	7.94	9
G7	25	5.4	41.98	3.32	75	2	5	-1	2	2	1.94	7
G8	20	4.9	30.69	2.96	95	1	5	-2	1	2	3.94	8
G11	20	5.0	18.28	3.85	90	2	5	-2	3	3	3.94	8
H6	30	4.5	36.20	2.98	80	2	5	-3	2	2	7.94	8
H7	14	4.6	32.42	1.83	33	2	5	-3	2	2	7.94	8
H10	25	5.1	22.20	6.37	100	2	5	-1	3	2	1.94	7
I7	18	5.4	25.93	5.32	5	0	5	-2	3	2	3.94	8
I9	15	5.0	11.67	4.69	10	-1	5	-4	3	2	15.937	10
J6	20	5.2	21.40	4.53	10	-1	5	-4	3	2	15.937	10
Mean	22	5.1	28	4	53	1	5	-3	2	2	8.64	9
Min	10	4.5	12	2	0	-1	5	-4	1	1	1.94	7
Max	30	5.7	42	6	100	2	5	-1	3	3	15.94	10
Stdev	5	0.4	8	1	38	1	0	1	1	1	5.29	1

Table 5.8: Substrate group 8 data and summary statistics.

Code	Soil depth (cm)	pH	SMC (%)	OMC (%)	Bare soil (%)	MEAN	MIN-DOM	MAX-DOM	MOD-OM	MED-OM	Range	Heterogeneity
F8	20	5.4	48.28	6.09	75	1	5	-2	3	2	3.94	8
F10	0	*	0.00	0.00	55	-3	-6	-7	-6	-3	65	3
G9	10	4.7	36.41	3.30	90	-1	5	-4	2	2	15.94	9
G10	15	4.9	42.54	5.39	0	-2	5	-4	-4	-1	15.937	10
G12	20	4.7	55.68	6.49	90	3	5	-1	3	3	1.94	7
I5	21	5.3	70.64	25.13	90	-1	4	-2	0	0	3.94	7
I6	15	4.6	51.03	5.66	75	0	5	-4	2	2	15.94	10
J4	0	*	0	0	0	*	*	*	*	*	0	0
J5	25	4.9	50.09	4.32	75	-1	5	-3	0	0	7.94	9
K3	0	*	0	0	0	*	*	*	*	*	0	0
K4	30	5.0	98.84	9.09	50	0	5	-2	0	0	3.94	8
L3	0	*	0	0	0	*	*	*	*	*	0	0
L4	20	5.0	63.40	5.94	60	2	5	-2	3	2	3.94	8
M2	0	*	0	0	0	*	*	*	*	*	0	0
M3	0	*	0	0	0	*	*	*	*	*	0	0
Mean	14	5	40	5	51	0	4	-3	0	1	11	6
Min	0	5	0	0	0	-3	-6	-7	-6	-3	0	0
Max	30	5	99	25	90	3	5	-1	3	3	65	10
Stdev	11	0	31	7	37	2	3	2	3	2	17	4

Appendix 6.
Geomorphic landform classification.

Table 6.1: Sample identity belonging to each landform type on Tomdachoille Island SSSI. Landforms were defined and mapped by field mapping and aerial photograph interpretation.

1	2	3		4	5		6
Backwater	Abandoned channel	Point bar		Abandoned point bar	Floodplain		Embankment
J4	G5	B7	E9	I7	B4	C4	J9
K3	G6	B8	E11	I8	B5	D1	K9
K4	G7	B9	E12	I9	B6	D2	L8
L3	G8	B10	F4	I10	C5	D3	M8
L4	G11	B11	F5	J5	D4	E1	
M2	G12	B12	F6	J6	E4	E2	
M3	H5	C6	F7	J7	I11	E3	
	H6	C7	F8	J8	I12	F1	
	H7	C8	F9	K5	J10	F2	
	H8	C9	F10	K6	J11	F3	
	H9	C10	F11	K7	J12	G1	
	H10	C11	F12	K8	K10	G2	
	H11	C12	G4	L5	K11	G3	
	H12	D5	G9	L6	K12	H1	
	I4	D6	G10	L7	L9	H2	
	I5	D7	H4	M4	L10	H3	
	I6	D8		M5	L11	I1	
		D9		M6	L12	I2	
		D10		M7	M9	I3	
		D11			M10	J1	
		E10			M11	J2	
		D12			M12	J3	
		E5			B1	K1	
		E6			B2	K2	
		E7			B3	L1	
		E8			C1	L2	
					C2	M1	
					C3		

Appendix 7.

Diversity analysis, Tomdachoille.

Table 7.1: Biodiversity and pedodiversity analysis on Tomdachoille Island SSSI. The index is calculated by the number of samples occurring within a given group. N= number of observations; S= 'species' richness; H' max= maximum negentropy; H' = negentropy (Shannon) index; J= evenness (Equitability) index.

Plant community	Soil types								Pedodiversity indices							
	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6	Gp 7	Gp 8	N	S	H'max	H'	J			
SHhr	4	1	3	0	0	4	1	0	13	5	1.6	1.5	0.9			
W23a	1	0	0	2	2	2	1	0	8	5	1.6	1.6	1.0			
W23	1	0	0	0	0	4	2	0	7	3	1.1	1.0	0.9			
MG1e	0	0	0	2	12	2	0	0	16	3	1.1	0.7	0.7			
U4b	0	0	0	5	2	0	1	0	8	3	1.1	0.9	0.8			
W11d	0	0	0	20	6	0	0	0	26	2	0.7	0.5	0.8			
W7c	0	0	0	3	1	0	1	1	6	4	1.4	1.2	0.9			
W6	5	3	1	0	0	0	0	0	9	3	1.1	0.9	0.9			
W7a	2	0	0	0	2	5	12	8	29	5	1.6	1.4	0.9			
M23	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0			
SHscb	10	1	1	0	0	0	0	0	12	3	1.1	0.6	0.5			
SHpc	3	0	2	0	0	0	0	0	5	2	0.7	0.7	1.0			
S22a	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0			
N	26	5	7	32	25	17	18	9								
S	7	3	4	5	6	5	6	2								
H'max	1.9	1.1	1.4	1.6	1.8	1.6	1.8	0.7								
H'	1.7	1.0	1.3	1.2	1.4	1.5	1.2	0.3								
J	0.9	0.9	0.9	0.7	0.8	1.0	0.6	0.5								

Table 7.2: Biodiversity and geodiversity analysis on Tomdachoille Island SSSI. The index is calculated by the number of samples occurring within a given group. N= number of observations; S= 'species' richness; H' max= maximum negentropy; H' = negentropy (Shannon) index; J= evenness (Equitability) index.

	Plant community	Landform					Geodiversity indices					
		Floodplain	Point bar	Backwater	Abandoned channel	Abandoned point bar	Embankment	N	S	H'max	H'	J
Plant community	SHhr	0	2	0	0	10	1	13	3	1.1	0.7	0.6
	W23a	3	2	0	0	0	3	8	3	1.1	1.1	1.0
	W23	0	2	0	2	2	1	7	4	1.4	1.4	1.0
	MG1e	15	0	0	0	0	1	16	2	0.7	0.2	0.3
	U4b	8	0	0	0	0	0	8	1	0.0	0.0	0.0
	W11d	26	0	0	0	0	0	26	1	0.0	0.0	0.0
	W7c	3	1	0	1	1	0	6	4	1.4	1.2	0.9
	W6	0	8	0	1	0	0	9	2	0.7	0.3	0.5
	W7a	0	9	1	18	1	0	29	4	1.4	0.9	0.6
	M23	0	0	1	0	0	0	1	1	0.0	0.0	0.0
	SHscb	0	12	0	0	0	0	12	1	0.0	0.0	0.0
	SHpc	0	5	0	0	0	0	5	1	0.0	0.0	0.0
	S22a	0	0	3	0	0	0	3	1	0.0	0.0	0.0
	N	55	41	5	22	14	6					
	S	5	8	3	4	3	4					
	H'max	1.6	2.1	1.1	1.4	1.1	1.4					
	H'	1.3	1.8	1.0	0.7	0.9	1.2					
	J	0.8	0.9	0.9	0.5	0.8	0.9					

Table 7.3: Geodiversity and pedodiversity analysis on Tomdachoille Island SSSI. The index is calculated by the number of samples occurring within a given group. N= number of observations; S= 'species' richness; H' max= maximum negentropy; H' = negentropy (Shannon) index; J= evenness (Equitability) index.

	Landform				Geodiversity indices							
	Soil type	Floodplain	Point bar	Backwater	Abandoned channel	Abandoned point bar	Embankment	N	S	H' max	H'	J
Soil type	Gp 1	0	22	0	1	3	0	26	3	1.1	0.5	0.5
	Gp 2	0	5	0	0	0	0	5	1	0.0	0.0	0.0
	Gp 3	0	4	0	0	3	0	7	2	0.7	0.7	1.0
	Gp 4	30	0	0	0	0	2	32	2	0.7	0.2	0.3
	Gp 5	20	1	0	2	0	1	24	4	1.4	0.6	0.5
	Gp 6	4	1	0	4	6	3	18	5	1.6	1.5	0.9
	Gp 7	1	5	0	9	2	0	17	4	1.4	1.1	0.8
	Gp 8	0	3	6	6	0	0	15	3	1.1	1.1	1.0
Pedodiversity indices	N	55	41	6	22	14	6					
	S	4	7	1	5	4	3					
	H' max	1.4	1.9	0.0	1.6	1.4	1.1					
	H'	1.0	1.4	0.0	1.4	1.3	1.0					
	J	0.7	0.7	0.0	0.9	0.9	0.9					

Table 7.4: Biodiversity calculations along transects showing variation (a) perpendicular and (b) parallel to the main channel.

Transect	Plant community											Diversity indices						
	SHhr	W23a	W23	MG1e	U4b	W11d	W7c	W6	W7a	M23	SHscb	SHpc	S22a	N	S	H'	H'max	J
B	0	0	0	0	3	3	0	0	0	0	3	3	0	12	4	1.4	1.4	1.0
C	0	0	0	0	2	3	0	0	1	0	5	1	0	12	5	1.6	1.4	0.9
D	1	1	0	0	1	3	0	2	0	0	3	1	0	12	7	1.9	1.8	0.9
E	0	1	1	0	1	3	0	2	3	0	1	0	0	12	7	1.9	1.8	0.9
F	0	0	2	0	1	2	0	2	5	0	0	0	0	12	5	1.6	1.5	0.9
G	0	0	0	1	0	2	1	2	6	0	0	0	0	12	5	1.6	1.4	0.8
H	0	0	3	0	0	3	0	1	5	0	0	0	0	12	4	1.4	1.3	0.9
I	3	0	1	2	0	3	0	0	3	0	0	0	0	12	5	1.6	1.5	1.0
J	3	1	0	2	0	2	0	0	1	1	0	0	0	12	7	1.9	1.9	1.0
K	2	2	0	3	0	2	0	0	2	0	0	0	1	12	6	1.8	1.7	1.0
L	2	2	0	3	0	0	0	2	2	0	0	0	1	12	6	1.8	1.7	1.0
M	2	1	0	5	0	0	1	0	1	0	0	0	2	12	6	1.8	1.6	0.9

Transect	Plant community											Diversity indices						
	SHhr	W23a	W23	MG1e	U4b	W11d	W7c	W6	W7a	M23	SHscb	SHpc	S22a	N	S	H'	H'max	J
1	0	0	0	0	0	10	2	0	0	0	0	0	0	12	2	0.7	0.5	0.7
2	0	0	0	0	0	10	1	0	0	0	0	0	1	12	3	1.1	0.6	0.5
3	0	0	0	1	1	6	1	0	0	0	0	0	3	12	5	1.6	1.3	0.8
4	1	0	0	0	4	0	0	3	3	1	0	0	0	12	5	1.6	1.5	0.9
5	2	0	0	0	2	0	0	3	5	0	0	0	0	12	4	1.4	1.3	0.9
6	3	0	0	0	1	0	1	2	4	0	1	0	0	12	6	1.8	1.6	0.9
7	3	0	0	1	0	0	0	1	6	0	1	0	0	12	5	1.6	1.3	0.8
8	2	3	0	0	0	0	0	0	4	0	2	1	0	12	5	1.6	1.5	0.9
9	2	3	2	1	0	0	0	0	1	0	1	2	0	12	7	1.9	1.9	1.0
10	0	1	1	3	0	0	1	0	2	0	2	2	0	12	7	1.9	1.9	1.0
11	0	0	2	5	0	0	0	0	2	0	3	0	0	12	4	1.4	1.3	0.9
12	0	1	2	5	0	0	0	0	2	0	2	0	0	12	5	1.6	1.5	0.9

Table 7.5: Pedodiversity calculations along transects showing variation (a) perpendicular and (b) parallel to the main channel.

a)

Transect	Soil type								Diversity indices				
	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6	Gp 7	Gp 8	N	S	H'max	H'	J
B	3	1	2	3	2	0	1	0	12	6	1.8	1.7	1.0
C	7	0	0	4	1	0	0	0	12	3	1.1	0.9	0.8
D	7	0	1	4	0	0	0	0	12	3	1.1	0.9	0.8
E	2	2	0	4	0	1	2	0	11	5	1.6	1.5	0.9
F	1	1	0	3	0	0	5	2	12	5	1.6	1.4	0.9
G	1	0	1	3	1	0	3	3	12	6	1.8	1.7	0.9
H	1	0	0	2	2	4	3	0	12	5	1.6	1.5	0.9
I	0	1	0	1	4	2	2	2	12	6	1.8	1.7	0.9
J	1	0	0	1	4	3	1	2	12	6	1.8	1.6	0.9
K	0	0	2	1	4	3	0	2	12	5	1.6	1.5	0.9
L	1	0	0	3	3	3	0	2	12	5	1.6	1.5	1.0
M	1	0	1	3	3	2	0	2	12	6	1.8	1.7	1.0

b)

Transect	Soil type								Diversity indices				
	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6	Gp 7	Gp 8	N	S	H'max	H'	J
1	0	0	0	9	3	0	0	0	12	2	0.7	0.6	0.8
2	0	0	0	8	3	0	0	1	12	3	1.1	0.8	0.8
3	0	0	0	8	1	0	0	3	12	3	1.1	0.8	0.8
4	2	1	1	3	0	1	1	3	12	7	1.9	1.8	0.9
5	3	2	0	1	2	2	0	2	12	6	1.8	1.7	1.0
6	3	1	2	0	2	0	3	1	12	6	1.8	1.7	1.0
7	3	0	1	0	0	3	5	0	12	4	1.4	1.3	0.9
8	2	0	2	2	1	3	1	1	12	7	1.9	1.9	1.0
9	3	0	0	0	2	3	3	1	12	5	1.6	1.5	1.0
10	3	0	1	0	2	3	1	2	12	6	1.8	1.7	1.0
11	3	1	0	0	4	2	2	0	12	5	1.6	1.5	0.9
12	3	1	0	1	4	1	1	1	12	7	1.9	1.7	0.9

Table 7.6: Geodiversity calculations along transects showing variation (a) perpendicular and (b) parallel to the main channel.

Transect	Landform				Diversity indices						
	Floodplain	Point bar	Back-water	Abandoned channel	Abandoned point bar	Embankment	N	S	H'max	H'	J
B	6	6	0	0	0	0	12	2	0.7	0.7	0.0
C	5	7	0	0	0	0	12	2	0.7	0.7	1.0
D	4	8	0	0	0	0	12	2	0.7	0.6	1.0
E	4	8	0	0	0	0	12	2	0.7	0.6	0.9
F	3	7	0	2	0	0	12	3	1.1	1.0	0.9
G	3	2	0	7	0	0	12	3	1.1	1.0	0.9
H	3	1	0	6	2	0	12	4	1.4	1.2	0.9
I	5	1	0	3	2	1	12	5	1.6	1.4	0.9
J	5	1	1	1	3	1	12	6	1.8	1.5	0.9
K	6	0	2	1	2	1	12	5	1.6	1.4	0.9
L	6	0	1	1	3	1	12	5	1.6	1.3	0.8
M	5	0	2	1	2	2	12	5	1.6	1.5	0.8

Transect	Landform				Diversity indices						
	Floodplain	Point bar	Back-water	Abandoned channel	Abandoned point bar	Embankment	N	S	H'max	H'	J
1	12	0	0	0	0	0	12	1	0.0	0.0	0.0
2	11	0	1	0	0	0	12	2	0.7	0.3	0.4
3	8	1	3	0	0	0	12	3	1.1	0.8	0.4
4	4	4	2	2	0	0	12	4	1.4	1.3	0.8
5	2	3	0	5	2	0	12	4	1.4	1.3	1.0
6	1	4	0	3	4	0	12	4	1.4	1.3	0.9
7	0	5	0	3	3	1	12	4	1.4	1.3	0.9
8	0	5	0	2	2	3	12	4	1.4	1.3	0.9
9	3	6	0	1	1	1	12	5	1.6	1.3	0.9
10	4	5	0	2	0	1	12	4	1.4	1.2	0.8
11	5	4	0	2	1	0	12	4	1.4	1.2	0.9
12	5	4	0	2	1	0	12	4	1.4	1.2	0.9

Appendix 8.
Species unique to landform units on Tomdachoille Island SSSI.

Table 8.1: Plant species identified within the Tomdachoille study area showing their distribution within the geomorphic land units. The rarity of each species within Perthshire is indicated, data on frequency was acquired from Smith *et al.* (1992).

		Backwater	Abandoned channel	Point bar	Abandoned point bar	Floodplain	Embankment	Total	Frequency
<i>Acer pseudoplatanus</i>	Sycamore	*	*	*	*	*	*	5	C
<i>Achillea millefolium</i>	Yarrow	*	*	*	*	*	*	5	VC
<i>Aegopodium podagraria</i>	Ground elder	*			*			2	F
<i>Agrostis capillaris</i>	Common bent		*					2	VC
<i>Agrostis stolonifera</i>	Creeping bent	*				*		2	C
<i>Ajuga reptans</i>	Bugle	*		*	*	*	*	4	C
<i>Alchemilla vulgaris</i>	Lady's mantle				*			1	C
<i>Alliaria petiolata</i>	Garlic mustard		*					1	O
<i>Allium ursinum</i>	Ramsons		*		*			2	F
<i>Alnus glutinosa</i>	Alder	*	*	*	*	*	*	6	C
<i>Amanita phalloides</i>	Death cap				*			1	
<i>Anemone nemorosa</i>	Wood anemone	*			*			2	VC
<i>Angelica sylvestris</i>	Wild angelica			*	*	*	*	3	VC
<i>Anthoxanthum odoratum</i>	Sweet vernal grass	*		*	*	*	*	4	VC
<i>Anthriscus sylvestris</i>	Cow parsley	*			*			2	F
<i>Anthyllis vulneria</i>	Kidney vetch			*				1	O
<i>Aquilegia vulgaris</i>	Comlumbine	*						1	R a
<i>Arrhenathrum elatius</i>	False oat grass	*	*	*	*	*	*	5	C
<i>Barbarea vulgaris</i>	Common winter cress		*					1	O
<i>Bellis perennis</i>	Daisy		*		*			2	VC
<i>Betula pendula</i>	Silver birch	*	*	*	*	*	*	5	VC
<i>Betula pubescens</i>	downy birch	*	*	*	*	*	*	4	VC
<i>Brizia media</i>	Quaking grass			*	*			2	F
<i>Bromus arvensis</i>	Field brome			*	*			1	O
<i>Bromus diandrus</i>	Great brome	*		*	*	*	*	4	O
<i>Calamagrostis canescens</i>	Purple small reed	*						1	VR
<i>Calliergon cuspidatum</i>		*						1	
<i>Callitriche stagnalis</i>	Common water starwort	*						1	F
<i>Calluna vulgaris</i>	Heather	*		*	*	*	*	3	VC
<i>Campanula rotundifolia</i>	Harebell	*		*	*	*	*	4	C
<i>Cardamine hirsuta</i>	Hairy bittercress	*						1	F
<i>Cardamine pratensis</i>	Cuckoo flower	*				*		2	VC
<i>Carex echinata</i>	Star sedge	*	*					2	VC
<i>Carex flacca</i>	Glaucous sedge					*		1	C
<i>Carex pallescens</i>	Pale sedge	*						1	F
<i>Carex panicea</i>	Carnation sedge				*			1	VC
<i>Carex remota</i>	Remote sedge	*						1	F
<i>Carex rostrata</i>	Bottle sedge	*						1	C
<i>Carex sylvatica</i>	Wood sedge				*			1	F
<i>Carex vesicaria</i>	Bladder sedge	*						1	O
<i>Centaurea nigra</i>	Common knapweed	*	*	*	*	*	*	6	VC
<i>Cerastium holosteoides</i>	Common mouse ear			*	*	*	*	1	VC
<i>Chrysanthemum leucanthemum</i>	Ox eye daisy	*	*	*	*	*	*	4	F
<i>Chrysanthemum parthenium</i>	Feverfew		*	*				2	O
<i>Chrysosplenium alternifolium</i>	Alternate-leaved golden saxifrage	*						1	O
<i>Circaea lutetiana</i>	Common enchanter's nightshade	*				*		2	F
<i>Cirsium eriophorum</i>	Woolly thistle				*			1	O
<i>Cirsium heterophyllum</i>	Melancholy thistle				*			1	F b
<i>Cirsium vulgare</i>	Spear thistle	*	*	*	*	*	*	4	C
<i>Cladonia ochrochlora</i>	Cladonia		*	*				2	
<i>Climacium dendrioides</i>		*						1	
<i>Conopodium majus</i>	Pignut	*			*			2	C
<i>Corylus avellana</i>	Hazel				*			1	C
<i>Crepis biennis</i>	Rough hawk's-beard				*			1	O
<i>Crepis paludos</i>	Marsh hawk's-beard	*						1	C
<i>Crepis vesicaria</i>	Beaked hawk's-beard	*			*			2	O
<i>Cretaceous monogyna</i>	Hawthorne			*	*			2	C

		Backwater	Abandoned channel	Point bar	Abandoned point bar	Floodplain	Embankment	Total	Frequency
<i>Dactylis glomerata</i>	Cocksfoot	*		*	*	*	*	4	C
<i>Dactylorhiza fuchsii</i>	Common spotted orchid		*	*	*			2	F
<i>Deschampsia cespitosa</i>	Tufted hair grass	*		*	*	*	*	4	VC
<i>Deschampsia flexuosa</i>	Wavy hair grass			*	*			2	VC
<i>Dianthus deltoides</i>	Maiden pink			*				1	R
<i>Dicranum scoparium</i>		*	*	*	*			4	
<i>Digitalis purpurea</i>	Foxglove	*	*	*	*	*	*	5	VC
<i>Dryopteris dilatata</i>	Broad buckler fern	*						1	VC
<i>Epilobium montanum</i>	Broad-leaved willowherb	*	*			*		3	C
<i>Equisetum arvense</i>	Field horsetail	*						1	C
<i>Equisetum fluviatile</i>	Water horsetail	*						1	C
<i>Equisetum palustre</i>	Marsh horsetail	*	*					2	F
<i>Equisetum pratense</i>	Shady horsetail	*						1	O
<i>Euphrasia nemorosa</i>	Eyebright			*				1	VR
<i>Fagus sylvatica</i>	Beech	*	*	*	*	*	*	4	F
<i>Festuca ovina</i>	Sheep's fescue			*	*	*	*	3	VC
<i>Festuca rubra</i>	Red fescue	*	*	*	*	*	*	5	VC
<i>Festuca vivipara</i>	Viviparous fescue				*	*		1	F
<i>Filipendula ulmaria</i>	Meadowsweet	*	*	*	*	*	*	5	VC
<i>Fragaria vesca</i>	Wild strawberry	*		*	*	*	*	2	O
<i>Fraxinus excelsior</i>	Ash	*	*	*	*	*	*	4	C
<i>Galium aparine</i>	Cleavers	*	*	*	*	*	*	4	C
<i>Galium boreale</i>	Northern bedstraw	*		*	*	*	*	2	F
<i>Galium cruciata</i>	Crosswort	*		*	*	*	*	3	F
<i>Galium palustre</i>	Marsh bedstraw	*						1	C
<i>Galium saxatile</i>	Heath bedstraw		*	*	*	*	*	2	VC
<i>Galium verum</i>	Lady's bedstraw	*	*	*	*	*	*	4	C
<i>Geranium robertianum</i>	Herb robert	*	*	*	*	*	*	4	C
<i>Geranium sylvaticum</i>	Wood cranesbill	*		*	*	*	*	2	C
<i>Geum rivale</i>	Water avens	*	*	*	*	*	*	3	C
<i>Geum urbanum</i>	Herb bennet	*	*	*	*	*	*	2	C
<i>Glyceria fluitans</i>	Floating sweet grass	*	*	*	*	*	*	2	F
<i>Glyceria maxima</i>	Reed sweet grass	*		*	*	*	*	2	O
<i>Helianthemum chamaecistus</i>	Common rockrose			*	*	*	*	2	O
<i>Heracleum sphondylium</i>	Hogweed	*	*	*	*	*	*	2	C
<i>Hesperis matronalis</i>	Dame's violet	*	*	*	*	*	*	2	O
<i>Hieracium perpropinquum</i>	Hawkweed			*	*	*	*	1	R
<i>Holcus lanatus</i>	Yorkshire fog	*	*	*	*	*	*	5	VC
<i>Holcus mollis</i>	Creeping soft grass	*	*	*	*	*	*	4	VC
<i>Hyacinthoides non-serotus</i>	Bluebell	*	*	*	*	*	*	2	C
<i>Hylocomium lanatum</i>		*	*	*	*	*	*	1	
<i>Hylocomium splendens</i>		*	*	*	*	*	*	5	
<i>Hypericum hirsutum</i>	Hairy St. John's wort		*	*	*	*	*	2	O
<i>Hypericum humifusum</i>	Trailing St. John's wort	*	*	*	*	*	*	2	O
<i>Hypericum maculatum</i>	Imperforate St. John's wort	*	*	*	*	*	*	2	O
<i>Hypericum perforatum</i>	Perforate St. John's wort	*	*	*	*	*	*	4	O
<i>Hypericum pulchrum</i>	Slender St. John's wort	*	*	*	*	*	*	2	VC
<i>Hypericum cupressiforme</i>		*	*	*	*	*	*	1	
<i>Hypochoeris radicata</i>	Common cat's ear			*	*	*	*	2	C
<i>Impatiens glandulifera</i>	Himalayan balsam	*	*	*	*	*	*	5	O
<i>Iris pseudocorus</i>	Yellow flag	*	*	*	*	*	*	1	F
<i>Isoetes myurum</i>		*	*	*	*	*	*	2	
<i>Juncus articulatus</i>	jointed rush	*	*	*	*	*	*	1	C
<i>Juncus bulbosus</i>	Bulbous rush	*	*	*	*	*	*	1	C
<i>Juncus conglomeratus</i>	Compact rush	*	*	*	*	*	*	2	C
<i>Juncus effusus</i>	Soft rush	*	*	*	*	*	*	3	VC
<i>Juncus inflexus</i>	hard rush	*	*	*	*	*	*	1	O
<i>Knautia arvensis</i>	Field scabious		*	*	*	*	*	2	O
<i>Lactarius rufus</i>	Rufus milk cap			*	*	*	*	1	
<i>Lathyrus pratensis</i>	Meadow vetchling			*	*	*	*	1	C
<i>Lepidium heterophyllum</i>	Smith's pepperwort	*	*	*	*	*	*	4	O
<i>Lepilata procera</i>			*	*	*	*	*	1	O
<i>Linaria repens</i>	Pale toadflax		*	*	*	*	*	2	O
<i>Lotus corniculatus</i>	Common birdsfoot trefoil	*	*	*	*	*	*	3	C
<i>Lotus pendiculatus</i>	Greater birdsfoot trefoil			*	*	*	*	1	O

		Backwater	Abandoned channel	Point bar	Abandoned point bar	Floodplain	Embankment	Total	Frequency
<i>Lupinus polyphyllus</i>	Garden lupin	*		*	*			3	O
<i>Luzula campestris</i>	Filed woodrush				*			1	C
<i>Luzula sylvatica</i>	Great woodrush	*		*	*			3	VC
<i>Lysimachia nemorum</i>	Yellow pimpernel	*		*				2	C
<i>Malus sylvestris</i>	Crab apple					*		1	O
<i>Meconopsis cambrica</i>	Welsh poppy		*					1	O d
<i>Medicago lupulina</i>	Black medic				*			1	O
<i>Mentha aquatica</i>	Water mint	*	*					2	F
<i>Mentha piperita</i>	Spear mint	*						1	R
<i>Mercurialis perennis</i>	Dog's mercury	*	*		*			2	C
<i>Mimulus guttatus</i>	Monkey flower	*	*	*				3	O
<i>Mnium hybrida</i>	Fine-leaved sandwort				*	*		2	O
<i>Mnium hornum</i>		*						1	
<i>Myosotis arvensis</i>	Filed forget-me-not		*	*	*	*	*	4	F
<i>Myosotis scorpioides</i>	Water forget-me-not	*	*	*	*	*	*	5	F
<i>Myosotis sylvatica</i>	Wood forget-me-not				*	*		2	R
<i>Nardus stricta</i>	Mat grass				*	*		1	VC
<i>Ononis repens</i>	Rest harrow	*	*	*	*	*	*	5	O
<i>Oxalis acetosella</i>	Wood sorrel	*			*			2	VC
<i>Parmelina saxatilis</i>					*			1	
<i>Parmelia sinuosa</i>					*			1	
<i>Pezizites albus</i>	White butterbur	*						1	O*
<i>Phalaris arundinacea</i>	Reed canary grass	*	*	*	*	*	*	5	C
<i>Pilosella officinarum</i>	Mouse-ear hawkweed	*		*	*			3	R
<i>Pimpinella saxifraga</i>	Burnet saxifrage			*				1	O
<i>Pinus sylvestris</i>	Scots pine			*				1	O
<i>Plagiommium rostratum</i>		*			*			2	
<i>Plagiommium undulatum</i>		*		*	*	*	*	4	
<i>Plantago lanceolata</i>	Ribwort plantain	*	*	*	*	*	*	6	VC
<i>Poa annua</i>	Annual meadow grass					*		1	VC
<i>Poa nemoralis</i>	Wood meadow grass	*			*			2	F
<i>Poa pratensis</i>	Smooth meadow grass	*		*	*	*	*	4	C
<i>Poa subcaerulea</i>	Spreading meadow grass	*			*	*	*	2	VR
<i>Poa trivialis</i>	Rough meadow grass	*		*	*	*	*	4	C
<i>Polygala vulgaris</i>	Common milkwort				*			1	O
<i>Polygonum viviparum</i>	Alpine bistort			*	*			2	F
<i>Polystichum aculeatum</i>	Hard shield fern			*				1	F
<i>Potentilla anserina</i>	Silverweed	*	*	*				3	F
<i>Potentilla argentea</i>	Hoary cinquefoil		*	*				2	O
<i>Potentilla erecta</i>	Tormentil	*			*			2	VC
<i>Potentilla sterilis</i>	Barren strawberry	*		*	*			3	F
<i>Primula veris</i>	Cowslip	*		*	*	*	*	4	O e
<i>Primula vulgaris</i>	Primrose				*			1	C
<i>Prunella vulgaris</i>	Self heal	*	*					2	C
<i>Prunus avium</i>	Wild cherry	*						1	O
<i>Prunus padus</i>	Bird cherry		*	*				2	F
<i>Prunus spinosa</i>	Blackthorn		*					1	F
<i>Pseudoscleropodium purum</i>			*	*				2	
<i>Pulicaria dysenterica</i>	Common fleabane	*		*	*			1	O
<i>Quercus robur</i>	Pedunculate oak	*		*	*			3	F
<i>Racomitrium canescens</i>		*	*	*	*			3	VR f
<i>Ranunculus acris</i>	Meadow buttercup	*	*	*	*			3	VC
<i>Ranunculus ficaria</i>	Lesser celandine	*			*			2	C
<i>Ranunculus flammula</i>	Lesser spearwort	*	*					2	C
<i>Ranunculus lingua</i>	Greater spearwort	*						1	R
<i>Ranunculus repens</i>	Creeping buttercup	*	*	*	*			3	VC
<i>Ranunculus sceleratus</i>	Celery-leaved buttercup	*						1	O
<i>Rhianthus minor</i>	Yellow rattle	*	*	*	*			4	F
<i>Rhodobryum roseum</i>					*			1	
<i>Rhynchospora alba</i>					*			1	
<i>Rhynchospora squarrosus</i>		*		*	*	*		4	
<i>Rhynchospora triquetrus</i>			*	*	*			2	
<i>Rorippa nasturtium-aquaticum</i>	Watercress	*						1	R
<i>Rosa canina</i>	Dog rose	*						1	O
<i>Rosa rubiginosa</i>	Sweet briar	*	*	*	*	*	*	4	O

		Backwater	Abandoned channel	Point bar	Abandoned point bar	Floodplain	Embankment	Total	Frequency
<i>Rosa tomentosa</i>	Downy rose		*	*	*			1	C
<i>Rubus fruticosus</i>	Blackberry	*	*	*	*	*	*	6	C
<i>Rubus idaeus</i>	Raspberry	*	*	*	*	*	*	6	C
<i>Rumex acetosa</i>	Common sorrel		*	*	*	*	*	4	VC
<i>Rumex acetosella</i>	Sheep's sorrel	*	*	*	*			4	C
<i>Rumex obtusifolius</i>	Broad-leaved dock	*	*		*			3	C
<i>Rumex sanguineus</i>	Wood dock				*			1	O
<i>Russula mairei</i>	Beechwood sickner				*			1	
<i>Salix aurita</i>	Eared willow		*	*				2	C
<i>Salix caprea</i>	Goat willow		*		*			2	C
<i>Salix cinerea ssp oleifolia</i>	Grey willow	*	*	*	*			4	C
<i>Salix purpurea</i>	Purple willow	*						1	O
<i>Salix viminalis</i>	Osier	*						1	O
<i>Salix myrsinifolia</i>	Dark-leaved willow	*	*	*	*	*	*	6	O
<i>Salix tetrapla</i>	(hybrid) <i>S. myrsinifolia x phyticifolia</i>	*	*					2	R
<i>Sambucus nigra</i>	Elder	*	*		*			3	F
<i>Sambucus racemosa</i>	Red-berried elder				*			1	O
<i>Sarothamnus scoparius</i>	Broom	*	*	*	*	*	*	5	C
<i>Sceleranthus annuus</i>	Annual knawel				*			1	O
<i>Scrophularia nodosa</i>	Common figwort	*						1	O
<i>Scutellaria galenculata</i>	Common skullcap				*			1	
<i>Senecio aquatious</i>	Marsh ragwort	*						1	O
<i>Senecio jacobaea</i>	Common ragwort		*	*	*	*	*	5	C
<i>Senecio viscosus</i>	Sticky groundsel		*					1	O
<i>Senecio vulgaris</i>	Groundsel		*					1	R
<i>Silene dioica</i>	Red campion	*			*	*	*	3	C
<i>Silene maritima</i>	Sea campion		*	*				2	R c
<i>Silene vulgaris</i>	Bladder campion	*	*	*				2	O
<i>Sinapis arvensis</i>	Charlock		*					1	O
<i>Solidago vigaurea</i>	Goldenrod	*	*					2	F
<i>Stachys sylvatica</i>	Hedge woundwort	*	*	*	*	*	*	4	C
<i>Stellaria graminac</i>	Lesser stitchwort	*	*	*	*	*	*	5	C
<i>Stellaria holostea</i>	Greater stitchwort				*	*	*	2	F
<i>Stellaria media</i>	Chickweed		*		*			2	C
<i>Succisa pratense</i>	Devilsbit scabious	*	*	*	*	*	*	3	VC
<i>Symphytum officinale</i>	Common comfrey	*		*				2	R g
<i>Taraxacum officinale</i>	Dandelion		*		*			2	C
<i>Teesdalia nudicaulis</i>	Shepherd's cress		*					1	R c
<i>Teucrium scorodonia</i>	Wood sage	*	*	*	*	*	*	5	C
<i>Thalictrum minus</i>	Lesser meadow rue	*	*	*	*	*	*	2	O e
<i>Thuidium tamarascinum</i>		*	*	*	*	*	*	4	
<i>Thymus drucei</i>	Wild thyme		*	*	*			3	C
<i>Thymus pulegioides</i>	Large thyme	*						1	O
<i>Tortilis japonica</i>	Hedge parsley					*		1	O
<i>Tortula ruraliformis</i>				*				1	
<i>Trifolium pratense</i>	Red clover	*		*				2	F
<i>Trifolium repens</i>	White clover	*	*	*	*	*	*	4	C
<i>Tussilago farfara</i>	Coltsfoot	*	*	*				3	F
<i>Ulex europaeus</i>	Gorse	*	*	*	*	*	*	5	C
<i>Urtica dioica</i>	Nettle	*	*			*		3	C
<i>Valaria officinalis</i>	Common valerian				*			1	C
<i>Veronica chamaedrys</i>	Germander speedwell	*	*	*	*	*	*	6	C
<i>Veronica officinalis</i>	Heath speedwell	*		*	*			3	C
<i>Vicia cracca</i>	Tufted vetch				*			1	F
<i>Vicia sativa</i>	Common vetch	*			*			2	O
<i>Viola riviniana</i>	Common dog violet	*	*	*	*	*	*	5	C
<i>Viola tricolor</i>	Wild pansy			*	*	*	*	3	O
Total number of species in each landform class		51	143	79	93	149	61		
Total number of species = 244									
a: Along River Tay									
b: Rare near River Tay									
c: Shingle islands of rivers Tay, Tummel and Garry									
d: Particularly on riverbanks									
e: Along rivers Tay, Tummel and Garry									
f: New record to Perthshire, 1997									
g: Only on Tomdachoille along R. Tummel									
* species thought not to be native to Perthshire									
o: pre-1970 record in the county									
VR: very rare									
R: rare									
O: occasional									
F: frequent									
C: common									
VC: very common									

Appendix 9.
Best sub-sets regression analysis for the Tomdachoille dataset.

Table 9.1: Results of best sub-sets regression analysis for the whole data set on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	Order of entry of variables	R ² (%)	p	
	Landform	Elevation (m)	Plant community	S	H'	J	Tree cover	Shrub cover	Tall herb cover	Herb cover	Moss cover	Soil group	Soil depth	pH	SMC	Shingle	Mean	MAX-DOM	MOD-OM	MED-OM	Range	Heterogeneity				
Plant community	-					-	+	-				+	+			+								2, 6, 7, 8, 13, 16, 12	52.3	***
S	-		+						+	+			+		-									3, 9, 10, 15, 16, 1, 13	31.5	***
H'		+	+	+						+	+										+			3, 2, 4, 10, 11	72.1	***
J		+	+	-	+		-												-	+				3, 2, 5, 4, 10, 19, 20, 7	85.4	***
Tree cover	-											-							+					2, 1, 18, 12	46.1	***
Shrub cover	+																							1, 14	96.5	*
Tall herb cover		+											+											2, 13, 17, 22	51.8	***
Herb cover	+	+										-								-				2, 1, 19, 21, 12	64.9	***
Moss cover	+																							1	25.9	***
Soil group													-									+		13, 21	99.8	*

Table 9.2: Results of best sub-sets regression analysis within the backwater landform on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * p<0.05; ** p<0.01; *** p<0.001.

	S	Tree cover	Soil depth	Order of entry of variables	R ² (%)	p
	(1)	(2)	(3)			
Plant community	-	-	-	1, 2, 3	100	***

Table 9.3: Results of best sub-sets regression analysis within the abandoned channel landform on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * p<0.05; ** p<0.01; *** p<0.001.

	S	H'max	Tree cover	Shrub cover	Tall herb cover	Soil depth	Order of entry of variables	R ² (%)	p
	(1)	(2)	(3)	(4)	(5)	(6)			
Plant community	-	+	+	-	-	(6)	2, 1, 3, 5	80.7	***
S				+			4	97.7	***
H					+		6	80.1	**
J	-		+	+			1, 3, 4	100	***
Tree cover						+	6	81.9	**
Tall herb cover						+	6	88.1	**
Herb cover					+	+	6	80.1	**

Table 9.4: Results of best sub-sets regression analysis within the point bar landform on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * p<0.05; ** p<0.01; *** p<0.001.

	Plant community	J	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover	Mean	MAX-DOM	MOD-OM	MED-OM	Range	CG	ST	Order of entry of variables	R ² (%)	p
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)			
Plant community		+			-		-	-	+	-			+		2, 5, 7, 8, 9, 10, 13	76.7	***
S	-			-		+									1, 6, 4	68.3	**
H'			+			+						+			3, 12, 6	82.7	***
J			+			+						+			3, 6, 12	72.6	**
Tall herb cover														+	14	29.5	*
Moss cover											+		+		11, 12, 13	90.1	***
Soil group								-			+	-	+		8, 11, 12	81.9	***

CG = coarse gravel; ST = silt.

Table 9.5: Results of best sub-sets regression analysis within the abandoned point bar landform on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)	Order of entry of variables	R ² (%)	p	
	Elevation (m)	Plant community	S	H	J	TSR	Tree cover	Tall herb cover	Herb cover	Moss cover	Soil group	Soil depth	SMC	Mean	MAXDOM	MINDOM	MODOM	MEDOM	Range	Heterogeneity	CG	MG	FG	ST				
Plant community	-						+								+													
S							-	+			+					+		-								1, 7, 15	78.9	***
H'																										7, 8, 11, 16, 17	66.5	***
J					+			-																		5, 3, 8	88.9	***
Tree cover	-																									2, 4, 3, 7	80.4	***
Shrub cover													+													1, 13, 19	85.5	**
Tall herb cover																							+			20, 23	29.9	**
Herb cover																								+		2, 24	45.9	***
Moss cover																										15, 19, 22	32.2	**
Soil group																							+			2, 18, 23	41.4	***
																										12, 13, 19	82.3	*

CG = coarse gravel; MG = medium gravel; FG = fine gravel; ST = silt.

Table 9.6: Results of best sub-sets regression analysis within the floodplain landform on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * p<0.05; ** p<0.01, *** p<0.001.

	Elevation (m)	S	H'	J	Tree cover	Shrub cover	Tall herb cover	Soil depth	OMC	MAX-DOM	MIN-DOM	MOD-OM	BR	SC	FG	Order of entry of variables	R ² (%)	p
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)			
Plant community		-	+	-	-	-	+	+								3, 4, 2, 7, 6, 8	82.5	***
S						-	-		+						+	6, 9, 15	65.4	*
H'	+	+														1, 2	54.7	**
J	+				-	+										1, 5, 6	53.6	**
Tree cover	-									+						1, 10	56.7	**
Tall herb cover								+								8	35.3	**
Herb cover											+		+			11, 13	43.6	*
Soil group					+											5, 12, 14	82.3	***

BR = boulders; SC = small cobbles; FG = fine gravel.

Table 9.7: Results of best sub-sets regression analysis within the embankment landform on Tomdachoille Island SSSI. Showing the independent variables having a significant influence on the environmental variables and diversity indices. The direction of the relationship is indicated by + for positive and - for negative. * p<0.05; ** p<0.01, *** p<0.001.

	Elevation (m)	S	Tree cover	Shrub cover	Tall herb cover	Soil group	Soil depth	pH	OMC	MAX-DOM	MOD-OM	Range	Heterogeneity	Order of entry of variables	R ² (%)	p
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)			
S								-						4, 8	99.8	*
H'		+												2	98.7	**
J		+	+		-	-								2, 3, 4, 6	62.4	***
Tree cover												-		6, 12, 7	22	**
Shrub cover										+		+		10, 12, 13, 8	34.1	***
Tall herb cover	+								-		+			1, 11, 9	24.4	**
Herb cover						-	+							6, 7	13.6	*

Appendix 10.
Floristic tables of species data from the Ballinluig dataset.

Table 10.1: TWINSpan end group 1, SHpc community

Code	Environmental variable	GB1	GB2	GB3	GB4	GB5	GB6	GB7	GB8	GB9	GB10
4	Elevation (m)	2.13	2.54	1.63	1.01	1.00	1.00	1.87	1.14	0.01	0.00
7	Soil depth (cm)	0	0	0	0	0	0	0	0	0	0
10	Shrub height (m)	1	1		1	1		2	1	2	1
11	Herb height (cm)	15	40	35	20	37	30	40	32	50	25
12	Moss height (mm)		3	3	3	3	4	4	4	3	
14	Shrub cover (%)	2	5		5	2		2	5	5	1
15	Herb cover (%)	20	25	95	5	20	2	50	10	25	5
16	Moss cover (%)		10	20	10	5	5	30	5	5	
21	Bare shingle (%)	100	95	2	95	100	10	30	10	50	80
22	Bare soil (including sand) (%)	0	0	3	2	0	0	30	0	45	0
23	Open water (%)	0	0	0	0	0	0	0	20	20	0
34	SMC (%)							5		9	
35	SOMC (%)							1		1	
38	Soil particle size range						7	94	3	94	
39	MODOM							5		5	
51	Litter (%)	2	0	2	0	2	0	3	0	5	0
52	CWD (%)	5	20	5	2	3	2	5	2	5	3
	Species name										
1239	<i>Senecio jacobaea</i>	1	4	2	3	3	2	4	3	3	4 V
391	<i>Chamerion angustifolium</i>	4	3	3	1	2		3	3	2	3 V
1256	<i>Silene uniflora</i>	1	3	8	3	3		6	1	2	2 V
708	<i>Impatiens glandulifera</i>			3	2	2	2	2	2	3	2 IV
1225	<i>Sedum acre</i>		3	4	3	2	1	4	2	1	IV
1321	<i>Teucrium scorodonia</i>			2		3	1	3	2	3	2 IV
574	<i>Festuca ovina</i>	1		3			1		1	2	1 III
1179	<i>Salix repens</i> agg.		3	4	2	2			4		2 III
1254	<i>Silene dioica</i>	2		1				2	1	2	3 III
1296	<i>Stellaria graminea</i>			1			1	1		1	1 III
1368	<i>Urtica dioica</i>	2			1			3	2	1	2 III
1939	<i>Rhytidadelphus loreus</i>		1	3			1	3	1	2	III
419	<i>Cirsium vulgare</i>			2				3		2	1 II
1761	<i>Hylocomium splendens</i>		1	4				1		2	II
1928	<i>Racomitrium canescens</i>		4		4	4	4				II
482	<i>Digitalis purpurea</i>			2						2	1 II
630	<i>Geranium robertianum</i>		1			1				1	II
680	<i>Holcus lanatus</i>			3	2					1	II
973	<i>Plantago lanceolata</i>					1	1			2	II
1118	<i>Rorippa nasturtium-aquaticum</i>	2						1		2	II
1175	<i>Salix myrsinifolia</i>		1	3		1					II
104	<i>Achillea millefolium</i>						2			2	I
127	<i>Ajuga reptans</i>			2						2	I
171	<i>Anthoxanthum odoratum</i>		1						1		I
1095	<i>Ranunculus repens</i>			2						2	I
1140	<i>Rumex acetosella</i>			2						1	I
1220	<i>Scrophularia nodosa</i>					1					I
1242	<i>Senecio viscosus</i>		4						1		I
1350	<i>Trifolium repens</i>							1		1	I
1429	<i>Viola riviniana</i>									1	I
2601	<i>Acer pseudoplatanus</i> (g)						3				I
2764	<i>Rubus idaeus</i> (g)			1						1	I
403	<i>Chrysanthemum leucanthemum</i>									2	I
583	<i>Filipendula ulmaria</i>									2	I
662	<i>Hesperis matronalis</i>	1									I
701	<i>Hypericum perforatum</i>									4	I
822	<i>Anchusa arvensis</i>							2			I
855	<i>Mentha aquatica</i>									1	I
868	<i>Mimulus guttatus</i>									3	I
889	<i>Myosotis scorpioides</i>									1	I
914	<i>Ononis repens</i>						1				I
1043	<i>Potentilla anserina</i>			2							I
1088	<i>Ranunculus ficaria</i>			1							I
1147	<i>Rumex obtusifolius</i>										I
1169	<i>Salix cinerea</i> (s)			2				2			I
1308	<i>Symphytum officinale</i>			1							I
1349	<i>Trifolium pratense</i>										I
1396	<i>Veronica chamaedrys</i>									1	I
1432	<i>Viola tricolor</i>			1						3	I
2602	<i>Alnus glutinosa</i> (s)			3							I
2606	<i>Betula pendula</i> (s)	2									I
2613	<i>Fagus sylvatica</i> (g)		1								I
2633	<i>Sambucus nigra</i> (g)					1					I
3042	<i>Sarothamnus scoparius</i> (g)						2				I
	Number of species per sample	9	13	27	9	13	13	16	13	33	15
	Mean number of species	16.1									
	Standard error of the mean	2.461									

Table 10.3: TWINSpan end group 3, U4b community

Code	Environmental Variable	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
4	Elevation (m)	1.13	1.76	1.54	1.79	1.82	1.62	1.54	1.01	0.94	0.99
7	Soil depth (cm)	40	25	13	15	20	24	124	28	24	34
9	Tree height (m)										
11	Herb height (cm)	10	12	22	10	4	10	17	14	25	22
12	Moss height (mm)	3	5	3	3	2	4	4	3	5	4
13	Tree cover (%)	2	5	3	4	2	5	2	2	3	2
15	Herb cover (%)	30	30	30	60	80	40	25	20	40	15
16	Moss cover (%)	80	60	85	40	25	85	90	60	85	55
17	pH	5.0	5.4	5.0	4.7	4.9	5.0	4.8	5.2	5.3	5.0
21	Bare shingle (%)	0	0	0	5	5	0	0	2	2	0
22	Bare soil (including sand) (%)	0	2	0	3	2	0	2	3	0	0
23	Open water (%)	0	0	0	0	0	0	0	0	0	0
34	SOMC (%)	17	29	50	40	35	31	17	41	39	38
35	SOMC (%)	2	4	9	6	5	6	3	7	4	6
36	Tall herb height (cm)	70	75	82	55	50	63	93	105	107	106
37	Tall herb cover (%)	70	75	70	40	25	80	75	80	80	90
38	Range	794		794	794	794		794		794	794
39	MODOM	6	5	5	3	5	5	6	5	3	5
51	Litter (%)	2	0	3	5	0	5	3	0	0	0
52	CWD (%)	0	0	0	0	0	0	0	0	0	0
	Species name										
171	<i>Anthoxanthum odoratum</i>	2	4	2	3	2	3	4	3	4	4
613	<i>Galium verum</i>	4	3	1	3	3	5	4	4	5	2
914	<i>Ononis repens</i>	4	4	3	4	5	3	4	4	3	3
1761	<i>Hylocomium splendens</i>	4	7	8	4	5	4	4	7	4	6
1940	<i>Rhynchospora squarrosus</i>	8	4	4	4	3	8	8	4	1	5
237	<i>Betula pendula (c)</i>	1	2	2	2	2	1	2			1
574	<i>Festuca ovina</i>	8	8	6	8	6	8	8		5	7
576	<i>Festuca rubra</i>	6		7	4	5	4	4	8	6	5
680	<i>Holcus lanatus</i>		4	3	1	2	5	3	3	5	4
973	<i>Plantago lanceolata</i>	2	3	3	4	4	2		3	4	4
465	<i>Dactylis glomerata</i>	3	5	4		2		5	4	4	3
477	<i>Deschampsia cespitosa</i>	1	2	4	3	3	3		4		2
1296	<i>Stellaria graminea</i>	3	4	4		2	3		4	2	1
1321	<i>Teucrium scorodonia</i>	2	2	4	3			4	2	2	3
371	<i>Centaurea nigra</i>	4	3	1			2		3	5	5
655	<i>Helictotrichon pratense</i>	2	4	5		3			5	2	2
965	<i>Pilosella officinarum agg.</i>	3	5	4	5	2	2	2			1
1051	<i>Potentilla sterilis</i>			3	4	2		3	2	3	3
1106	<i>Rhinanthus minor</i>		2	1	3	1	2	1	2		1
1305	<i>Succisa pratensis</i>	4	4	2			4	2	2	4	1
1396	<i>Veronica chamaedrys</i>	3				2	3	3	4	4	3
104	<i>Achillea millefolium</i>	3	5	4	3		4	3			1
197	<i>Arrhenatherum elatius</i>	6	4				6	8		5	8
1333	<i>Thymus drucei</i>	3	2	2	2	5	2		1		1
1429	<i>Viola riviniana</i>	2	3		4	1	2	3			1
153	<i>Alnus glutinosa (c)</i>				1	1	2	2			2
403	<i>Chrysanthemum leucanthemum</i>			2	2				2	4	2
578	<i>Festuca vivipara</i>	4		5			3	1	4		1
971	<i>Pinus sylvestris (c)</i>		3	2	1				3		1
455	<i>Galium cruciatum</i>	1	2				2	4			1
1056	<i>Primula veris</i>		1					2		1	2
2776	<i>Euphrasia nemorosa</i>			3	3			2			3
288	<i>Campanula rotundifolia</i>		2					2			2
478	<i>Deschampsia flexuosa</i>			4	4						1
701	<i>Hypericum perforatum</i>	2	1	2							1
800	<i>Lotus corniculatus</i>					2	4	2			1
1139	<i>Rumex acetosa</i>					3				2	2
103	<i>Acer pseudoplatanus (c)</i>			1							1
251	<i>Briza media</i>				3		2				1
583	<i>Filipendula ulmaria</i>					2		3			1
589	<i>Fraxinus excelsior (c)</i>	1					1				1
1046	<i>Potentilla erecta</i>	1									1
1081	<i>Ranunculus acris</i>		3				1				1
1175	<i>Salix myrsinifolia</i>						1				1
1239	<i>Senecio jacobaea</i>	1						1			1
1350	<i>Trifolium repens</i>		2			2					1
1363	<i>Ulex europaeus (s)</i>				2			1			1
167	<i>Angelica sylvestris</i>								1		1
174	<i>Anthyllus vulneraria</i>			2							1
278	<i>Calluna vulgaris</i>				2						1
482	<i>Digitalis purpurea</i>								1		1
606	<i>Galium boreale</i>							2			1
633	<i>Geum rivale</i>							1			1
654	<i>Helianthemum chamaestris</i>						3				1
681	<i>Holcus mollis</i>	2									1
757	<i>Lathyrus pratensis</i>										3
864	<i>Mercurialis perennis</i>							1			1
1043	<i>Potentilla anserina</i>			2							1
1140	<i>Rumex acetosella</i>	4									1
1270	<i>Solidago virgaurea</i>				1						1
1297	<i>Stellaria holostea</i>							1			1
1401	<i>Veronica officinalis</i>	1									1
1638	<i>Dicranum scoparium</i>								2		1
1941	<i>Rhynchospora triquetra</i>				5						1
2602	<i>Alnus glutinosa (s)</i>			1							1
2614	<i>Fraxinus excelsior (s)</i>							1			1
2639	<i>Ulex europaeus (g)</i>	2									1
2954	<i>Rosa rubiginosa</i>										1
4435	<i>Pinus sylvestris</i>								1		1
	Number of species per sample	29	29	31	31	24	31	34	27	21	32
	Mean number of species	28.9									
	Standard error of the mean	1.242									

Table 10.4: TWINSpan end group 4, W11c community

Code	Environmental variable	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	
4	Elevation (m)	1.05	1.50	1.28	1.94	0.64	1.24	1.22	1.45	1.64	1.19	
7	Soil depth (cm)	90	70	86	30	40	80	105	73	120	105	
9	Tree height (m)	27	22	10	14	20	32	8	26	23	25	
11	Herb height (cm)	25	31	22	15	25	30	15	25	20	25	
12	Moss height (mm)	3	3	4	3	4	5	3	5	0	3	
13	Tree cover (%)	60	60	50	90	60	50	60	80	80	90	
15	Herb cover (%)	35	30	70	25	35	45	25	25	33	25	
16	Moss cover (%)	50	70	85	90	80	10	90	40	0	15	
17	pH	4.6	4.8	4.4	4.8	4.9	4.8	4.5	4.3	4.5	4.5	
21	Bare soil (including sand) (%)	0	0	0	0	0	2	0	2	0	0	
34	SMC (%)	16	13	14	32	24	21	21	20	12	10	
35	SOMC (%)	3	2	3	10	5	3	4	4	3	3	
36	Tall herb height (cm)	82	87	95	70	72	87	100	95	90	85	
37	Tall herb cover (%)	90	85	40	70	70	70	90	75	90	95	
38	MEAN	1	0	1	0	1	0	1	1	2	3	
39	MINDOM	5	5	5	4	5	5	5	5	5	5	
40	MAXDOM	-1	-2	-1	-2	-1	-2	-2	-2	-1	-1	
41	MEDOM	2	0	2	0	1	0	2	2	3	3	
42	MODOM	2	0	2	1	1	0	3	2	3	3	
43	Range	3.9	7.9	3.9	7.9	3.9	7.9	7.9	7.9	3.9	1.9	
44	Heterogeneity	8	9	8	8	7	9	9	9	8	7	
51	Litter (%)	0	0	0	5	2	3	5	2	3	2	
52	CWD (%)	2	5	2	5	10	5	5	5	10	5	
	Species name											
171	<i>Anthoxanthum odoratum</i>	6	5	4	4	7	5	4	5	6	6	V
197	<i>Arrhenatherum elatius</i>	7	7	7	4	5	4	3	7	7	6	V
236	<i>Betula pubescens (c)</i>	4	4	6	4	7	7	7	8	7	6	V
237	<i>Betula pendula (c)</i>	5	7	3	2	4	3	2	3	2	2	V
574	<i>Festuca ovina</i>	8	8	8	8	8	8	6	7	7	6	V
1429	<i>Viola riviniana</i>	3	4	4	3	4	4	3	4	4	4	V
445	<i>Cretaeus monogyna (s)</i>	3	3	3		1	1	3	3	3	3	V
681	<i>Holcus mollis</i>		6	7	3	3	4	8	6	6	6	V
1051	<i>Potentilla sterilis</i>	3	2	2		4	3	3	3	4	4	V
1293	<i>Stachys sylvatica</i>		4	4	3	4	4	3	3	4	2	V
1396	<i>Veronica chamaedrys</i>	3	3	3	3	3	3	3		3	3	V
1761	<i>Hylocomium splendens</i>	4	7	7	4	7	4	7	6		3	V
1940	<i>Rhydiadelphus squarrosus</i>	5	7	8	5	7	3	8	5		6	V
477	<i>Deschampsia cespitosa cespitosa</i>	3		3		4	4	4	6	5	4	IV
680	<i>Holcus lanatus</i>	4		3	5	5		3	2	3	6	IV
971	<i>Pinus sylvestris (c)</i>	5	3	4	7	1	2			2	7	IV
465	<i>Dactylis glomerata</i>	4			4	4	4	4	3	4	4	IV
613	<i>Galium verum</i>	2	3	2		2	3	2	1			IV
986	<i>Poa nemoralis</i>		3		3	6	4	2	5	3		IV
1363	<i>Ulex europaeus (s)</i>		3			1	2	2	3	2	3	IV
655	<i>Helictotrichon pratense</i>		4		4	5	5	5			5	III
864	<i>Mercurialis perennis</i>			7				1	4	1	1	III
932	<i>Oxalis acetosella</i>	2		2	3			4	4		3	III
1046	<i>Potentilla erecta</i>	3	3			3	3		3	3		III
1305	<i>Succisa pratensis</i>		2		3	3	4			2	2	III
1321	<i>Teucrium scorodonia</i>	4	2		1	2			2		3	III
2707	<i>Vicia sativa</i>	2	3	1					2	2	1	III
417	<i>Cirsium heterophyllum</i>	2		3		3			2	4		III
455	<i>Galium cruciata</i>			3		3	2		4	3		III
578	<i>Festuca vivipara</i>				3	7	5		3	4		III
701	<i>Hypericum perforatum</i>	2	2			1	3		3			III
800	<i>Lotus corniculatus</i>		3			2	3	2		2		III
2472	<i>Parmelia sinuosa</i>	3	3	4				3		3		III
2604	<i>Betula pubescens (s)</i>	3	2						2	2	2	III
2764	<i>Rubus idaeus (g)</i>	4		5	3			4	6			III
4435	<i>Pinus sylvestris</i>	1				4		4	4	2		III
153	<i>Alnus glutinosa (c)</i>			4	5			3			3	II
371	<i>Centauria nigra</i>			2	1		4	2				II
605	<i>Galium aparine</i>	3		3				3			3	II
1296	<i>Stellaria graminea</i>		3	1		1			2			II
1368	<i>Urtica dioica</i>			1	1			3			2	II

Code	Species name	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	
2003	<i>Thuidium tamariscinum</i>			4	6			4			3	II
2633	<i>Sambucus nigra (g)</i>	2			1			2			1	II
606	<i>Galium boreale</i>			2	3	3						II
630	<i>Geranium robertianum</i>			2		1					2	II
633	<i>Geum rivale</i>			1			2			1		II
988	<i>Poa pratensis</i>			3	4						3	II
1254	<i>Silene dioica</i>			1				2			2	II
1941	<i>Rhytidadelphus triquetrus</i>				7		4				4	II
2752	<i>Prunus padus (c)</i>			2	2						1	II
123	<i>Agrostis capillaris</i>	3			3							I
278	<i>Calluna vulgaris</i>		2				3					I
431	<i>Conopodium majus</i>					2			2			I
478	<i>Deschampsia flexuosa</i>	4	4									I
499	<i>Dryopteris dilatata</i>							4	4			I
654	<i>Helianthemum chamaeastris</i>								2	1		I
807	<i>Luzula campestris</i>					1	4					I
812	<i>Luzula sylvatica</i>		4						3			I
973	<i>Plantago lanceolata</i>				2		3					I
1064	<i>Prunus padus (s)</i>							1	2			I
1088	<i>Ranunculus ficaria</i>							1				I
1297	<i>Stellaria holostea</i>								2	1		I
1298	<i>Stellaria media</i>		2		1							I
1350	<i>Trifolium repens</i>		2				2					I
2603	<i>Alnus glutinosa (g)</i>							2	2			I
103	<i>Acer pseudoplatanus (c)</i>							1				I
104	<i>Achillea millefolium</i>		2									I
127	<i>Ajuga reptans</i>								1			I
167	<i>Angelica sylvestris</i>								2			I
338	<i>Carex pallescens</i>		2									I
419	<i>Cirsium vulgare</i>					2						I
466	<i>Dactylorhiza fuchsii</i>								1			I
482	<i>Digitalis purpurea</i>								1			I
576	<i>Festuca rubra</i>								4			I
589	<i>Fraxinus excelsior (c)</i>				2							I
632	<i>Geranium sylvaticum</i>								1			I
965	<i>Pilosella officinarum agg</i>							3				I
982	<i>Poa chaixii</i>			2								I
1056	<i>Primula veris</i>										3	I
1081	<i>Ranunculus acris</i>						1					I
1175	<i>Salix myrsinifolia</i>				3							I
1807	<i>Plagiomnium undulatum</i>						3					I
2610	<i>Corylus avellana (g)</i>							2				I
2611	<i>Cretaeus monogyna (g)</i>	1										I
2623	<i>Prunus padus (g)</i>									2		I
2754	<i>Rosa canina (g)</i>				1							I
	Number of species per sample	31	34	37	36	36	34	41	44	33	36	
	Mean number of species combined	36.2										
	Standard error of the mean	1.2										

Table 10.5: TWINSPAN end group 5, W7 community

Code	Environmental variable	WW1	WW2	WW3	WW4	WW5	WW6	WW7	WW8	WW9	WW10	
4	Elevation (m)	0.12	-0.06	-0.19	0.37	0.61	0.44	0.58	1.04	1.39	1.10	
7	Soil depth (cm)	74	83	30	47	23	0	11	38	33	60	
9	Tree height (m)	15	20	9	21	13	12	10	6	12	9	
11	Herb height (cm)	10	25	10	25	30	10	15	20	15	15	
12	Moss height (mm)	4		3	4		20	15			5	
13	Tree cover (%)	85	90	95	90	80	80	80	95	95	90	
15	Herb cover (%)	30	15	30	20	20	25	10	30	20	10	
16	Moss cover (%)	5		3	3		3	5			3	
17	pH	3.7	4	5.3	4.2	4.8		4.6	5	5.4	3.9	
21	Bare shingle	0	0	2	0	2	85	3	2	40	5	
22	Bare soil (including sand) (%)	5	10	0	10	5	0	5	5	10	10	
23	Open water (%)	25	30	20	0	5	95	50	30	50	40	
34	SMC (%)	26	46	43	28	47		34	27	14	36	
35	SOMC (%)	4	5	5	4	9		4	1	1	4	
36	Tall herb height (cm)	110	100	110	115	80	130	90	120	90	115	
37	Tall herb cover (%)	75	90	80	85	90	10	40	80	80	90	
38	Range	794	794	794	794	794		394	794		794	
39	MODOM	5	5	5	5	9		4	5	9	5	
51	Litter (%)	5	10	5	5	5	0	5	10	5	0	
52	CWD (%)	15	25	10	10	15	20	30	30	25	10	
	Species name											
103	<i>Acer pseudoplatanus (c)</i>	2	3	4	1	1	6	7	6	7	4	V
589	<i>Fraxinus excelsior (c)</i>	2	3	5	6	4	3	3	4	4	5	V
605	<i>Galium aparine</i>	5	4	5	4	4	2	4	4	2	3	V
414	<i>Circaea lutetiana</i>	5	3	4	3	3		3	3	3	4	V
477	<i>Deschampsia cespitosa cespitosa</i>	3	4	6	7	4	3		8	5	5	V
864	<i>Mercurialis perennis</i>	4	4	4	3	5		3	3	3	4	V
1429	<i>Viola riviniana</i>	3	2	3	2	3		2	2	4	2	V
606	<i>Galium boreale</i>	2	3		2		1	3	2	1	2	IV
655	<i>Helictotrichon pratense</i>	7	6	5	4	6			5	6	7	IV
807	<i>Luzula campestris</i>	4	2		2	2		2	1	1	2	IV
889	<i>Myosotis scorpioides</i>	2		3	3	2	3	3	3	2		IV
197	<i>Arrhenatherum elatius</i>	7	6	7	4	7			3		6	IV
465	<i>Dactylis glomerata</i>		1	4	4	3		2	3		1	IV
583	<i>Filipendula ulmaria</i>		2	4			2	2	3	2	2	IV
1254	<i>Silene dioica</i>	1	2		2	3		2	2	1		IV
1293	<i>Stachys sylvatica</i>	4	5		4	4		5		3	3	IV
151	<i>Allium ursinum</i>	2	2	3		3	2			3		III
236	<i>Betula pubescens (c)</i>	3	3		2	1		1	2			III
630	<i>Geranium robertianum</i>	3		1	3	2	2	2				III
1368	<i>Urtica dioica</i>	2		3	2	3		2		3		III
2752	<i>Prunus padus (c)</i>	2	2	2				2		2	1	III
2757	<i>Corylus avellana (c)</i>	2		2				2	3	3	1	III
574	<i>Festuca ovina</i>	4	3	4	4	4						III
1175	<i>Salix myrsinifolia</i>						5	4	4	3	3	III
1360	<i>Tussilago farfara</i>					2		2		3	2	III
350	<i>Carex remota</i>		2		1	2			1			II
419	<i>Cirsium vulgare</i>						2	2	1	2		II
499	<i>Dryopteris dilatata</i>	1	2							2	2	II
730	<i>Juncus effusus</i>		1			3	2					II
932	<i>Oxalis acetosella</i>	3	4		5	5						II
971	<i>Pinus sylvestris (c)</i>	2	3	1	1							II
990	<i>Poa trivialis</i>	3	4	4						6		II
1051	<i>Potentilla sterilis</i>	4		3	3			2				II
1095	<i>Ranunculus repens</i>			5				1	3	2		II
1940	<i>Rhynchospora squarrosus</i>	3		3	3						3	II
127	<i>Ajuga reptans</i>				1		2			2		II
408	<i>Chrysosplenium oppositifolium</i>			3				3			2	II
445	<i>Crataegus monogyna (s)</i>	2			1						1	II
633	<i>Geum rivale</i>						2		2		1	II
855	<i>Mentha aquatica</i>						5	2		1		II
955	<i>Phalaris arundinacea</i>						3			3	3	II
1064	<i>Prunus padus (s)</i>					2	2				1	II
1396	<i>Veronica chamaedrys</i>	3					2	1				II
1761	<i>Hylocomium splendens</i>	2						2	3			II
2633	<i>Sambucus nigra (g)</i>	3							1		1	II
455	<i>Galium cruciata</i>				2				2			I
639	<i>Glyceria fluitans</i>					3				3		I
722	<i>Juncus articulatus</i>			1	2							I
986	<i>Poa nemoralis</i>	3		4								I
1081	<i>Ranunculus acris</i>						1			1		I

Table 10.6: TWINSpan end group 6, M23 community

Code	Environmental variable	1	
4	Elevation (m)	-1.00	
7	Soil depth (cm)	0	
10	Shrub height (m)	2	
11	Herb height (cm)	30	
14	Shrub cover (%)	5	
15	Herb cover (%)	40	
21	Bare shingle (%)	30	
22	Bare soil (including sand) (%)	10	
23	Open water (%)	75	
51	Litter (%)	5	
52	CWD (%)	5	
	Species name		
123	<i>Agrostis capillaris</i>	2	V
127	<i>Ajuga reptans</i>	3	V
228	<i>Barbarea vulgaris</i>	3	V
391	<i>Chamerion angustifolium</i>	1	V
419	<i>Cirsium vulgare</i>	1	V
522	<i>Epilobium montanum</i>	1	V
583	<i>Filipendula ulmaria</i>	3	V
605	<i>Galium aparine</i>	2	V
662	<i>Hesperis matronalis</i>	1	V
680	<i>Holcus lanatus</i>	3	V
701	<i>Hypericum perforatum</i>	4	V
708	<i>Impatiens glandulifera</i>	3	V
730	<i>Juncus effusus</i>	5	V
773	<i>Lepidium heterophyllum</i>	1	V
855	<i>Mentha aquatica</i>	6	V
868	<i>Mimulus guttatus</i>	5	V
889	<i>Myosotis scorpioides</i>	4	V
955	<i>Phalaris arundinacea</i>	6	V
973	<i>Plantago lanceolata</i>	1	V
1043	<i>Potentilla anserina</i>	3	V
1095	<i>Ranunculus repens</i>	3	V
1098	<i>Ranunculus sceleratus</i>	4	V
1140	<i>Rumex acetosella</i>	2	V
1147	<i>Rumex obtusifolius</i>	1	V
1220	<i>Scrophularia nodosa</i>	1	V
1239	<i>Senecio jacobaea</i>	3	V
1254	<i>Silene dioica</i>	2	V
1256	<i>Silene uniflora</i>	3	V
1296	<i>Stellaria graminea</i>	1	V
1308	<i>Symphytum officinale</i>	2	V
1349	<i>Trifolium pratense</i>	2	V
1350	<i>Trifolium repens</i>	3	V
1368	<i>Urtica dioica</i>	3	V
2602	<i>Alnus glutinosa (s)</i>	3	V
2764	<i>Rubus idaeus (g)</i>	2	V
2785	<i>Alchemilla vulgaris agg.</i>	1	V
	Number of species per sample	36	
	Mean number of species	36	
	Standard error of the mean	-1	

Appendix 11.
Soil/substrate classification, Ballinluig.

Table 11.1.: Substrate group 1 data and summary statistics.

Sample	Bare gravel %	Bare soil %	Soil Depth (cm)	% stones	SMC %	OMC %	pH	MEAN	MIN-DOM	MAX-DOM	MEDOM	MODOM	RANGE	HETERO-GENEITY
GB1	100	0	0	0	0	0	0.0	-2	-3	-8	-1	-3	248.00	11
GB4	95	2	0	0	0	0	0.0	-2	-2	-8	-2	-7	252.00	13
GB5	100	0	0	0	0	0	0.0	-2	-3	-8	-1	-6	174.40	11
GB6	100	0	0	0	0	0	0.0	-2	-3	-8	-2	-6	248.00	11
GB9	50	45	0	0	0	0	0.0	-3	-4	-8	-2	-7	255.94	17
GB10	80	0	0	0	0	0	0.0	-2	-3	-8	-1	-4	172.00	10
GB7	30	30	0	0	0	0	0.0	0	-1	-6	0	-4	89.94	17
GB8	100	0	0	0	0	0	0.0	-1	-1	-6	0	-4	87.00	11
mean	81.88	9.63	0.00	0.00	0.00	0.00	0.00	-2.00	-3.00	-8.00	-1.00	-5.00	190.91	12.63
min	30.00	0.00	0.00	0.00	0.00	0.00	0.00	-3.00	-4.00	-8.00	-2.00	-7.00	87.00	10.00
max	100.00	45.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.00	-6.00	0.00	-3.00	255.94	17.00
st. dev	27.25	17.68	0.00	0.00	0.00	0.00	0.00	0.89	1.07	0.93	0.83	1.55	71.82	2.83

Table 11.2.: Substrate group 3 data and summary statistics.

Sample	Bare gravel %	Bare soil %	Soil Depth (cm)	% stones	SMC %	OMC %	pH	MEAN	MIN-DOM	MAX-DOM	MEDOM	MODOM	RANGE	HETERO-GENEITY
WW6	85	0	0	0	0	0	0.0	*	*	*	*	*	0.00	0
SB9	0	2	0	0	0	0	0.0	*	*	*	*	*	0.00	0
GB2	95	0	0	0	0	0	0.0	*	*	*	*	*	0.00	0
GB3	2	3	0	0	0	0	0.0	*	*	*	*	*	0.00	0
BW1	30	10	0	0	0	0	0.0	*	*	*	*	*	0.00	0
mean	42.40	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
min	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
max	95.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
st. dev	45.18	4.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 11.3: Soil group 5 data and summary statistics.

Sample	Bare gravel		Soil Depth		OMC %	pH	MEAN	MIN-DOM	MAX-DOM	MEDOM	MODOM	RANGE	HETERO-GENEITY
	%	Bare soil %	(cm)	% stones									
W1	0	0	90	0	16.27	4.6	1	5	-1	2	2	3.94	8
W2	0	0	70	0	13.02	4.8	0	5	-2	0	0	7.94	9
W3	0	0	86	0	13.53	4.8	2	5	-1	2	2	3.94	8
W6	0	2	80	0	21.02	4.8	0	5	-2	0	0	7.94	9
W7	0	0	105	0	21.06	4.5	1	5	-2	2	3	7.94	9
W8	0	2	73	0	19.66	4.3	1	5	-2	2	2	7.94	9
W9	0	0	120	0	12.15	4.5	2	5	-1	3	3	3.94	8
W10	0	0	105	0	10.31	4.5	3	5	-1	3	3	1.94	7
WW1	0	5	74	0	26.42	3.7	0	5	-2	1	1	1.94	9
WW2	0	10	83	0	46.06	4.0	-1	4	-2	0	1	7.94	8
WW10	5	10	60	5	36.25	3.9	0	4	-2	1	1	7.94	8
G7	0	2	124	0	16.90	4.8	0	5	-2	0	0	7.94	9
mean	0.42	2.58	89.17	0.42	21.05	4.43	0.75	4.83	-1.67	1.33	1.50	5.94	8.42
min	0.00	0.00	60.00	0.00	10.31	3.70	-1.00	4.00	-2.00	0.00	0.00	1.94	7.00
max	5.00	10.00	124.00	5.00	46.06	4.80	3.00	5.00	-1.00	3.00	3.00	7.94	9.00
st. dev	1.44	3.78	20.24	1.44	10.63	0.91	1.14	0.39	0.49	1.15	1.17	2.56	0.67

Table 11.4: Soil group 6 data and summary statistics.

Sample	Bare gravel		Soil depth		OMC %	pH	MEAN	MIN-DOM	MAX-DOM	MEDOM	MODOM	RANGE	HETERO-GENEITY
	%	Bare soil %	(cm)	% stones									
W5	0	0	40	0	23.73	4.9	1	5	-1	1	1	3.94	7
SB10	0	2	42	2	22.39	5.3	-1	4	-2	0	0	7.94	8
G1	0	0	40	0	17.22	5.0	0	5	-2	0	0	7.94	9
WW8	2	5	38	0	27.40	5.0	0	5	-2	1	1	7.94	8
SB8	10	5	30	0	24.25	5.4	-1	4	-2	0	0	7.94	8
SB6	2	5	44	5	6.90	5.3	0	4	-2	0	0	7.94	9
SB7	0	20	31.5	5	16.67	5.5	-1	4	-3	-1	-1	15.94	9
mean	2.00	5.29	37.93	1.71	19.79	5.20	-0.29	4.43	-2.00	0.14	0.14	8.51	8.29
min	0.00	0.00	30.00	0.00	6.90	4.90	-1.00	4.00	-3.00	-1.00	-1.00	3.94	7.00
max	10.00	20.00	44.00	5.00	27.40	5.50	1.00	5.00	-1.00	1.00	1.00	15.94	9.00
st. dev	3.65	6.87	5.26	2.36	6.86	1.24	0.76	0.53	0.58	0.69	0.69	3.60	0.76

Table 11.5: Soil group 7 data and summary statistics.

Sample	Bare gravel %	Bare soil %	Soil depth (cm)	% stones	SMC %	OMC %	pH	MEAN	MIN-DOM	MAX-DOM	MEDOM	MODOM	RANGE	HETERO-GENEITY
W4	0	0	30	0	31.72	9.67	4.8	0	4	-2	0	1	7.94	8
WW3	2	0	29.5	20	42.95	5.03	5.3	-1	4	-2	0	1	7.94	8
WW4	0	10	47	50	28.38	4.21	4.2	0	4	-2	1	1	7.94	8
WW5	2	5	23	20	47.08	8.88	4.8	-1	5	-2	0	-2	7.94	8
WW7	3	5	11	5	34.06	4.24	4.6	1	5	-1	2	2	3.94	8
WW9	40	10	33	50	14.17	1.29	5.4	-2	5	-3	-2	-2	15.94	10
G2	0	2	24.5	10	28.94	4.43	5.4	-1	4	-3	0	1	15.94	9
G3	0	0	13	13	50.30	23.34	5.0	1	4	-2	1	1	7.94	8
G4	5	3	15	30	40.08	6.42	4.7	-1	5	-2	0	3	7.94	9
G5	5	2	20	20	35.49	5.44	4.9	-1	4	-2	0	1	7.94	8
G6	0	0	24	20	30.79	5.73	5.0	-2	4	-3	-1	1	15.94	9
G8	2	3	28	40	41.27	6.72	5.2	-1	5	-3	-1	1	15.94	10
G9	2	0	24	10	38.96	3.51	5.5	-1	5	-2	0	3	7.94	9
G10	0	0	34	10	37.62	6.49	5.0	-1	4	-2	0	1	7.94	8
SB1	0	0	21	0	28.63	4.00	5.4	1	4	-1	2	3	3.94	9
SB2	0	0	18	0	28.28	4.04	5.3	1	5	-2	2	4	7.94	8
SB3	3	2	18	0	13.77	2.13	5.2	0	4	-2	0	1	7.94	7
SB4	0	5	18	0	10.28	1.68	5.2	0	4	-1	0	0	3.94	9
SB5	0	5	28	2	13.66	1.89	5.3	0	4	-3	0	0	15.94	9
mean	3.37	2.74	24.16	15.79	31.39	5.74	5.06	0.00	4.00	-2.00	0.00	1.00	9.41	8.53
min	0.00	0.00	11.00	0.00	10.28	1.29	4.20	-2.00	4.00	-3.00	-2.00	-2.00	3.94	7.00
max	40.00	10.00	47.00	50.00	50.30	23.34	5.50	1.00	5.00	-1.00	2.00	4.00	15.94	10.00
st. dev	9.03	3.23	8.54	16.43	11.62	4.82	0.34	0.96	0.50	0.66	1.03	1.52	4.26	0.77

Appendix 12.
Diversity Analysis, Ballinluig.

Table 12.1: Biodiversity and pedodiversity analysis on the Ballinluig dataset. The index is calculated by the number of samples occurring within a given group. N = number of observations; S = species richness; H'max = maximum negentropy; H' = Shannon index; J = evenness (Equitability) index.

	Plant community	Soil types							Pedodiversity indices						
		Gp1	Gp3	Gp5	Gp6	Gp7	N	S	H'max	H'	J				
Plant community	SHpc	8	2	0	0	0	10	2	0.7	0.5	0.7				
	MG5b	0	1	0	4	5	10	3	1.1	0.9	0.9				
	U4b	0	0	1	1	8	10	3	1.1	0.6	0.6				
	W11c	0	0	8	1	1	10	3	1.1	0.6	0.6				
	W7	0	1	3	1	5	10	4	1.4	1.2	0.8				
	M23	1	0	0	0	0	1	1	0.0	0.0	0.0				
	N	9	4	12	7	19									
Biodiversity Indices	S	2	3	3	4	4									
	H'max	0.7	1.1	1.1	1.4	1.4									
	H'	0.3	0.7	0.8	0.6	0.9									
	J	0.5	0.6	0.8	0.4	0.6									

Table 12.2: Biodiversity and geodiversity analysis on the Ballinluig dataset. The index is calculated by the number of samples occurring within a given group. N = number of observations; S = species richness; H'max = maximum negetropy; H' = Shannon index; J = evenness (Equitability) index.

	Plant community	Landform types			Geodiversity indices					
		Side-arm	Abandoned channel	Point bar	Floodplain	N	S	H'max	H'	J
Plant community	SHpc	0	0	10	0	10	1	0.0	0.0	0.0
	MG5b	0	0	0	10	10	1	0.0	0.0	0.0
	U4b	0	0	0	10	10	1	0.0	0.0	0.0
	W11c	0	0	0	10	10	1	0.0	0.0	0.0
	W7	5	5	0	0	10	2	0.7	0.7	1.0
	M23	1	0	0	0	1	1	0.0	0.0	0.0
	N	6	5	10	30					
Biodiversity indices	S	2	1	1	3					
	H'max	0.7	0.0	0.0	1.1					
	H'	0.5	0.0	0.0	1.1					
	J	0.7	0.0	0.0	1.0					

Table 12.3: Geodiversity and pedodiversity analysis on the Ballinluig dataset. The index is calculated by the number of samples occurring within a given group. N = number of observations; S = species richness; H'max = maximum negentropy; H' = Shannon index; J = evenness (Equitability) index.

	Landform	Soil types					Pedodiversity indices					
		Gp1	Gp3	Gp5	Gp6	Gp7	N	S	H'max	H'	J	
Landform	Side-arm	0	2	1	1	2	6	4	1.4	1.3	1.0	
	Abandoned channel	0	0	2	0	3	5	2	0.7	0.7	1.0	
	Point bar	8	2	0	0	0	10	2	0.7	0.5	0.7	
	Floodplain	0	1	9	6	14	30	4	1.4	1.2	0.8	
Geodiversity indices	N	8	5	12	7	19						
	S	1	3	3	2	3						
	H'max	0.0	1.1	1.1	0.7	1.1						
	H'	0.0	0.7	0.5	0.4	0.8						
	J	0.0	0.6	0.5	0.6	0.7						

Appendix 13.

Species unique to landform units and plant community types within the Ballinluig dataset.

Table 13.1: Plant species identified within the Ballinluig dataset showing their distribution within the geomorphic land units. The rarity of each species within Perthshire is indicated, data on frequency was acquired from Smith *et al.* (1992).

		Backwater	Abandoned channel	Point bar	Floodplain	Total	Frequency
<i>Acer pseudoplatanus</i>	Sycamore	1	1	1	1	4	C
<i>Achillea millefolium</i>	Yarrow			1	1	2	VC
<i>Agrostis capillaris</i>	Common bent	1			1	2	VC
<i>Ajuga reptans</i>	Bugle	1	1	1	1	4	C
<i>Alchemilla vulgaris</i>	Lady's mantle	1			1	2	C
<i>Allium ursinum</i>	Ramsons	1	1			2	F
<i>Alnus glutinosa</i>	Alder	1	1	1	1	4	C
<i>Anchusa arvensis</i>	Bugloss			1		1	O
<i>Anemone nemorosa</i>	Wood anemone		1			1	VC
<i>Angelica sylvestris</i>	Wild angelica				1	1	VC
<i>Anthoxanthum odoratum</i>	Sweet vernal grass			1	1	2	VC
<i>Anthyllis vulneria</i>	Kidney vetch				1	1	O
<i>Arrhenathrum elatius</i>	False oat grass	1	1		1	3	C
<i>Barbarea vulgaris</i>	Common winter cress	1				1	O
<i>Betula pendula</i>	Silver birch			1	1	2	VC
<i>Betula pubescens</i>	Downy birch	1	1		1	3	VC
<i>Briza media</i>	Quaking grass				1	1	F
<i>Calluna vulgaris</i>	Heather				1	1	VC
<i>Campanula rotundifolia</i>	Harebell				1	1	C
<i>Carex pallescens</i>	Pale sedge				1	1	F
<i>Carex remota</i>	Remote sedge	1	1			2	F
<i>Carex vesicaria</i>	Bladder sedge		1			1	O
<i>Centaurea nigra</i>	Common knapweed				1	1	VC
<i>Chamerion angustifolium</i>	Rosebay Willowherb	1		1		2	VC
<i>Chrysanthemum leucanthemum</i>	Ox eye daisy			1	1	2	F
<i>Chrysosplenium oppositifolium</i>	Opposite-leaved golden saxifrage	1	1			2	VC
<i>Circaea lutetiana</i>	Common enchanter's nightshade	1	1			2	F
<i>Cirsium heterophyllum</i>	Melancholy thistle		1		1	2	F b
<i>Cirsium vulgare</i>	Spear thistle	1		1	1	3	C
<i>Climacium dendrioides</i>		1				1	
<i>Conopodium majus</i>	Pignut		1		1	2	C
<i>Corylus avellana</i>	Hazel	1	1		1	3	C
<i>Cretageous monogyna</i>	Hawthorne		1		1	2	C
<i>Cynosurus cristatus</i>	Crested dogs-tail				1	1	C
<i>Dactylis glomerata</i>	Cocksfoot	1	1		1	3	C
<i>Dactylorhiza fuchsii</i>	Common spotted orchid				1	1	F
<i>Deschampsia cespitosa</i>	Tufted hair grass	1	1		1	3	VC
<i>Deschampsia flexuosa</i>	Wavy hair grass				1	1	VC
<i>Dicranum scoparium</i>		1				1	
<i>Digitalis purpurea</i>	Foxglove	1		1	1	3	VC
<i>Dryopteris dilata</i>	Broad buckler fern	1	1		1	3	VC
<i>Epilobium montanum</i>	Broad-leaved willowherb	1				1	C
<i>Euphrasia nemorosa</i>	Eyebright				1	1	VR
<i>Fagus sylvatica</i>	Beech			1		1	F
<i>Festuca ovina</i>	Sheep's fescue		1	1	1	3	VC
<i>Festuca pratensis</i>	Meadow fescue				1	1	O
<i>Festuca rubra</i>	Red fescue				1	1	VC
<i>Festuca vivipara</i>	Viviparous fescue				1	1	F
<i>Filiendula ulmaria</i>	Meadowsweet	1	1	1	1	4	VC
<i>Fraxinus excelsior</i>	Ash	1	1		1	3	C
<i>Galium aparine</i>	Cleavers	1	1		1	3	C
<i>Galium boreal</i>	Northern bedstraw	1	1		1	3	F
<i>Galium cruciata</i>	Crosswort	1	1		1	3	F
<i>Galium verum</i>	Lady's bedstraw				1	1	C
<i>Geranium robertianum</i>	Herb robert	1	1	1	1	4	C
<i>Geranium sylvaticum</i>	Wood cranesbill				1	1	C
<i>Geum rivale</i>	Water avens	1			1	2	C
<i>Glyceria fluitans</i>	Floating sweet grass	1	1			2	F
<i>Helianthemum chamaecistus</i>	Common rockrose				1	1	O
<i>Helictotrichon pratense</i>	Meadow oat-grass	1	1		1	3	O
<i>Hesperis matronalis</i>	Dame's violet	1		1		2	O d
<i>Holcus lanatus</i>	Yorkshire fog	1		1	1	3	VC
<i>Holcus mollis</i>	Creeping soft grass		1		1	2	VC

		Backwater	Abandoned channel	Point bar	Floodplain	Total	Frequency
<i>Hylocomnium splendens</i>		1	1	1	1	4	
<i>Hypericum perforatum</i>	Perforate St. John's wort	1		1	1	3	O
<i>Hypochoeris glabra</i>	Smooth cat's-ear				1	1	O
<i>Impatiens glandulifera</i>	Himalayan balsam	1		1		2	O
<i>Iris pseudocorus</i>	Yellow flag	1				1	F
<i>Juncus articulatus</i>	jointed rush		1			1	C
<i>Juncus effusus</i>	Soft rush	1	1			2	VC
<i>Lathyrus pratensis</i>	Meadow vetchling				1	1	C
<i>Lepidium heterophyllum</i>	Smith's pepperwort	1			1	2	O
<i>Lotus corniculatus</i>	Common birdsfoot trefoil				1	1	C
<i>Luzula campestris</i>	Field woodrush	1	1		1	3	C
<i>Luzula sylvatica</i>	Great woodrush				1	1	VC
<i>Mentha aquatica</i>	Water mint	1		1		2	F
<i>Mercurialis perennis</i>	Dog's mercury	1	1		1	3	C
<i>Minulus guttatus</i>	Monkey flower	1		1		2	O
<i>Mniun hornum</i>		1				1	
<i>Myosotis scorpioides</i>	Water forget-me-not	1	1	1		3	F
<i>Ononis repens</i>	Rest harrow			1	1	2	O
<i>Oxalis acetosella</i>	Wood sorrel		1		1	2	VC
<i>Parmelia sinuosa</i>			1		1	2	
<i>Phalaris arundinacea</i>	Reed canary grass	1				1	C
<i>Pilosella officinarum</i>	Mouse-ear hawkweed				1	1	R
<i>Pinus sylvestris</i>	Scots pine		1		1	2	O
<i>Plagionnium undulatum</i>					1	1	
<i>Plantago lanceolata</i>	Ribwort plantain	1		1	1	3	VC
<i>Poa chaixii</i>	Broad-leaved meadow grass				1	1	R
<i>Poa nemoralis</i>	Wood meadow grass		1		1	2	F
<i>Poa pratensis</i>	Smooth meadow grass				1	1	C
<i>Poa trivialis</i>	Rough meadow grass	1	1			2	C
<i>Potentilla anserina</i>	Silverweed	1		1	1	3	F
<i>Potentilla erecta</i>	Tormentil				1	1	VC
<i>Potentilla sterillis</i>	Barren strawberry	1	1		1	3	F
<i>Primula veris</i>	Cowslip	1			1	2	O
<i>Prunus padus</i>	Bird cherry	1	1		1	3	F
<i>Racomitrium canescens</i>				1	1	2	VR
<i>Ranunculus acris</i>	Meadow buttercup	1			1	2	VC
<i>Ranunculus ficaria</i>	Lesser celandine	1	1	1	1	4	C
<i>Ranunculus flammula</i>	Lesser spearwort	1				1	C
<i>Ranunculus repens</i>	Creeping buttercup	1	1	1		3	VC
<i>Ranunculus sceleratus</i>	Celery-leaved buttercup	1				1	O
<i>Rhianthus minor</i>	Yellow rattle				1	1	F
<i>Rhynchospora alba</i>				1		1	
<i>Rhynchospora alba</i>		1	1		1	3	
<i>Rhynchospora alba</i>		1			1	2	
<i>Rorippa nasturtium-aquaticum</i>	Watercress			1		1	R
<i>Rosa canina</i>	Dog rose				1	1	O
<i>Rosa rubiginosa</i>	Sweet briar				1	1	O
<i>Rubus idaeus</i>	Raspberry	1	1	1	1	4	C
<i>Rumex acetosa</i>	Common sorrel				1	1	VC
<i>Rumex acetosella</i>	Sheep's sorrel	1		1	1	3	C
<i>Rumex obtusifolius</i>	Broad-leaved dock	1		1		2	C
<i>Salix cinerea ssp oleifolia</i>	Grey willow			1		1	C
<i>Salix repens</i>	Creeping willow			1	1	2	O
<i>Salix myrsinifolia</i>	Dark-leaved willow	1		1	1	3	O
<i>Sambucus nigra</i>	Elder		1	1	1	3	F
<i>Sarothamnus scoparius</i>	Broom			1	1	2	C
<i>Scrophularia nodosa</i>	Common figwort	1		1		2	O
<i>Scutellaria galenculata</i>	Common skullcap	1	1			2	O
<i>Sedum acre</i>	Biting stoncrop			1		1	O
<i>Senecio jacobaea</i>	Common ragwort	1		1	1	3	C
<i>Senecio viscosus</i>	Sticky groundsel			1		1	O
<i>Silene dioica</i>	Red campion	1	1	1	1	4	C
<i>Silene vulgaris</i>	Bladder campion	1		1	1	3	O
<i>Solidago vigaurea</i>	Goldenrod				1	1	F
<i>Stachys sylvatica</i>	Hedge woundwort	1	1		1	3	C
<i>Stellaria gramineae</i>	Lesser stitchwort	1		1	1	3	C
<i>Stellaria holostea</i>	Greater stitchwort				1	1	F
<i>Stellaria media</i>	Chickweed				1	1	C
<i>Succisa pratense</i>	Devilsbit scabious	1		1		2	VC

		Backwater	Abandoned channel	Point bar	Floodplain	Total	Frequency	
<i>Symphytum officinale</i>	Common comfrey	1	1	1		3	R	g
<i>Taraxacum officinale</i>	Dandelion	1	1			2	C	
<i>Teucrium scorodonia</i>	Wood sage	1	1	1	1	4	C	
<i>Thuidium tamarascinum</i>			1		1	2		
<i>Thymus drucei</i>	Wild thyme				1	1	C	
<i>Trifolium pratense</i>	Red clover	1		1		2	F	
<i>Trifolium repens</i>	White clover	1		1	1	3	C	
<i>Tussilago farfara</i>	Coltsfoot	1	1			2	F	
<i>Ulex europaeus</i>	Gorse				1	1	C	
<i>Urtica dioica</i>	Nettle	1	1	1	1	4	C	
<i>Valaria officinalis</i>	Common valerian	1				1	C	
<i>Veronica chamaedrys</i>	Germander speedwell	1	1	1	1	4	C	
<i>Veronica officinalis</i>	Heath speedwell				1	1	C	
<i>Vicia sativa</i>	Common vetch				1	1	O	
<i>Viola riviniana</i>	Common dog violet	1	1	1	1	4	C	
<i>Viola tricolor</i>	Wild pansy			1		1	O	
Total number of species in each landform class		80	58	54	107			
Total number of species = 148								
a: Along River Tay								
b: Rare near River Tay								
c: Shingle islands of rivers Tay, Tummel and Garry								
d: Particularly on riverbanks								
e: Along rivers Tay, Tummel and Garry								
f: New record to Perthshire, 1997								
g: Only on Tomdachoille along R. Tummel								
* species thought not to be native to Perthshire								
o: pre-1970 record in the county								
VR: very rare								
R: rare								
O: occasional								
F: frequent								
C: common								
VC: very common								

Table 13.2: Plant species identified within the Ballinluig dataset showing their distribution within the plant communities. The rarity of each species within Perthshire is indicated, data on frequency was acquired from Smith *et al.* (1992).

		SHpc	MG5b	U4b	W11c	W7	M23	Total	Frequency
<i>Acer pseudoplatanus</i>	Sycamore	1		1	1	1		4	C
<i>Achillea millefolium</i>	Yarrow	1	1	1	1			4	VC
<i>Agrostis capillaris</i>	Common bent				1		1	2	VC
<i>Ajuga reptans</i>	Bugle	1			1	1	1	4	C
<i>Alchemilla vulgaris</i>	Lady's mantle		1				1	2	C
<i>Allium ursinum</i>	Ramsons					1		1	F
<i>Alnus glutinosa</i>	Alder	1		1	1	1	1	5	C
<i>Anchusa arvensis</i>	Bugloss	1						1	O
<i>Anemone nemorosa</i>	Wood anemone					1		1	VC
<i>Angelica sylvestris</i>	Wild angelica		1	1	1			3	VC
<i>Anthoxanthum odoratum</i>	Sweet vernal grass	1	1	1	1			4	VC
<i>Anthyllis vulneria</i>	Kidney vetch		1	1				2	O
<i>Arrhenathrum elatius</i>	False oat grass		1	1	1	1		4	C
<i>Barbarea vulgaris</i>	Common winter cress						1	1	O
<i>Betula pendula</i>	Silver birch	1	1	1	1			4	VC
<i>Betula pubescens</i>	Downy birch				1	1		2	VC
<i>Briza media</i>	Quaking grass		1	1				2	F
<i>Calluna vulgaris</i>	Heather			1	1			2	VC
<i>Campanula rotundifolia</i>	Harebell		1	1				2	C
<i>Carex pallescens</i>	Pale sedge				1			1	F
<i>Carex remota</i>	Remote sedge					1		1	F
<i>Carex vesicaria</i>	Bladder sedge					1		1	O
<i>Centaurea nigra</i>	Common knapweed		1	1	1			3	VC
<i>Chamerion angustifolium</i>	Rosebay Willowherb	1					1	2	VC
<i>Chrysanthemum leucanthemum</i>	Ox eye daisy	1	1	1				3	F
<i>Chrysosplenium oppositifolium</i>	Opposite-leaved golden saxifrage					1		1	VC
<i>Circaea lutetiana</i>	Common enchanter's nightshade					1		1	F
<i>Cirsium heterophyllum</i>	Melancholy thistle				1	1		2	F b
<i>Cirsium vulgare</i>	Spear thistle	1			1	1	1	4	C
<i>Climacium dendrioides</i>						1		1	
<i>Conopodium majus</i>	Pignut				1	1		2	C
<i>Corylus avellana</i>	Hazel				1	1		2	C
<i>Cretageous monogyna</i>	Hawthorne				1	1		2	C
<i>Cynosurus cristatus</i>	Crested dogs-tail		1					1	C
<i>Dactylis glomerata</i>	Cocksfoot		1	1	1	1		4	C
<i>Dactylorhiza fuchsii</i>	Common spotted orchid				1			1	F
<i>Deschampsia cespitosa</i>	Tufted hair grass		1	1	1	1		4	VC
<i>Deschampsia flexuosa</i>	Wavy hair grass		1	1	1			3	VC
<i>Dicranum scoparium</i>				1				1	
<i>Digitalis purpurea</i>	Foxglove	1		1	1	1		4	VC
<i>Dryopteris dilata</i>	Broad buckler fern				1	1		2	VC
<i>Epilobium montanum</i>	Broad-leaved willowherb						1	1	C
<i>Euphrasia nemorosa</i>	Eyebright		1	1				2	VR
<i>Fagus sylvatica</i>	Beech	1						1	F
<i>Festuca ovina</i>	Sheep's fescue	1	1	1	1	1		5	VC
<i>Festuca pratensis</i>	Meadow fescue		1					1	O
<i>Festuca rubra</i>	Red fescue		1	1	1			3	VC
<i>Festuca vivipara</i>	Viviparous fescue		1	1	1			3	F
<i>Filiendula ulmaria</i>	Meadowsweet	1		1		1	1	4	VC
<i>Fraxinus excelsior</i>	Ash			1	1	1		3	C
<i>Galium aparine</i>	Cleavers				1	1	1	3	C
<i>Galium boreal</i>	Northern bedstraw		1	1	1	1		4	F

		SHpc	MG5b	U4b	W11c	W7	M23	Total	Frequency
<i>Galium cruciata</i>	Crosswort			1	1	1		3	F
<i>Galium verum</i>	Lady's bedstraw		1	1	1			3	C
<i>Geranium robertianum</i>	Herb robert	1			1	1		3	C
<i>Geranium sylvaticum</i>	Wood cranesbill				1			1	C
<i>Geum rivale</i>	Water avens			1	1	1		3	C
<i>Glyceria fluitans</i>	Floating sweet grass					1		1	F
<i>Helianthemum chamaecistus</i>	Common rockrose			1	1			2	O
<i>Helictotrichon pratense</i>	Meadow oat-grass			1	1	1		3	O
<i>Hesperis matronalis</i>	Dame's violet	1					1	2	O d
<i>Holcus lanatus</i>	Yorkshire fog	1	1	1	1		1	5	VC
<i>Holcus mollis</i>	Creeping soft grass			1	1	1		3	VC
<i>Hylocomnium splendens</i>		1	1	1	1	1		5	
<i>Hypericum perforatum</i>	Perforate St. John's wort	1	1	1	1		1	5	O
<i>Hypochoeris glabra</i>	Smooth cat's-ear		1					1	o
<i>Impatiens glandulifera</i>	Himalayan balsam	1				1	1	3	O
<i>Iris pseudocorus</i>	Yellow flag					1		1	F
<i>Juncus articulatus</i>	jointed rush					1		1	C
<i>Juncus effusus</i>	Soft rush					1	1	2	VC
<i>Lathyrus pratensis</i>	Meadow vetchling		1	1				2	C
<i>Lepidium heterophyllum</i>	Smith's pepperwort		1				1	2	O
<i>Lotus corniculatus</i>	Common birdsfoot trefoil		1	1	1			3	C
<i>Luzula campestris</i>	Field woodrush				1	1		2	C
<i>Luzula sylvatica</i>	Great woodrush				1			1	VC
<i>Mentha aquatica</i>	Water mint	1				1	1	3	F
<i>Mercurialis perennis</i>	Dog's mercury			1	1	1		3	C
<i>Mimulus guttatus</i>	Monkey flower	1					1	2	O
<i>Mnium hornum</i>						1		1	
<i>Myosotis scorpioides</i>	Water forget-me-not	1				1	1	3	F
<i>Ononis repens</i>	Rest harrow	1	1	1				3	O
<i>Oxalis acetosella</i>	Wood sorrel				1	1		2	VC
<i>Parmelia sinuosa</i>					1	1		2	
<i>Phalaris arundinacea</i>	Reed canary grass					1	1	2	C
<i>Pilosella officinarum</i>	Mouse-ear hawkweed		1	1	1			3	R
<i>Pinus sylvestris</i>	Scots pine			1	1	1		3	O
<i>Plagiomnium undulatum</i>					1			1	
<i>Plantago lanceolata</i>	Ribwort plantain	1	1	1	1		1	5	VC
<i>Poa chaixii</i>	Broad-leaved meadow grass				1			1	R
<i>Poa nemoralis</i>	Wood meadow grass				1	1		2	F
<i>Poa pratensis</i>	Smooth meadow grass		1		1			2	C
<i>Poa trivialis</i>	Rough meadow grass					1		1	C
<i>Potentilla anserina</i>	Silverweed	1	1	1			1	4	F
<i>Potentilla erecta</i>	Tormentil			1	1			2	VC
<i>Potentilla sterillis</i>	Barren strawberry		1	1	1	1		4	F
<i>Primula veris</i>	Cowslip		1	1	1	1		4	O e
<i>Prunus padus</i>	Bird cherry				1	1		2	F
<i>Racomitrium canescens</i>		1	1					2	VR f
<i>Ranunculus acris</i>	Meadow buttercup		1	1	1	1		4	VC
<i>Ranunculus ficaria</i>	Lesser celandine	1			1	1		3	C
<i>Ranunculus flammula</i>	Lesser spearwort					1		1	C
<i>Ranunculus repens</i>	Creeping buttercup	1				1	1	3	VC
<i>Ranunculus sceleratus</i>	Celery-leaved buttercup						1	1	O
<i>Rhianthus minor</i>	Yellow rattle		1	1				2	F
<i>Rhizidadelphus loveus</i>		1						1	
<i>Rhizidadelphus squarrosus</i>			1	1	1	1		4	
<i>Rhizidadelphus triquetrus</i>				1	1	1		3	
<i>Rorippa nasturtium-aquaticum</i>	Watercress	1						1	R
<i>Rosa canina</i>	Dog rose		1		1			2	o
<i>Rosa rubiginosa</i>	Sweet briar			1				1	o
<i>Rubus idaeus</i>	Raspberry	1			1	1	1	4	C

		Stpc	MG5b	U4b	W11c	W7	M23	Total	Frequency
<i>Rumex acetosa</i>	Common sorrel		1	1				2	VC
<i>Rumex acetosella</i>	Sheep's sorrel	1		1			1	3	C
<i>Rumex obtusifolius</i>	Broad-leaved dock	1					1	2	C
<i>Salix cinerea ssp oleifolia</i>	Grey willow	1						1	C
<i>Salix repens</i>	Creeping willow	1	1					2	O
<i>Salix myrsinifolia</i>	Dark-leaved willow	1		1	1	1		4	O
<i>Sambucus nigra</i>	Elder	1			1	1		3	F
<i>Sarothamnus scoparius</i>	Broom	1	1					2	C
<i>Scrophularia nodosa</i>	Common figwort	1					1	2	O
<i>Scutellaria galunculata</i>	Common skullcap					1		1	O
<i>Sedum acre</i>	Biting stonecrop	1						1	O
<i>Senecio jacobaea</i>	Common ragwort	1	1	1			1	4	C
<i>Senecio viscosus</i>	Sticky groundsel	1						1	O
<i>Silene dioica</i>	Red campion	1			1	1	1	4	C
<i>Silene vulgaris</i>	Bladder campion	1	1				1	3	O
<i>Solidago vigaurea</i>	Goldenrod		1	1				2	F
<i>Stachys sylvatica</i>	Hedge woundwort				1	1		2	C
<i>Stellaria graminea</i>	Lesser stitchwort	1	1	1	1		1	5	C
<i>Stellaria holostea</i>	Greater stitchwort			1	1			2	F
<i>Stellaria media</i>	Chickweed		1		1			2	C
<i>Succisa pratense</i>	Devilsbit scabious		1	1	1	1		4	VC
<i>Symphytum officinale</i>	Common comfrey	1				1	1	3	R ^g
<i>Taraxacum officinale</i>	Dandelion					1		1	C
<i>Teucrium scorodonia</i>	Wood sage	1	1	1	1	1		5	C
<i>Thuidium tamarascinum</i>					1	1		2	
<i>Thymus drucei</i>	Wild thyme		1	1				2	C
<i>Trifolium pratense</i>	Red clover	1					1	2	F
<i>Trifolium repens</i>	White clover	1		1	1		1	4	C
<i>Tussilago farfara</i>	Coltsfoot					1		1	F
<i>Ulex europaeus</i>	Gorse		1	1	1			3	C
<i>Urtica dioica</i>	Nettle	1			1		1	3	C
<i>Valaria officinalis</i>	Common valerian			1		1		2	C
<i>Veronica chamaedrys</i>	Germander speedwell	1	1	1	1	1		5	C
<i>Veronica officinalis</i>	Heath speedwell				1			1	C
<i>Vicia sativa</i>	Common vetch				1			1	O
<i>Viola riviniana</i>	Common dog violet	1	1	1	1	1		5	C
<i>Viola tricolor</i>	Wild pansy	1						1	O
Total number of species in each landform class		54	55	65	81	72	36		
Total number of species = 148									
a: Along River Tay									
b: Rare near River Tay									
c: Shingle islands of rivers Tay, Tummel and Garry									
d: Particularly on riverbanks									
e: Along rivers Tay, Tummel and Garry									
f: New record to Perthshire, 1997									
g: Only on Tomdachoille along R. Tummel									
* species thought not to be native to Perthshire									
o: pre-1970 record in the county									
VR: very rare									
R: rare									
O: occasional									
F: frequent									
C: common									
VC: very common									

Appendix 14.
Bonferroni post-hoc tests results for ANOVA.

Table 14: Bonferroni post hoc test for ANOVA showing the significant mean differences between landform types in bold at the 5% significance level. Analysis was performed for significant ANOVA results. Landform 1 = side-arm; 2 = abandoned channel; 3 = point bar; 5 = floodplain.

a) Elevation (m)

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	0.43	0.38	1.000	-0.61	1.46
	3	-0.61	0.32	0.377	-1.49	0.27
	5	-1.08	0.28	0.002	-1.85	-0.32
2	1	-0.43	0.38	1.000	-1.46	0.61
	3	-1.04	0.34	0.022	-1.97	-0.10
	5	-1.51	0.30	0.000	-2.33	-0.68
3	1	0.61	0.32	0.377	-0.27	1.49
	2	1.04	0.34	0.022	0.10	1.97
	5	-0.47	0.23	0.263	-1.09	0.15
5	1	1.08	0.28	0.002	0.32	1.85
	2	1.51	0.30	0.000	0.68	2.33
	3	0.47	0.23	0.263	-0.15	1.09

b) H'

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	-0.22	0.15	0.851	-0.63	0.19
	3	0.30	0.13	0.132	-0.05	0.65
	5	-0.19	0.11	0.581	-0.49	0.12
2	1	0.22	0.15	0.851	-0.19	0.63
	3	0.52	0.13	0.002	0.15	0.89
	5	0.04	0.12	1.000	-0.29	0.36
3	1	-0.30	0.13	0.132	-0.65	0.05
	2	-0.52	0.13	0.002	-0.89	-0.15
	5	-0.49	0.09	0.000	-0.73	-0.24
5	1	0.19	0.11	0.581	-0.12	0.49
	2	-0.04	0.12	1.000	-0.36	0.29
	3	0.49	0.09	0.000	0.24	0.73

c) S

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	-1.03	3.35	1.000	-10.26	8.19
	3	15.07	2.86	0.000	7.20	22.93
	5	-0.17	2.47	1.000	-6.98	6.65
2	1	1.03	3.35	1.000	-8.19	10.26
	3	16.10	3.03	0.000	7.76	24.44
	5	0.87	2.67	1.000	-6.49	8.22
3	1	-15.07	2.86	0.000	-22.93	-7.20
	2	-16.10	3.03	0.000	-24.44	-7.76
	5	-15.23	2.02	0.000	-20.80	-9.67
5	1	0.17	2.47	1.000	-6.65	6.98
	2	-0.87	2.67	1.000	-8.22	6.49
	3	15.23	2.02	0.000	9.67	20.80

d) Soil depth (cm)

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	-27.63	17.90	0.776	-76.94	21.67
	3	23.67	15.27	0.767	-18.38	65.72
	5	-22.87	13.22	0.542	-59.28	13.55
2	1	27.63	17.90	0.776	-21.67	76.94
	3	51.30	16.19	0.016	6.70	95.90
	5	4.77	14.28	1.000	-34.57	44.10
3	1	-23.67	15.27	0.767	-65.72	18.38
	2	-51.30	16.19	0.016	-95.90	-6.70
	5	-46.53	10.79	0.000	-76.27	-16.80
5	1	22.87	13.22	0.542	-13.55	59.28
	2	-4.77	14.28	1.000	-44.10	34.57
	3	46.53	10.79	0.000	16.80	76.27

e) Mean particle size

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	0.35	0.72	1.000	-1.64	2.34
	3	1.50	0.66	0.163	-0.32	3.32
	5	-0.35	0.57	1.000	-1.93	1.23
2	1	-0.35	0.72	1.000	-2.34	1.64
	3	1.15	0.61	0.399	-0.54	2.84
	5	-0.70	0.52	1.000	-2.14	0.73
3	1	-1.50	0.66	0.163	-3.32	0.32
	2	-1.15	0.61	0.399	-2.84	0.54
	5	-1.85	0.43	0.001	-3.04	-0.67
5	1	0.35	0.57	1.000	-1.23	1.93
	2	0.70	0.52	1.000	-0.73	2.14
	3	1.85	0.43	0.001	0.67	3.04

f) MINDOM

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	0.35	1.21	1.000	-2.99	3.69
	3	-2.20	1.10	0.315	-5.25	0.85
	5	0.23	0.96	1.000	-2.43	2.89
2	1	-0.35	1.21	1.000	-3.69	2.99
	3	-2.55	1.03	0.102	-5.39	0.29
	5	-0.12	0.87	1.000	-2.53	2.30
3	1	2.20	1.10	0.315	-0.85	5.25
	2	2.55	1.03	0.102	-0.29	5.39
	5	2.43	0.72	0.009	0.44	4.42
5	1	-0.23	0.96	1.000	-2.89	2.43
	2	0.12	0.87	1.000	-2.30	2.53
	3	-2.43	0.72	0.009	-4.42	-0.44

g) MAXDOM

(I) LANDFORM	(J) LANDFORM	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	0.00	20.02	1.000	-55.43	55.43
	3	-197.50	18.27	0.000	-248.10	-146.90
	5	-0.07	15.92	1.000	-44.14	44.00
2	1	0.00	20.02	1.000	-55.43	55.43
	3	-197.50	17.01	0.000	-244.60	-150.40
	5	-0.07	14.45	1.000	-40.08	39.94
3	1	197.50	18.27	0.000	146.90	248.10
	2	197.50	17.01	0.000	150.40	244.60
	5	197.43	11.92	0.000	164.43	230.43
5	1	0.07	15.92	1.000	-44.00	44.14
	2	0.07	14.45	1.000	-39.94	40.08
	3	-197.43	11.92	0.000	-230.43	-164.43

h) MEDOM

(I) LANDFORM	(J) LANDFORM	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	0.10	0.75	1.000	-1.97	2.17
	3	1.63	0.68	0.131	-0.26	3.51
	5	-0.09	0.59	1.000	-1.73	1.56
2	1	-0.10	0.75	1.000	-2.17	1.97
	3	1.53	0.64	0.125	-0.23	3.28
	5	-0.19	0.54	1.000	-1.68	1.31
3	1	-1.63	0.68	0.131	-3.51	0.26
	2	-1.53	0.64	0.125	-3.28	0.23
	5	-1.71	0.44	0.002	-2.94	-0.48
5	1	0.09	0.59	1.000	-1.56	1.73
	2	0.19	0.54	1.000	-1.31	1.68
	3	1.71	0.44	0.002	0.48	2.94

i) MODOM

(I) LANDFORM	(J) LANDFORM	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	0.10	0.93	1.000	-2.47	2.67
	3	5.63	0.85	0.000	3.28	7.97
	5	-0.74	0.74	1.000	-2.78	1.30
2	1	-0.10	0.93	1.000	-2.67	2.47
	3	5.53	0.79	0.000	3.34	7.71
	5	-0.84	0.67	1.000	-2.70	1.01
3	1	-5.63	0.85	0.000	-7.97	-3.28
	2	-5.53	0.79	0.000	-7.71	-3.34
	5	-6.37	0.55	0.000	-7.90	-4.84
5	1	0.74	0.74	1.000	-1.30	2.78
	2	0.84	0.67	1.000	-1.01	2.70
	3	6.37	0.55	0.000	4.84	7.90

j) Range

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	0.41	28.76	1.000	-78.87	79.70
	3	-145.58	24.90	0.000	-214.24	-76.91
	5	-0.86	21.96	1.000	-61.41	59.70
2	1	-0.41	28.76	1.000	-79.70	78.87
	3	-145.99	24.90	0.000	-214.66	-77.33
	5	-1.27	21.96	1.000	-61.83	59.29
3	1	145.58	24.90	0.000	76.91	214.24
	2	145.99	24.90	0.000	77.33	214.66
	5	144.72	16.60	0.000	98.94	190.50
5	1	0.86	21.96	1.000	-59.70	61.41
	2	1.27	21.96	1.000	-59.29	61.83
	3	-144.72	16.60	0.000	-190.50	-98.94

k) Soil group

(I) LANDFORM	(J) LANDFORM	Mean	Std. Error	Sig.	95% Confidence Interval	
		Difference (I-J)			Lower Bound	Upper Bound
1	2	-1.03	0.68	0.824	-2.92	0.85
	3	3.77	0.58	0.000	2.16	5.37
	5	-0.90	0.50	0.487	-2.29	0.49
2	1	1.03	0.68	0.824	-0.85	2.92
	3	4.80	0.62	0.000	3.10	6.50
	5	0.13	0.55	1.000	-1.37	1.64
3	1	-3.77	0.58	0.000	-5.37	-2.16
	2	-4.80	0.62	0.000	-6.50	-3.10
	5	-4.67	0.41	0.000	-5.80	-3.53
5	1	0.90	0.50	0.487	-0.49	2.29
	2	-0.13	0.55	1.000	-1.64	1.37
	3	4.67	0.41	0.000	3.53	5.80

Appendix 15.
Summary statistics of temporal analysis of landscape patches along the River Tummel between 1946-1994.

Table 15.1: Temporal variations in the mean area (ha²) of landscape patches within the Tomdachoille reach of the River Tummel.
 - land cover type absent

Land cover	1946	Stdev	1968	Stdev	1971	Stdev	1988	Stdev	1994	Stdev
Abandoned point bar	-	-	-	-	-	-	2.07	0	0.28	2561
<i>Betula</i> woodland	3.54	0	4.17	0	3.96	0	5.99	0	1.85	24160
<i>S. scoparius</i> scrub	0.09	0	0.88	3090	0.52	4675	0.44	2945	0.24	5352
Coarse grassland	-	-	4.54	0	4.28	0	2.80	0	2.10	0
Cut-off channel	0.74	1873	-	-	-	-	1.86	0	-	-
Herb rich grassland	3.32	29319	2.40	10688	1.05	11467	1.35	1705	0.61	5801
Mid-channel bar	-	-	0.19	0	0.24	1376	0.22	0	0.05	499
Open water	-	-	-	-	-	-	-	-	0.02	186
Pasture	16.34	0	7.11	15190	7.12	52483	9.90	29415	9.13	18495
Riparian woodland (gravel)	0.48	5343	0.28	1381	0.20	984	0.38	1237	0.22	2415
Riparian woodland (sandy)	0.30	0	0.14	0	0.15	689	1.68	3175	0.73	5652
River	10.95	0	11.44	0	14.78	0	10.97	0	14.11	0
Scrub	0.23	3021	0.44	0	0.15	1712	0.44	0	0.21	2188
Gravel (herb rich)	-	-	-	-	-	-	-	-	0.16	1392
Gravel (partially colonised)	-	-	0.71	0	0.34	3639	-	-	0.22	0
Backwater	-	-	-	-	-	-	0.25	0	0.72	6682
Swamp <i>G. fluitans</i>	-	-	-	-	-	-	-	-	0.05	0
Unvegetated gravel	1.35	7410	1.12	12000	0.57	6916	2.2	10178	1.03	13137
Vegetated mid-channel bar	-	-	0.17	0	-	-	0.45	0	0.43	0

Table 15.2: Temporal variation in shape indices $S1$ and $S2$ within the Tomdachoille reach on the River Tummel between 1946-1994.

- land cover type absent.

a) $S1$

Land cover	1946	Stdev	1968	Stdev	1971	Stdev	1988	Stdev	1994	Stdev
Abandoned point bar	-	-	-	-	-	-	0.06	0.00	0.20	0.06
<i>Betula</i> woodland	0.05	0.00	0.04	0.00	0.06	0.00	0.05	0.00	0.09	0.07
<i>S. scoparius</i> scrub	0.24	0.00	0.09	0.02	0.14	0.04	0.11	0.01	0.33	0.17
Coarse grassland	-	-	0.02	0.00	0.02	0.00	0.03	0.00	0.04	0.00
Cut-off channel	0.19	0.02	-	-	-	-	0.10	0.00	-	-
Herb rich grassland	0.06	0.03	0.04	0.00	0.15	0.12	0.05	0.00	0.20	0.15
Mid-channel bar	-	-	0.24	0.00	0.13	0.05	0.15	0.00	0.34	0.18
Open water	-	-	-	-	-	-	-	-	0.56	0.28
Pasture	0.01	0.00	0.02	0.01	0.06	0.03	0.01	0.00	0.01	0.00
Riparian woodland (gravel)	0.16	0.01	0.14	0.03	0.17	0.04	0.10	0.02	0.21	0.06
Riparian woodland (sandy)	0.15	0.00	0.24	0.00	0.18	0.04	0.09	0.02	0.17	0.04
River	0.05	0.00	0.06	0.00	0.05	0.00	0.05	0.00	0.04	0.00
Scrub	0.47	0.37	0.08	0.00	0.23	0.11	0.07	0.00	0.33	0.23
Gravel (herb rich)	-	-	-	-	-	-	-	-	0.18	0.07
Gravel (partially colonised)	-	-	0.06	0.00	0.13	0.03	-	-	0.15	0.00
Backwater	-	-	-	-	-	-	0.26	0.00	0.17	0.04
Swamp <i>G. fluitans</i>	-	-	-	-	-	-	-	-	0.43	0.00
Unvegetated gravel	0.11	0.04	0.16	0.11	0.32	0.31	0.07	0.02	0.56	0.65
Vegetated mid-channel bar	-	-	0.12	0.00	-	-	0.07	0.00	0.08	0.00

b) $S2$

Land cover	1946	Stdev	1968	Stdev	1971	Stdev	1988	Stdev	1994	Stdev
Abandoned point bar	-	-	-	-	-	-	1.27	0.00	1.46	0.39
<i>Betula</i> woodland	2.45	0.00	1.32	0.00	3.12	0.00	2.10	0.00	0.93	0.14
<i>S. scoparius</i> scrub	2.00	0.00	1.33	0.04	1.30	0.42	1.08	0.31	1.30	0.72
Coarse grassland	-	-	0.74	0.00	1.22	0.00	0.89	0.00	0.85	0.00
Cut-off channel	4.52	0.07	-	-	-	-	2.23	0.00	-	-
Herb rich grassland	2.41	0.98	0.95	0.12	1.18	0.23	0.94	0.01	1.60	0.69
Mid-channel bar	-	-	1.65	0.00	0.92	0.14	0.90	0.00	0.90	0.07
Open water	-	-	-	-	-	-	-	-	0.87	0.10
Pasture	1.46	0.00	0.72	0.18	1.79	0.30	0.65	0.15	0.68	0.10
Riparian woodland (gravel)	2.92	2.17	1.22	0.54	1.21	0.53	0.97	0.07	1.24	0.42
Riparian woodland (sandy)	2.36	0.00	2.29	0.00	1.09	0.35	1.95	0.57	2.04	0.92
River	4.24	0.00	1.25	0.00	3.12	0.00	2.37	0.00	2.25	0.00
Scrub	3.31	0.98	1.28	0.00	0.91	0.09	0.74	0.00	1.67	0.87
Gravel (herb rich)	-	-	-	-	-	-	-	-	0.94	0.09
Gravel (partially colonised)	-	-	0.28	0.47	1.02	0.30	-	-	1.11	0.00
Backwater	-	-	-	-	-	-	2.08	0.00	1.97	0.56
Swamp <i>G. fluitans</i>	-	-	-	-	-	-	-	-	1.46	0.00
Unvegetated gravel	3.24	0.63	2.87	1.19	1.56	0.52	1.45	0.51	1.60	0.73
Vegetated mid-channel bar	-	-	1.23	0.18	-	-	0.77	0.15	0.80	0.00

Table 15.3: Temporal variation in the mean area (ha²) of land cover types within the River Tummel study area between 1946-1994 (excluding 1971).

- Land cover type absent.

Land cover	1946	Stdev	1968	Stdev	1988	Stdev	1994	Stdev
Abandoned point bar	1.56	0	-	-	2.07	0	0.28	2561
Aquatic vegetation <i>E. fluviatile</i>	-	-	-	-	0.07	0	0.02	0
Arable	10.20	0	10.42	0	9.12	0	-	-
<i>Betula</i> woodland	1.93	15790	5.71	21743	5.80	2653	1.38	19686
<i>S. scoparius</i> scrub	0.15	948	0.65	4554	0.39	2256	0.21	29719
Coarse grassland	3.31	23250	1.78	16313	0.99	15672	0.84	9083
Cut-off channel	0.96	3405	-	-	1.16	9928	0.42	3832
Herb rich grassland	2.59	28207	1.82	12470	1.00	9381	0.70	6501
Mid-channel bar	0.37	2167	0.51	2956	0.77	7857	0.32	5053
Open water	0.06	26	0.27	0	-	-	0.02	691
Pasture	12.13	119842	8.53	69437	10.13	66253	9.77	33542
Riparian woodland (gravel)	0.45	3512	1.08	13393	0.48	1852	0.36	4760
Riparian woodland (sandy)	2.09	24673	3.13	51136	8.20	95032	2.80	35001
River	25.84	0	24.83	0	25.95	0	31.73	0
Scot's pine wood	-	-	-	-	0.67	0	1.48	0
Scrub	0.39	4312	0.64	2837	0.85	7050	0.18	2384
Gravel (herb rich)	-	-	-	-	-	-	0.33	3678
Gravel (partially colonised)	0.08	968	0.88	2348	-	-	0.22	0
Backwater	0.23	0	0.51	1444	0.36	1462	0.34	3915
Swamp <i>G. fluitans</i>	-	-	-	-	-	-	0.05	0
Unvegetated gravel	1.30	17508	1.39	10729	1.75	10384	0.53	9118
Vegetated mid-channel bar	-	-	0.17	0	0.45	0	0.26	1722

Table 15.4: Temporal variation in shape indices *S1* and *S2* within the River Tummel study area between 1946-1994 (excluding 1971).

- land cover type absent

a) *S1*

Land cover	1946	Stdev	1968	Stdev	1988	Stdev	1994	Stdev
Abandoned point bar	0.12	0.00	-	-	0.06	0.00	0.20	0.06
Aquatic vegetation <i>E. fluviatile</i>	-	-	-	-	0.22	0.00	0.51	0.00
Arable	0.02	0.00	0.02	0.00	0.02	0.00	-	-
<i>Betula</i> woodland	0.08	0.03	0.05	0.01	0.04	0.01	0.14	0.08
<i>S. scoparius</i> scrub	0.19	0.09	0.11	0.04	0.11	0.01	0.32	0.16
Coarse grassland	0.07	0.02	0.06	0.03	0.15	0.11	0.14	0.09
Cut-off channel	0.18	0.02	-	-	0.13	0.04	0.24	0.05
Herb rich grassland	0.14	0.04	0.06	0.03	0.11	0.08	0.16	0.11
Mid-channel bar	0.11	0.04	0.12	0.10	0.10	0.07	0.25	0.22
Open water	0.30	0.06	0.10	0.00	-	-	0.56	0.28
Pasture	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.00
Riparian woodland (gravel)	0.18	0.04	0.11	0.04	0.10	0.02	0.20	0.09
Riparian woodland (sandy)	0.10	0.04	0.10	0.06	0.07	0.03	0.14	0.06
River	0.05	0.00	0.05	0.00	0.05	0.00	0.04	0.00
Scot's pine wood	-	-	-	-	0.06	0.00	0.06	0.00
Scrub	0.27	0.24	0.08	0.00	0.08	0.02	0.30	0.21
Gravel (herb rich)	-	-	-	-	-	-	0.16	0.07
Gravel (partially colonised)	0.35	0.22	0.08	0.03	-	-	0.15	0.00
Backwater	0.24	0.00	0.14	0.03	0.21	0.07	0.26	0.11
Swamp <i>G. fluitans</i>	-	-	-	-	-	-	0.43	0.00
Unvegetated gravel	0.16	0.11	0.11	0.09	0.08	0.05	0.41	0.39
Vegetated mid-channel bar	-	-	0.06	0.00	0.05	0.03	0.15	0.08

b) *S2*

Land cover	1946	Stdev	1968	Stdev	1988	Stdev	1994	Stdev
Abandoned point bar	2.38	0.00	-	-	1.27	0.00	1.46	0.39
Aquatic vegetation <i>E. fluviatile</i>	-	-	-	-	0.94	0.00	1.18	0.00
Arable	0.89	0.00	0.89	0.00	0.79	0.00	-	-
<i>Betula</i> woodland	1.56	0.74	1.75	0.61	1.71	0.55	1.08	0.37
<i>S. scoparius</i> scrub	1.00	0.18	1.24	0.17	1.04	0.24	1.27	0.62
Coarse grassland	1.74	0.88	1.05	0.23	0.90	0.09	1.16	0.46
Cut-off channel	2.68	0.17	-	-	1.98	0.35	2.25	0.72
Herb rich grassland	2.52	0.51	1.01	0.13	1.05	0.40	1.46	0.66
Mid-channel bar	0.90	0.09	1.10	0.48	0.97	0.20	1.04	0.20
Open water	1.15	0.21	0.82	0.00	-	-	0.87	0.10
Pasture	0.98	0.21	0.85	0.01	0.78	0.03	0.81	0.15
Riparian woodland (gravel)	1.75	0.72	1.39	0.58	1.07	0.17	1.32	0.48
Riparian woodland (sandy)	1.88	1.28	1.60	0.45	2.26	0.55	1.93	0.79
River	3.86	0.00	4.34	0.00	4.09	0.00	4.09	0.00
Scot's pine wood	-	-	-	-	0.82	0.00	1.23	0.00
Scrub	1.32	0.53	0.96	0.24	1.10	0.32	1.24	0.56
Gravel (herb rich)	-	-	-	-	-	-	1.09	0.31
Gravel (partially colonised)	1.08	0.22	1.27	0.65	-	-	1.11	0.00
Backwater	1.84	0.00	1.54	0.11	1.89	0.27	1.85	0.37
Swamp <i>G. fluitans</i>	-	-	-	-	-	-	1.46	0.00
Unvegetated gravel	3.61	0.94	2.60	0.96	2.52	0.92	2.47	1.13
Vegetated mid-channel bar	-	-	0.39	0.00	0.77	0.01	1.03	0.27

Table 15.5: Temporal variation in the mean area (ha²) of landscape patches within the River Tummel study area between 1946-1994 (excluding 1971).

- Land cover type absent.

Land cover	1946	Stdev	1968	Stdev	1988	Stdev	1994	Stdev
Abandoned channel	0.70	1515	1.51	4089	0.30	0	0.91	0
Abandoned point bar	3.51	0	-	-	4.15	0	3.02	0
Alluvial plug	-	-	-	-	0.72	0	-	-
Channel	26.07	0	24.83	0	25.95	0	31.75	0
Cut-off channel	1.28	2084	-	-	1.16	9928	0.33	3146
Embankment	1.11	0	0.88	3090	0.72	0	0.39	0
Floodplain (agriculture)	11.66	85128	8.65	56746	9.88	54329	9.74	52470
Floodplain (semi-natural)	5.52	34600	7.53	62227	10.76	98673	6.07	70189
Mid-channel bar (unvegetated)	0.37	2167	0.58	1912	0.77	7857	0.37	5421
Mid-channel bar (vegetated)	-	-	0.37	0	0.45	0	0.43	0
Point bar	2.07	12065	2.68	23815	3.44	20197	2.62	17797
River banks	0.87	7619	1.15	9559	1.46	0	1.35	11884
Lateral bar	1.54	19534	0.48	4037	0.65	6110	0.37	5901
Backwater	0.18	726	0.51	1444	0.36	1462	0.32	4036

Table 15.6: Temporal variation in the shape indices $S1$ and $S2$ of the geomorphic landforms within the River Tummel study area between 1946-1994.

- Land cover type absent

a) $S1$

Land cover	1946	Stdev	1968	Stdev	1988	Stdev	1994	Stdev
Abandoned channel	0.18	0.02	0.09	0.02	0.15	0.00	0.10	0.00
Abandoned point bar	0.04	0.00	-	-	0.04	0.00	0.04	0.00
Alluvial plug	-	-	-	-	0.08	0.00	-	-
Channel	0.05	0.00	0.05	0.00	0.05	0.00	0.04	0.00
Cut-off channel	0.15	0.01	0.00	0.00	0.13	0.04	0.29	0.09
Embankment	0.13	0.00	0.09	0.02	0.10	0.00	0.15	0.00
Floodplain (agriculture)	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01
Floodplain (semi-natural)	0.04	0.02	0.04	0.02	0.03	0.01	0.04	0.01
Mid-channel bar (unvegetated)	0.11	0.04	0.08	0.03	0.10	0.07	0.26	0.23
Mid-channel bar (vegetated)	-	-	0.08	0.00	0.07	0.00	0.08	0.00
Point bar	0.07	0.02	0.07	0.04	0.04	0.02	0.07	0.05
River banks	0.14	0.06	0.11	0.07	0.08	0.00	0.12	0.08
Lateral bar	0.14	0.16	0.17	0.11	0.17	0.07	0.37	0.26
Backwater	0.26	0.03	0.14	0.03	0.21	0.07	0.26	0.11

b) $S2$

Land cover	1946	Stdev	1968	Stdev	1988	Stdev	1994	Stdev
Abandoned channel	4.17	0.61	3.16	0.17	2.36	0.00	2.81	0.00
Abandoned point bar	2.19	0.00	-	-	2.27	0.00	2.00	0.00
Alluvial plug	-	-	-	-	1.95	0.00	-	-
Channel	6.65	0.00	7.69	0.00	6.68	0.00	6.71	0.00
Cut-off channel	4.75	0.57	-	-	3.51	0.63	4.04	0.90
Embankment	3.98	0.00	2.36	0.06	2.30	0.00	2.70	0.00
Floodplain (agriculture)	1.57	0.37	1.44	0.13	1.38	0.04	1.40	0.11
Floodplain (semi-natural)	1.90	0.36	2.16	0.65	2.58	1.20	2.23	1.05
Mid-channel bar (unvegetated)	1.59	0.16	1.61	0.28	1.72	0.36	1.67	0.24
Mid-channel bar (vegetated)	-	-	1.44	0.00	1.37	0.00	1.43	0.00
Point bar	2.74	0.43	2.55	0.42	2.04	0.65	2.23	0.48
River banks	3.17	0.78	2.49	0.45	2.75	0.00	3.28	1.51
Lateral bar	2.32	1.50	2.36	0.70	3.28	0.55	2.68	1.34
Backwater	3.06	0.29	2.73	0.20	3.35	0.49	2.85	0.70