Supporting conservation policy and management for protected woodland species in Britain

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DECLARATION

I hereby declare that this thesis has been completed by myself, and it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

Alice C. Broome

Summary

Conservation action is urgently required to address global decline in biological diversity. Research evidence underpins approaches to prioritize and conserve biodiversity, assists in setting strategic international policy, guides country policy and actions plans, and informs conservation management, formulation of incentives and adherence to legislation. Appropriate and sound evidence, accessible to policymakers and practitioners is therefore required and the challenge to fill knowledge gaps remains.

Research evidence has to be delivered at the level where conservation policies and actions are applied. This is often at a sector by country level. I have used the forestry sector in Britain to illustrate this ‘downscaling’ of evidence appropriate to its application. Consequently, the focus of this thesis is British woodlands. The underlying research theme is the identification of woodland protected species resource needs and understanding how woodland management influences these resources.

Chapter 1 considers the types and qualities of research that is appropriate to my thesis topic and introduces five sequential stages in accumulating and reviewing knowledge (five ‘*Knowledge Acquisition Stages’*) required in providing an evidence base to species conservation policy and practice. Chapters 2 to 9 describe individual studies and provide examples of each of the five stages, appropriate to the maturity of knowledge that is already held on the species.

Even for relative well studied taxa, information about their distribution is needed to report on status and trends. Species surveys can additionally aid our understanding of species habitat requirements (*Knowledge Acquisition Stage 1 and 2*). Examples are provided for Scottish crossbill (Chapter 1) and juniper (Chapter 3). Understanding how species may respond to habitat change (*Knowledge Acquisition Stage 3*) is a key component of evidence-based conservation and importantly whether management interventions considered beneficial have unintended consequences for the protected species using habitats where management is applied. I report on the outcomes for moths of coppice management (Chapter 4) and epiphytic lichens of woodland restoration

(Chapter 5). Conservation evidence needs to be accessible and research findings disseminated in a form that is relevant to the end user (*Knowledge Acquisition Stage 4*). I synthesize knowledge to provide a system to assess the value of lowland broadleaved woodlands for declining woodland birds (Chapter 6) and another to map the potential of the native woodland resource to support 179 of the 208 woodland species identified for protection in Scotland (Chapter 7). Reliability of evidence for conservation decision-making is important for ensuring efficacy of conservation actions. I illustrate field-testing of management recommendations (*Knowledge Acquisition Stage 5)* for creating brood habitat for capercaillie in pine plantations (Chapter 8), and for encouraging natural regeneration of juniper in upland acid grassland habitats (Chapter 9).

Supporting conservation policy and management for protected woodland species in Britain requires a varied research approach, as the level of baseline knowledge on different taxa (*Knowledge Acquisition Stages*) is diverse. I found ecological theory, particularly the niche concept and plant succession, provided a sound basis for my work. In Chapter 10, I reflect on the impact of my research and the scale at which the information is delivered to meet end-user needs. My research is of instrumental, symbolic and conceptual use to the forestry sector. The information is provided for end users at strategic, tactical and finer scales for policy advisors, forest planners and operational decision-makers, respectively.

Although my thesis describes a framework for gathering and assessing knowledge of high utility to forestry decision-makers, it does not provide an answer to all woodland conservation policy and management needs. Further, whilst I provide examples of single species and multi-species focused research, I do not make an overall choice between delivering specific action for individual protected species or undertaking management that benefits multiple species. Instead, I suggest adopting a scaled approach based on the level of legal protection a species has. Otherwise, delivering effective policy and management recommendations, which meet both these needs, is too challenging without further research to accumulate, review and disseminate evidence.

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Table of Contents

Chapter One: Introduction **19**
1.1 Biodiversity in crisis 19
1.1.1 A challenge for research 19
1.1.2 What to conserve 20
1.1.3 Where to focus conservation effort 20
1.1.4 Approaches to the conservation of biological diversity in forests 21
1.2 Building the evidence to support policy and practice 24
1.2.1 Evidence-based conservation 24
1.2.2 Ecological theory and concepts 24
1.2.3 Boundary science and a Knowledge Acquisition framework 28
2.1 Thesis aims and objectives 30

Chapter Two: Association between crossbills and North American conifers in Scotland **33**
2.1 Abstract 34
2.2 Introduction 35
2.3 Methods 37
2.3.1 Study area and sampling design 37
2.3.2 Cone characteristics 40
2.3.3 Analysis 40
2.4 Results 41
2.4.1 The conifer resource 41
2.4.2 Associations between crossbills and habitat variables 44
2.4.3 Cone characteristics 47
2.4.4 Bill sizes of crossbills 48
2.5 Discussion 48
2.6 Acknowledgments 52

Chapter Three: Can the site conditions required for successful natural regeneration of juniper (*Juniperus communis* L.) be determined from a single species survey? **53**
3.1 Abstract 54
3.2 Introduction 54
3.3 Materials and methods 56
3.4 Results 59
3.4.1 Principal component analysis 59
3.4.2 Maxent modeling 64
3.5 Discussion 64
3.5.1 Detecting natural regeneration 64
3.5.2 Site conditions associated with the natural regeneration of juniper 65
3.5.3 Inferred change in site conditions over time 66
3.5.4 Appropriate conservation management of sites with juniper 67
3.5.5 Usefulness of national survey data in informing conservation action 68
3.6 Conclusions 71
3.7 Acknowledgements 71

Chapter Four: The effect of coppice management on moth assemblages in an English woodland. **73**
4.1 Abstract 74
4.2 Introduction 74
4.3 Materials and methods 77
4.3.1 Study area 77

4.3.2 Moth trapping ... 77
4.3.3 Vegetation surveys ... 80
4.3.4 Data analysis ... 80
4.4 Results ... 81
4.4.1 Moth species and assemblages ... 81
4.4.2 Habitat conditions characterising the coupe stages ... 88
4.5 Discussion ... 92
4.6 Conclusions ... 97
4.7 Acknowledgments ... 98

Chapter Five: Epiphytic lichens of Atlantic oakwood remnants can survive early stages of woodland restoration ... **101**
5.1 Abstract ... 102
5.2 Introduction ... 103
5.3 Material and methods ... 106
5.3.1 Study site ... 106
5.3.2 Experimental design ... 107
5.3.3 Ground flora assessment ... 108
5.3.4 Lichen assessment ... 108
5.4 Data analysis ... 109
5.4.1 Evaluating restoration success through ground flora species and functional trait composition ... 109
5.4.2 Evaluating the impact of clear-felling on lichen survival ... 111
5.5 Results ... 112
5.5.1 Evaluation of change in ground vegetation and functional-trait composition ... 112
5.5.2 Impact of clear-felling on epiphytic lichens ... 116
5.6 Discussion ... 120
5.6.1 Overview ... 120
5.6.2 Ground vegetation response measures of restoration success and timeframe of restoration ... 120
5.6.3 Lichen response ... 122
5.7 Conclusion ... 124
5.8 Acknowledgements ... 124

Chapter Six: Implications of lowland broadleaved woodland management for the conservation of target bird species ... **129**
6.1 Abstract ... 130
6.2 Introduction ... 130
6.3 Lowland broadleaved woodland study ... 134
6.3.1 Design and survey methods ... 134
6.3.2 Results of the field study ... 136
6.4 Resource requirements and woodland features for the target bird species ... 141
6.4.1 Methods ... 141
6.4.2 Results ... 142
6.5 Discussion and conclusions ... 146

Chapter Seven: Niches for Species, a multi-species model to guide woodland management: an example based on Scotland's native woodlands ... **149**
7.1 Abstract ... 150
7.2 Introduction ... 150
7.3 Material and methods ... 154
7.3.1 The Niches for Species framework ... 154
7.3.2 This woodland application ... 154
7.3.3 Validation of model ... 165
7.3.4 Choice of Niches for Species model outputs ... 166

7.4 Results 167
7.4.1 Spatial environmental data used to map niche occurrence in polygons 167
7.4.2 Validation 167
7.4.3 Example Niches for Species model outputs 169
7.5 Discussion 172
7.5.1 Adequacy of data and model strengths 172
7.5.2 Model validation 173
7.5.3 Application 174
7.6 Acknowledgments 176

Chapter Eight: An evaluation of thinning to improve habitat for capercaillie (*Tetrao urogallus*) **185**
8.1 Abstract 186
8.2 Introduction 187
8.3 Methods 190
8.3.1 Study sites 190
8.3.2 Thinning treatments 192
8.3.3 Measuring herbivore effects 193
8.3.4 Vegetation assessments 195
8.3.5 Data analysis 195
8.4 Results 198
8.4.1 Bilberry response to thinning treatments 198
8.4.2 Comparison with conservation management thinning guidance 199
8.5 Discussion 203
8.5.1 Bilberry response to thinning and clearfell treatments in study 203
Scots pine plantations 203
8.5.2 Management guidance for thinning 205
8.5.3 Compatibility between capercaillie brood habitat enhancement 205
measures and other plantation management objectives 205
8.6 Acknowledgements 207

Chapter Nine: Promoting natural regeneration for the restoration of *Juniperus communis*: a synthesis of knowledge and evidence for conservation practitioners **209**
9.1 Abstract 210
9.2 Introduction 211
9.3 Methods 214
9.3.1 Literature search and general review methods 214
9.3.2 Study areas 215
9.3.3 Management treatments 216
9.3.4 Direct sowing 216
9.3.5 Germination and regeneration assessments 218
9.3.6 Vegetation monitoring 218
9.3.7 Data analysis 218
9.4 Results 221
9.4.1 Site conditions associated with J. communis *regeneration from the review of regeneration surveys and studies* 221
9.4.2 Results from the review of regeneration surveys 221
9.4.3 Management interventions used to encourage natural regeneration of J. communis *from the review of management studies* 224
9.4.4 Germination of directly sown J. communis *seed in the field trials* 225
9.4.5 Response of J. communis *natural regeneration to intervention observed in the field trials* 225
9.4.6 Vegetation cover and composition characterizing regeneration microsites at one cattle-grazed field trial site (Fungarth) 225

9.4.7 Creation of regeneration microsites by scarification and grazing treatments used in the field trial 228
9.5 Discussion 230
9.5.1 Site and microsite conditions associated with J. communis *regeneration.* 231
9.5.2 Management methods that create site and microsite conditions for J. communis *regeneration* 232
9.5.3 Wider constraints on J. communis *regeneration* 234
9.6 Conclusions 235
9.7 Acknowledgements 236

Chapter Ten: Discussion and Conclusions 249
10.1 Introduction 249
10.2 Building on current knowledge of species to direct appropriate research 249
10.2.1 Knowledge Acquisition stages 1 and 2 249
10.2.2 Knowledge Acquisition stages 3 and 4 251
10.2.3 Knowledge Acquisition stage 5 252
10.3 Using ecological theory to provide a sound basis for research 253
10.3.1 Niche concept 254
10.3.2 Succession and disturbance 256
10.4 Information accessibility and end-user needs 257
10.4.1 Research impact 257
10.4.2 Scale and detail of information to match end-user needs 261
10.5 Single versus multi species conservation approach 262
10.6 Conclusions 263

Literature Cited 265

List of Figures

Figure 1.1 Sequence of woodland stand stage development following a successional process. 26
Figure 1.2 Woodland stand structures. 27
Figure 1.3 Stages of knowledge acquisition. 29
Figure 2.1 The distribution of sample points for crossbills. 37
Figure 2.2 The percentage of areas of different conifers. 42
Figure 2.3 Planting years for different conifers. 43
Figure 2.4 The structure of the different conifer stands. 44
Figure 2.5 Cone indices for conifers. 45
Figure 2.6 The modelled effect of the percentage of lodgepole pine on the probability of a survey point having Scottish crossbills. 47
Figure 2.7 The relationship between mid-cone scale thickness and cone length for different conifers. 49
Figure 2.8 Mean bill depths of North American and western Palearctic male crossbill taxa . 49
Figure 3.1 Principal component analysis bi-plot. 61
Figure 3.2 Age structure of juniper populations and site conditions for natural regeneration. 62
Figure 3.3 Partial dependence plots showing the marginal response of juniper to the seven variables. 63
Figure 4.1 Map of Rewell Wood, West Sussex, showing layout of the coupes. 79
Figure 4.2 Correspondence analysis of the night-flying moth species sampled by light-trapping over a 3 year period. 84
Figure 4.3 Change in habitat conditions described by coppice growth and structure and ground vegetation. 90
Figure 5.1 Location of Glencripesdale oak woodland and of the nine other Scottish oak woodlands. 107
Figure 5.2 ASNW/PAWS/remnant matrix and experiment design 107
Figure 5.3 Principal Components Analysis conducted on functional trait data 115
Figure 5.4 Chlorophyll fluorescence measured in two Lobarion lichen species. 117
Figure 5.5 Bootstrapped confidence intervals (95%) for mean change in epiphyte cover. 119
Figure 6.1 Approximate locations of sites in southern England and the Welsh Marches that were sampled in the extensive field study of lowland broadleaved woodland.. 135
Figure 6.2 Characteristic stand structure types (A–F). 144
Figure 7.1 A schematic flow chart illustrating the steps involved in Niches for Species expert-based habitat suitability modeling framework 156
Figure 7.2 Hierarchical representation of the breakdown of a species resource requirement 159
Figure 7.3 Graphical representation of the Niches for Species model development for Stage 4. 160
Figure 7.4 Species richness of native woodlands in Scotland. 169

Figure 7.5 Sample output from the Niches for Species model showing predicted distribution of protected woodland species richness by native woodland polygon in a 10 km x 10 km. 170
Figure 7.6 Sample output from the Niches for Species model showing predicted location of a protected woodland species in native woodland polygons in a 10 km x 10 km area. 171
Figure 8.1 Plan of study sites with locations of 50 m x 50 m treatment plots. 194
Figure 8.2 Plot layout used at both study sites (Inshriach and Novar) showing area thinned/clearfelled or left unthinned. 196
Figure 8.3 Bilberry response to variable intensity thinning, to clearfell treatment) and to control. 200
Figure 8.4 Stem density and tree heights in a model Scots pine plantation. 201
Figure 8.5 Bilberry response at Inshriach to thinning applied according to Parlane et al. (2006) prescription, not to prescription and to control. 203
Figure 9.1 Generic design for trial layout at the two Scottish trial sites receiving scarification treatment and two Scottish trial sites receiving cattle grazing treatment. 220
Figure 9.2 PCA bi-plot showing the distribution of ground vegetation cover variables at the field trial site. 227
Figure 9.3 Vegetation composition of the *J. communis* regeneration microsites and root collar diameter of seedlings. 227
Figure 9.4 Change in exposed bare ground over six years at the two trial sites subject to initial scarification treatment. 228
Figure 9.5 Change in occurrence of exposed bare ground and exposed moss cover over six years at the cattle grazed trial sites. 229
Figure 9.6 Change in vegetation height at two annually cattle grazed sites. 230
Figure 10.1 Impact of my research within the context of response options for sustainable management of British forests. 259

List of Tables

Table 2.1. A correlation matrix between the explanatory variables used in the analysis 41
Table 2.2 Maximum likelihood estimates from logistic regressions 46
Table 2.3 Lengths of conifer cones in Highland Scotland.. 47
Table 3.1 Descriptions of four morphological growth stages of juniper 57
Table 3.2 Summary information for the juniper (*Juniperus communis*) sites managed under four land use types derived from survey data. 60
Table 4.1 Coppice age at time of night flying moth survey 79
Table 4.2 Numbers of scarcer moth species listed with a conservation status 82
Table 4.3 Examples of moths associated with different stages of coppice development 85
Table 4.4 Numbers of moth species and numbers of individuals associated with three different stages of coppice development. 89
Table 4.5 Tree, shrub, climber and ground flora species recorded during the vegetation surveys. 91
Table 5.1 Total species richness in quadrats 112
Table 5.2 Quadrat frequency of desired invader and precursor ground flora species.. 114
Table 5.3 Change in percentage of cover for each species of lichen. 118
Table 6.1 Summary of resource requirements for 17 target bird species. 132
Table 6.2 Summary of literature review on effects of woodland management on birds. 133
Table 6.3 An overview of positive or negative effects of structural habitat features based on multivariate model weights 138
Table 6.4 Numbers of bird species for which associations with individual structural habitat features were identified. 139
Table 6.5 Target bird species for which negative or positive effects of increasing amounts of habitat features were detected 140
Table 6.6 Occurrence of the six characteristic stand types in different stages of stand development. 143
Table 7.1 Number of sources of evidence by evidence type used in identifying habitat requirements, by taxon. 157
Table 7.2 Summary of structure types used in the classification of niches providing habitat for 179 protected woodland species in Scotland 159
Table 7.3 Rule-set for combining spatial environmental data 162
Table 7.4 Correspondence between the habitat availability for ten validation species predicted using Niches for Species model and records of species occurrence and pseudo-absence 168
Table 8.1 Summary of site and stand information for the two study sites 191
Table 8.2 Mean values for measures of stand variables within the plots at the two study sites before and after thinnin treatments 199
Table 9.1 Summary descriptions of sites used, management interventions applied and monitoring in the *Juniperus communis* regeneration trial 217
Table 9.2 Support for the effects of site variables on promoting or restricting regeneration of *Juniperus communis* 222

List of Appendices

Appendix 4.1 Scarcer night-flying moth species recorded from managed sweet chestnut coppice (1 to 19 year old coppice coupes) in Rewell Wood, West Sussex between 2002 and 2004. 99
Appendix 5.1 Climatic data for Scottish oak woodlands........ 125
Appendix 5.2 Technical details on lichen data collection and processing......... 126
Appendix 5.3 Baseline vegetation pre-felling: distribution of species-specific functional traits along the PAWS to ASNW transect........ 127
Appendix 7.1 A small sample of database of ecological information associated with species included in the Niches for Species model............ 177
Appendix 7.2 Protected woodland species occurring in Scotland which are included in Niches for Species model and approach used to constrain predicted distribution (lack of 'X' indicates no constraints applied). 180
Appendix 9.1 *Juniperus communis* regeneration surveys conducted within the Atlantic North and the Atlantic Central environmental zones of Europe 237
Appendix 9.2 *Juniperus communis* management studies conducted within the Atlantic North and the Atlantic Central environmental zones of Europe. 243
Appendix 9.3 Loading values (superior to 0.1) for species groups used in the Principal Component Analysis (Figure 1) . The Principal Component Analysis investigated the distribution of ground vegetation cover variables at the field trial site, Fungarth (both grazed and ungrazed area), in samples with and without *Juniperus communis* natural regeneration; regeneration indicated by the presence of 1 to 2 year old seedlings. 247

Chapter One: Introduction

1.1 Biodiversity in crisis

Intensification measures causing habitat loss and degradation have taken their toll on biodiversity with an average of 70% decline globally in populations of c. 4000 species of birds, mammals, amphibians and reptiles, reported since 1970 (Zoological Society of London and WWF, 2018). The intensification of agriculture across the western world through the ‘Green Revolution’, forest removal to provide grazing lands for beef production in South America and the logging of tropical forests for quality hard woods globally, are all well known examples of what is now recognised as non-sustainable land management prevalent in the 20th and 21st centuries (Ormerod et al, 2003; PAB; FAO 2015; Keenan et al, 2015). The impact of humans on biodiversity is however believed to stretch back to before the Quaternary Period and a sevenfold reduction in biomass of wild animals and a two fold decline in plant biomass since the start of human civilisation has been calculated (Bar-On et al, 2018). Currently the rate of species’ population decline outweighs that of species extinctions, but some believe declines signal the sixth mass extinction (Briggs 2017; Ceballos et al, 2017; Thomas et al, 2004, IUCN, 2018).

1.1.1 A challenge for research

Historically, research and associated technological development has formed the basis of management policies and practices aimed to maximise exploitation and production of resources for humans. With human population levels anticipated to rise by another 50% by 2100 (UN DESA 2017) and the extreme levels of global environmental change which now faces humanity, finding solutions to redressing environmental damage and to deliver sustainable intensification to meet future population needs is evermore challenging (e.g. Pretty 2018; Wilson et al, 2007; DeFries et al, 2012).

The continued global decline in biodiversity and the limited resources with which to tackle the problem, heightens the requirement to address the question ‘what is the most effective way to achieve the conservation of biological diversity?’ Evidence is urgently needed to guide policy and management decisions on the ‘what’, ‘where’ and ‘how’ of biodiversity conservation. To provide such evidence when time and resources are limited, I propose that research needs to be conducted which is well targeted and appropriate to the state of knowledge, as well as being sound and accessible to the end-users.

1.1.2 What to conserve

A primary question underpinning the conservation of biological diversity is ‘what’ should be conserved. Species have dominated as the most widespread unit of measure of biodiversity since the beginning of the conservation movement (e.g. Cadotte et al, 2010). Given the pressure on time to identify and inventory species (UNEP/Bio.Div.2/3, 1990) and the limited resources available for this, the need to prioritise species for protection has intensified and the system of triage is recommended to sort and choose the most urgent cases for conservation when there is insufficient resources to conserve everything (Rudd 2011; Marris 2007). Views differ on how species are rated for prioritisation. For example, features such as identification of species making significant contributions to phylogenetic diversity or species indicating the presence of a large habitat area and an associated wide array of species (umbrella species) or species providing a pivotal function in the ecosystem (keystone species) have been suggested (Simberloff 1998; Winter et al, 2013). Or more frequently, prioritisation is by an assessment of rarity and/or risk of extinction of species and also the chances of successful conservation (Botrtril et al, 2008; Cadotte et al, 2010; Favaro et al, 2014; Vane-Wright et al, 1991).

1.1.3 Where to focus conservation effort

The delimitation of areas for the protection of the species has been part of national and international conservation planning for decades and networks of protected areas exist globally (Orlikowska et al., 2016). These were originally based on targeting 10% of the major biomes a target that was exceeded by 1.5% in 2003 (Dinerstein et al., 2017; Rodrigues et al., 2004). An alternative to a percentage area base approach is to identify areas with specific features: containing high levels of biodiversity, representing biodiversity not protected elsewhere, or where biodiversity is threatened (Margules and Pressey 2000; Rodrígues et al, 2011).

1.1.4 Approaches to the conservation of biological diversity in forests

Habitat level conservation actions

Setting forest areas with high natural values aside as reserves, where management and use becomes restricted, is a key approach to area based conservation measures, and globally areas of protected forest of high ecological values has increased (from 7.7% in 1990 to 16.3% in 2015) (Morales-Hidalgo et al, 2015; Bernes et al, 2015). Countries with high levels of biodiversity and endemism, such as Indonesia often aim to meet conservation objectives primarily through designating areas for protection and ex-situ conservation e.g. botanical gardens (Darajati et al, 2016).

The effectiveness of protected area networks has been questioned as the protection afforded varies with species group, habitat and country e.g. most of the European endangered wetland vertebates were adequate covered but only 7% of the endangered saproxylic beetles in Italy are afforded protection (e.g. D'Amen et al, 2013; Davis et al, 2014). Besides non enforcement of the protection, reasons for failure in meeting these objectives of protecting species by area based conservation include: decline in condition of habitat within protected areas (Zehetmair et al, 2015, Hedwall and Mikusiński 2015) and insufficiency of area, leading to the risk of extinction of species with either large core area requirements (e.g. wolves) or species existing as meta populations with the need for multiple connected sites (Hanski 1988). Approaches to address these shortcomings include reinstatement of natural processes such as fire, and actively applying interventions to create disturbance to maintain the protected areas in a condition which continues to support biodiversity (Zehetmair et al, 2015; Kovac et al, 2018). Further, integrating protected areas in to the wider landscape by adopting sustainable management of habitats within matrix surrounding protected areas as well as creating habitat connectivity, are actions set out in the 2011 to 2020 Strategic plan for biodiversity (CBD 2011). For forests, Sustainable Forest Management (SFM) is recognised as a guiding principle on how to "manage forests to provide for today's needs and not compromise (i.e. reduce) the options of future generations" (Forest Principles, UN Rio, 1992- see MacDicken et al, 2015). SFM-related policies and regulations are reported to be in place on 97% of the global forest area (MacDicken et al, 2015), (see Box 1 for British forestry example).

Box 1: Designated woodland areas in Britain and policies for their management

In Britain, 287 thousand hectares of woodland are designated for biological conservation in the form of Sites of Special Scientific Interest, National and Local Nature Reserves, Special Protection Areas and Special Areas of Conservation, and the intention of increasing the extent of areas for nature conservation has been adopted in to national policy in England (FAO, 2015; Defra, 2011; Lawton et al, 2010).

From 2000, Sustainable Forest Management (SFM) has been the main driver of forest policy as articulated by the UK Forestry Standard (FC, 2017) which sets out the requirements for how forestry is conducted in the UK.

Habitat restoration is seen as an essential tool to redress the changes made through intensification policies and practices of earlier decades which were unsustainable (SER 2004). A review of the 200 restoration projects from around the world registered on the Society of Ecological Restoration's database, showed a quarter to be forest habitats, indicating the extent of forest degradation and the efforts to improve it (Hallett et al, 2013). Habitat restoration is identified as a priority for biodiversity protection in temperate broadleaved and mixed forests (Dinerstein et al, 2017), (see Box 1 for British forestry example).

Box 2: Intensification of British forestry and policy response

In Britain, intensification of timber production usually by afforestation was aimed at building a strategic timber reserve when less than 5% of Britain's land area was wooded (early 1900's), and at supporting a domestic timber industry (mid 1900's). Multiple objective forestry arose in the 1980's as a policy in recognition of the collateral damage that afforestation was having particularly on the uplands and ancient woodlands, and to incorporate conservation objectives as well as cultural and aesthetic values in to forestry policy. Restoration of planted ancient woodland sites is now a policy priority and one to redress the effects of timber production 'intensification' policies of the 20th century (Sutherland et al, 2000).

Species level conservation actions

Whilst restoring habitat condition is seen by some as the most efficient method of conserving biodiversity (Egoh et al, 2014), doubts still remain whether broad-level habitat management delivers effective conservation for rare and protected species as many have very specific requirements, and more directly targeted action for single species conservation may offer clearer more tractable management goals (Boersma et al, 2001; Lundquist et al., 2002; Taylor et al., 2005). Species protection legislation provides a key mechanism for delivering conservation for individual species (e.g. Favaro et al, 2014). Decisions taken under the Multilateral Environmental Agreements are informed by the IUCN Red

List of Threatened Species and, being legally binding, are transposed in to country legislation providing a mechanism for enforcement (IUCN 2018). Signatory countries to the CDB, for example, have developed national strategies listing protected habitat and species for their various countries and written associated action plans for the list species maintenance or population recovery (CBD 2018). Delivery of the actions identified, if not required by law, are largely incentivized (see Box 3 for British forestry example).

Box 3: The UK's action on protected species and the enabling options available for sustainable management of forest

In the UK, targets to halt the loss of biodiversity and reverse previous losses through action targeted at species and habitat is outlined in the National Biodiversity Framework and, following a review of species in 2007 (BRIG, 2007), around 3000 species (marine and terrestrial) are identified as having some level of legal protection in the UK (JNCC and Defra, 2012). Of these, c. 420 species are associated with woodlands in Britain. Only a quarter of the woodland species are represented by better known taxa (birds, mammals amphibians, reptiles and vascular plants) whereas the remainder are species of invertebrates and non-vascular plants (bryophytes, lichens, liverworts, fungi) which tend to be more cryptic and less well studied (Di Minin and Moilanean, 2014; DiMarco et al., 2017).

Over the last two decades, policies on rare species conservation have been guided by detailed action plans for recovery of single species by incentivising conservation action for natural resource managers. (e.g. before 2007 the Forestry Commission was a listed as a partner in delivery of 135 species action plans (Broome et al, 2005)). With the rise in the number of rare species recognised for protection (BRIG, 2007), conservation action is increasingly dependent on legislation, licencing and clauses attached to grants and other management programmes (e.g. Natural England, 2013). For example:

- all woodland owners have personal responsibility to work within the wildlife laws when managing woodlands e.g. not killing or harming (schedules of the Wildlife and Countryside Act (W&CA)), avoiding damage, disturbance of breeding sites (all wild birds) and resting places (European Protected Species) (Directive 2009/147/EC, Directive 92/43/EEC, W&CA (see http://jncc.defra.gov.uk/page-1377))
- there is an expectation that a 'duty of care' for all priority listed species will be exercised on all public land, and on private land by managers in receipt of public funding (e.g. woodland management grants) (Natural Environment and Rural Communities (NERC) Act 2006 (England), Environment Act (Wales), Nature Conservation (Scotland) Act 2004)
- there is an overarching expectation that all woodland management will be conducted according the UK Forestry Standard, this is enforced through regulation (e.g. issuing felling licences) (FC, 2017)
- certain conservation actions are still incentivised through targeted grants usually associated with woodland creation or management but these can also be targeted specifically for woodland species (e.g. Woodland Improvement Grants to benefit priority species (FC Scotland, 2017); East Midlands Woodland Bird Project (FC England, 2011)).

1.2 Building the evidence to support policy and practice

1.2.1 Evidence-based conservation

Evidence-based conservation is defined as ‘the practice of accumulating, reviewing and disseminating evidence with the aim of formulating appropriate management strategies’ (Sutherland 2006). There is an aspiration that all policies and management actions for conservation should be evidence-based (CBD 2006; Defra 2014; Sutherland et al, 2004). Sutherland (2006) identifies several methods by which effects of management actions on environmental change can be predicted before they are widely applied. These methods include: extrapolation, experiments, modeling and use of expert opinion. He reports each as having their uses and shortcomings. Extrapolation (e.g. of a current observed trend) using data already collected by monitoring programmes does not capture what the responses to a new change in environmental conditions might be. Experiments applying the ‘new’ environmental change can provide a causal link between action and effect but are expensive when long-term and large-scale. A variety of modeling approaches can accommodate complex situations but often not all the parameters are known and therefore can contain high levels of uncertainty. Expert opinion is useful only where there is a paucity of data but conservation decisions need to be taken. This latter approach is however quite common.

1.2.2 Ecological theory and concepts

Generating an evidence base to develop policy and practice for conservation of rare and declining species may be challenging as the effects of habitat management for species may not be immediate but take years or decades to occur e.g. 6 year time lag between agricultural change in England and Wales and response of farmland bird populations (Chamberlain et al, 2000), but could be longer in woodlands. Researchers, in an attempt to provide timely guidance are often required to predict the outcomes when the evidence base is lacking. In such cases established ecological theory or concepts are essential in underpinning rationale to making projections and drawing conclusions. Perring et al, (2015) identifies 12 ecological theories or concepts applicable to conservation decision-making as they relate to the processes which policy and management aim to influence. Of those well established in practice, I propose four as being of most relevance to species conservation: the niche concept, plant succession and disturbance, recruitment limitation and herbivory/predation.

Niche concept

Central to our understanding of species conservation is the niche concept (Hutchinson, 1957). A ‘fundamental’ niche defines a location (actual or conceptual) in which the set of conditions present allow for a species’ long-term survival. The ‘realized niche’ describes such locations where the species actually occupies given other constraints such as dispersal limitations and competition (Phillips et al, 2006). Based on the niche concept, a major area of research on understanding species interactions enabling coexistence has developed (e.g. Atkinson and Shorrocks 1981; Levine and HilleRisLamber 2009). In relation to conservation management of rare species, this research lends support to the importance of microhabitats or ‘minor habitats’ (as first described by Elton, 1949), the resolution at which they occur and how they are dispersed through the landscape (Dymytrova et al, 2016; Harvey and Platenberg, 2009, Phillips et al 2006). Further development through species distribution modelling has led to the application of the niche concept in conservation planning and management (Elith and Leathwick 2009; Guisan and Thuiler 2005; Guisan and Zimmermann 2000). For example, in guiding designation of area networks selected to conserve habitat for the rare species and describing species habitat requirements and identifying new areas for survey for rare species monitoring (Carroll et al, 2010; Franco et al, 2009; DiMinin and Moilanen 2014 Dymytrova et al, 2016; Harvey and Platenberg 2009; Buechling and Tobalske 2011).

Plant succession

Plant succession is an orderly process of plant community development over time (Odum 1969). Founding theory on plant succession states that succession results from:

1. modification of the physical environment by the community;

2. the process of community development follows a predictable direction;

3. the rate of change and end point of succession is determined by the characteristics of the physical environment (Odum 1969).

Disturbance acts upon succession, interrupting or re-starting the process (Christensen 2014). This process is pertinent to woodland environments due to the long timeframe of their existence and histories of frequent anthropogenic and natural disturbance (Bradshaw et al, 2015). Stages of woodland succession have been widely adopted in vegetation classifications (Clements 1936) and is a key concept supporting silvicultural practices (Harmer et al, 2010) (Box 4). Woodland management guidance is formulated around driving the stand from one stage to the next in a successional sequence (Figure 1.1) (Box 4). The different stages in woodland development provide the variety of habitats important for the conservation of species. The ‘all sized’ or ‘old growth’ stand structures are considered to represent an end point of the succession as it can be maintained in relative perpetuity (e.g. for periods of 600 to 1000 years) (Figure 1.2; Harmer et al, 2010; Mason et al, 2004).

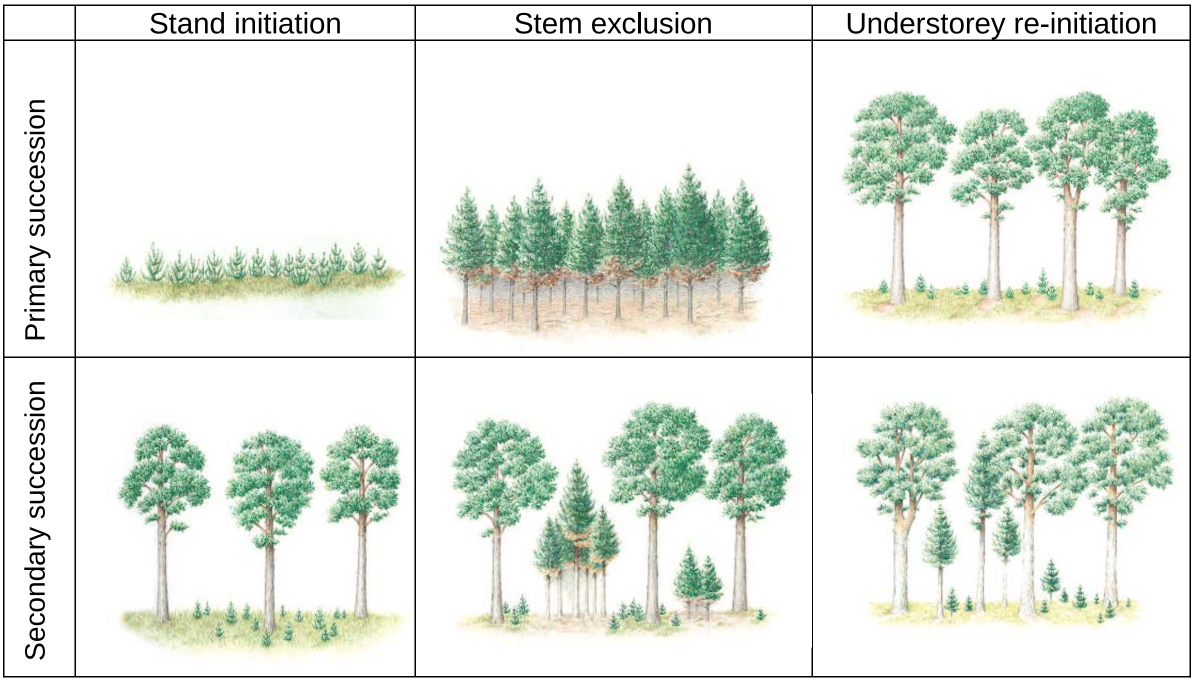


Figure 1.1 Sequence of woodland stand stage development following a successional process (source Mason et al, 2004): ‘Stand initiation stage’ -established tree seedlings begin to grow; ‘Stem exclusion stage’ - dense stands of immature trees with a regeneration/scrub or thicket structure, ‘Pole stage’ - new cohort of trees grow and weaker individuals are out-competed; ‘Understorey re-initiation stage’ - both ‘mature stand stage’ with understorey development and ‘over mature stand stage’ where canopy gaps begin to occur, permitting tree recruitment. Primary succession- tree seedlings are recruited on open (non-wooded) ground (or temporary open ground following the removal of the previous stand of trees); Secondary succession - seedlings are recruited under the canopies of the existing stand of trees.

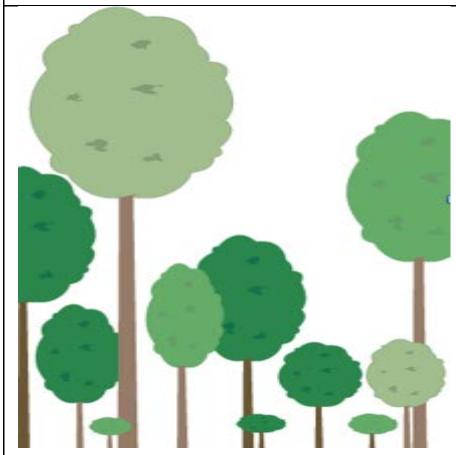
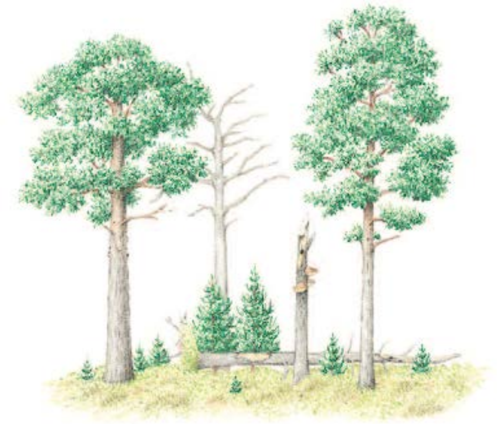
All sized broadleaved woodland	Old growth pine woodland
	

Figure 1.2 Woodland stand structures representing a stable end point in the successional stages of woodland development illustrated for broadleaved woodlands (source Harmer et al, 2010) or conifers (source Mason et al, 2004). This structure can be maintained by natural disturbance events e.g. storm damage or by silvicultural interventions (felling singly or in groups).

Box 4: Typical silvicultural interventions applied in Britain

a. Plant, prepare a seed bed and protect seedlings to assist the stage of tree recruitment

b. Tend (protection, replanting) or coppice (cut to the ground) of shrub or thicket stage trees (15 year cycle),

c. Thin at pole stage in place of natural stem exclusion, thin stands regularly (every 5 to 10 years) to maintain maximum volume increment of the mature trees,

d. Harvest the crop when volume increment ceases. At harvesting, trees are removed singly or in groups of various sizes (a few trees to a whole stand).

Environmental conditions and management objective shape the application of these typical silvicultural interventions. For example, management of a Scots pine forest for timber production by patch clearfelling would require application of most of the interventions listed above, compared to fewer interventions used in the management of an ancient semi-natural broadleaved woodland as a nature reserve.

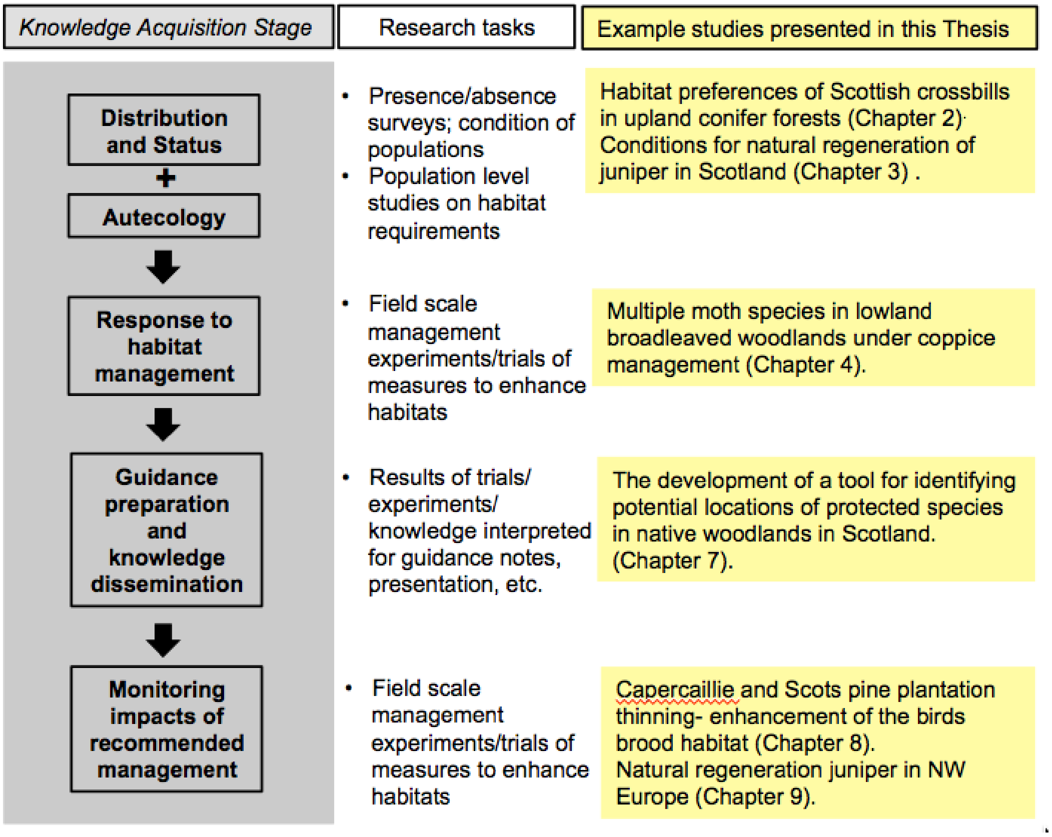
Recruitment limitation and herbivory/predation

Facilitating or enhancing recruitment is critical in the maintenance of any population but the process of recruitment in long-lived plant species, if achieved by natural regeneration, is seen to have several benefits for plant conservation e.g. enabling species to adapt to climate change and avoiding the risks associated with introducing plant material, such as novel pests and pathogens (Lefèvre et al, 2013; Cavers and Cottrell 2015). Conservation managers experience the ecological concept of herbivory/predation both as a tool to work with and a hindrance to progress. Whilst invertebrate seed-eaters can have a major influence on seed availability and subsequent tree recruitment and growth, it is the mammalian herbivores that are more commonly managed either for their beneficial effects on seed bed creation and competitive vegetation or to reduce the negative effect they can have on seedling recruitment, tree establishment and understorey development (Gill 1992; Mayle 1999; Pollock et al, 2005).

1.2.3 Boundary science and a Knowledge Acquisition framework

The ultimate value of the evidence to support decisions on biodiversity conservation is contingent on its utility and up-take by the policymaker or practitioner (Pullin and Knight 2012; Cook et al, 2013). Boundary science attempts to increase scientific understanding within the research community and contribute to decision-making (Cook et al, 2013). Awareness of the policy needs, governance and management systems into which evidence will fit can provide the ‘dual reference’ (i.e. scientifically rigorous, aligned to and/or realistically deliverable through policy or practice) which will make adoption of evidence easier (Bainbridge 2014; Rose 2015; Lawton and Rudd 2016). As well as in the design of research, researchers have to be cogniscent of the users’ needs in the way evidence is disseminated. Strategic decision-makers tend to require summarized answers to general questions rather than narrow ones, as the issues driving policy tend to be broad rather than specific (Sutherland et al, 2006). Similarly, Cook et al, (2013) assert that decisions will be made by managers even in the face of high uncertainty especially where there is a risk of delaying actions resulting in more expensive actions being needed, ultimately.

For protected species conservation, boundary science delivering evidence-based conservation can be conducted by following a framework of five ‘knowledge acquisition’ stages, which relate to the maturity of knowledge on a given species, and informs the type of research conducted (Figure 1.3) (Broome et al, 2005, Grice et al, 2004).



Knowledge Acquisition Stage	Research tasks	Example studies presented in this Thesis
Distribution and Status **+** **Autecology**	Presence/absence surveys; condition of populations Population level studies on habitat requirements	Habitat preferences of Scottish crossbills in upland conifer forests (Chapter 2) Conditions for natural regeneration of juniper in Scotland (Chapter 3) .
Response to habitat management	Field scale management experiments/trials of measures to enhance habitats	Multiple moth species in lowland broadleaved woodlands under coppice management (Chapter 4).
Guidance preparation and knowledge dissemination	Results of trials/ experiments/ knowledge interpreted for guidance notes, presentation, etc.	The development of a tool for identifying potential locations of protected species in native woodlands in Scotland. (Chapter 7).
Monitoring impacts of recommended management	Field scale management experiments/trials of measures to enhance habitats	Capercaillie and Scots pine plantation thinning- enhancement of the birds brood habitat (Chapter 8). Natural regeneration juniper in NW Europe (Chapter 9).

Figure 1.3 Stages of knowledge acquisition used in research on protected species and the type of tasks carried out at each stage (research on the first two stages often occurs together, feedback of information between stages is also expected).

Knowledge Acquisition stage 1: The initial evidence which needs to be gathered relates to where the species occurs, its population status and trends (Wilson et al 2015; Pocock et al, 2015). Often used to meet a statutory requirement to report on conservation targets, surveillance monitoring may also provide basic information on species' relationship with environmental variables (Lindenmayer and Likens 2010; Holland et al, 2012) which can be useful in *Knowledge Acquisition stage 2,* although this stage is more often supported by autecological studies. Autecological studies involve intensive study techniques such as monitoring recruitment success, detailed habitat recording, and for vagile species, mark-recapture studies, diet analysis, and radio-tracking (Connell and Yallop 2002; Jewell 2013). These studies can provide very convincing evidence of the importance of specific habitats and of the impacts of particular practices on key species, and so can diagnose the causes of adverse trends and suggest what land management measures are likely to be beneficial (Grice et al, 2004).

Knowledge Acquisition stage 3 assesses the species' level of tolerance to an imposed environmental change, which may result from ongoing management or interventions assumed as improvements of habitat for the species. Sometimes referred to as ecological effects monitoring, this form of study is designed to uncover unintended ecological consequences of management actions (Hutto and Belote 2013). Sutherland (2006) and Grice et al (2004), recommend an experimental approach as appropriate for this Knowledge Acquisition stage in the form of fine scale field experiments and especially where little is known about how a species may react to environmental change, to help in understanding cause and effect. Knowledge on species conservation gained from this stage can then be disseminated (*Knowledge Acquisition stage 4*) as advice or guidance for policy and practice, with the necessary caveats based on the limitations of knowledge gathered.

Knowledge Acquisition stage 5 relies on the advice and guidance being applied and monitoring and feedback being provided on the outcomes for the species it is aimed at. Such effectiveness monitoring is designed to evaluate whether a given management action helped meet a stated management objective (Hutto and Belote; 2013). Findings from effectiveness monitoring can refine the guidance used by decision makers either at a strategic policy level e.g. for incentivised conservation measures or applied at a tactical or operational level following adaptive management or management effectiveness evaluation approaches (Grice et al, 2004; Addison et al, 2015; Defra 2014; Larson et al, 2013).

2.1 Thesis aims and objectives

In this thesis, I use a series of case studies to provide evidence supporting conservation policy and management for woodland protected species. I illustrate how evidence for protected species conservation decision-making is built following the '*Knowledge Acquisition*' framework which facilitates the accumulation, reviewing and dissemination of evidence. I ask whether this approach directs research and provides evidence which is:

- Well-targeted: research appropriate to the maturity of knowledge
- Sound: based on ecological theory

- Accessible: information is suitable for the end-users needs.

In each chapter I identify the policy driver or evidence need and reflect on the tractability of guidance that the evidence may underpin as well as the target audience. In Chapter 2 and 3 (national surveys for Scottish crossbill (*Loxia scotica*) and juniper (*Juniperus communis*), respectively), I describe how studies of species occurrence provide knowledge on species resource needs which can inform conservation policy and practice. In Chapter 4 and 5, I investigate the impact woodland management practices have on two groups of species, moths in lowland woodlands that are subject to coppicing (Chapter 4) and epiphytic lichens in planted ancient woodlands which are subject to restoration management (Chapter 5). Chapters 6 and 7 are examples of knowledge transfer of relevant findings. Chapter 6 reports on an investigation of lowland woodland birds, setting the findings in the context of woodland management to create appropriate woodland structures. Chapter 7 assembles the habitat needs classified as woodland niches for c. 200 protected species and maps the availability of the niches across an entire country. In Chapter 8 and 9, the effectiveness of management guidance is tested. Chapter 8 reports field trials of thinning prescriptions for Scots pine (*Pinus sylvestris*) plantations to benefit capercaillie (*Tetrao urogallus*) and Chapter 9 provides a review as well as field testing of management prescriptions for juniper in several different habitat types. Reflecting the policy shifts that have occurred in biodiversity conservation in Britain over the last two decades, I present research specific to single species conservation as well as multi-species and habitat level conservation approaches. The eight data chapters also attempt to represent the range of British taxa and woodland habitats.

The data chapters are followed by a synthesis which discusses the results and reflects on the three evidence qualities I have identified above, along with the impact of my research.

Chapter Two: Association between crossbills and North American conifers in Scotland

An adapted version of this chapter has been published as:

Ron W. Summers and Alice Broome. 2012. Associations between crossbills and North American Conifers in Scotland *Forest Ecology and Management*, 271: 37-45.

Contributions: AB contributed the cone density data (collected, analysed and provided associated text), facilitated access to woodland datasets and commented on drafts of the manuscript. RS contributed all other elements of the research and wrote the manuscript.

2.1 Abstract

Understanding the habitat requirements of the Scottish crossbill *Loxia scotica* is fundamental to the conservation of this endemic bird which, like other crossbills, specialises in feeding on conifer seeds extracted from cones. Habitat associations of Scottish crossbills and common crossbills *Loxia curvirostra* were determined from a systematic survey of conifer woodland within the range of the Scottish crossbill during January to April 2008. All the commonly planted conifers were producing cones. Scottish crossbills were associated with the amount of coning lodgepole pine *Pinus contorta*, whilst common crossbills were associated with coning Sitka spruce *Picea sitchensis*, lodgepole pine and to a small extent with larches *Larix* spp. The Scottish crossbill's association with lodgepole pine is interesting in view of the notion that Scottish crossbills are adapted to Scots pine *Pinus sylvestris*. Likewise, there was no evidence that common crossbills in the study area during January to April 2008 had an association with Norway spruce *Picea abies*, the tree with which they are normally associated in continental Europe. Lodgepole pine and Sitka spruce cones have thinner scales than those of Scots pine and Norway spruce, respectively, so are probably easier to exploit for seeds than the conifers to which they are assumed to be adapted. This may explain the associations we found. North American crossbills that specialise on lodgepole pine and Sitka spruce have smaller bills than even common crossbills (the smallest of the western Palearctic crossbills, apart from the two-barred crossbill *Loxia leucoptera bifasciata*). Adaptation to Sitka spruce by common crossbills is unlikely because common crossbills in Scotland largely arrive during irruptions from continental Europe, after which they return in a subsequent season. Therefore, their association with North American conifers in Scotland is temporary. For the resident Scottish crossbills, there is a greater possibility of adaptation to lodgepole pine. However, given the difficulties in identification of old specimens in museums, it was not possible to examine trends in bill size; the prediction is that bill size should decline. Future research needs to distinguish which conifer Scottish crossbills are adapted to as opposed to those which may be temporarily preferred when most profitable.

2.2 Introduction

An understanding of habitat requirements is often important for wildlife management, especially for species of conservation concern, where there is the potential for habitat management (Sutherland et al., 2004; Eaton et al., 2005). For most European birds, there is a basic understanding of the main habitats used and diet (Birds of the Western Palearctic series; Fuller, 1982). Therefore, one can infer habitat requirements from where birds occur and what they eat, though detailed research is usually required to confirm inferences (Sutherland, 2000).

One British bird of conservation interest, for which our understanding of habitat requirements is incomplete, is the endemic Scottish crossbill *Loxia scotica*. This species, along with other crossbills, feeds primarily on the seeds of conifers (Newton, 1972; Benkman, 1987). Our poor knowledge of the type of conifer woodland required stemmed from the difficulty in distinguishing Scottish crossbills from common crossbills on appearance (Knox, 1990a). They have a similar plumage and only small differences in size. It was generally believed that semi-natural Scots pine *Pinus sylvestris* forest was the main habitat of Scottish crossbills (Nethersole- Thompson, 1975; Knox in Gibbons et al., 1993), because the species was thought to have evolved within Scots pine woodland after the last glaciation and when the land bridge with mainland Europe was severed, c. 7000 BP (Nethersole-Thompson, 1975; Edwards and Ralston, 2003). No other conifers suitable for crossbills colonised Britain at this time. Yew *Taxus baccata* and juniper *Juniperus communis* are also native conifers but their seeds are not eaten by crossbills. By evolving in isolation, the Scottish crossbill became Britain’s only endemic bird species (Knox in Nethersole-Thompson, 1975; BOU, 1980).

There was concern over the conservation status of the Scottish crossbill because its population size was thought to be small (1500 birds) and its range restricted to the Highlands of Scotland (Nethersole-Thompson, 1975). In addition, ancient native or semi-natural pinewoods are small in extent (18,000 ha) so the habitat itself is threatened (Anon, 1995; Mason et al., 2004). Therefore, the Scottish crossbill was red-listed and placed in category 1 as a species of European conservation concern (BirdLife International, 2004; Eaton et al., 2005). In the

Biodiversity Action plan, there is emphasis on more research into its habitat and food requirements (Anon, 1995).

Studies in North America indicate that the different crossbill taxa are adapted to single (‘key’) conifer species through their bill size (reflected in bill depth) and the width between the palate ridges for de-husking seeds (Benkman, 1989, 1993). On that continent, the habitats (tree species and stand structures) have been less modified by man so that adaptations and co-evolution have taken place uninterrupted over a long period (Benkman, 1999; Benkman et al., 2003). In Scotland, natural woodland cover was perhaps about 50% of the land area during the Mesolithic but, starting in the Neolithic, most was cut down by farmers and/or lost due to climate change (Smout, 1993; Tipping, 1994) so that Scotland had only about 5% woodland cover by the 17th century (Walker and Kirby, 1989), a situation that did not improve until the 20th century (Mather, 1993). The Forestry Commission was formed in 1919 and undertook a concerted effort to increase the amount of conifer woodland (Anderson, 1967). In addition, from the 1950s, the private sector also embarked on large-scale planting of conifers (Warren, 2002). As well as native Scots pine, North American conifers (mainly Sitka spruce *Picea sitchensis* and lodgepole pine *Pinus contorta*) were planted over large areas. Both grow faster than the native Scots pine, and are adapted to a wet climate (Anderson, 1967). Smaller amounts of other non-native conifers (Douglas fir *Pseudotsuga menziesii*, Norway spruce *Picea abies*, European larch *Larix decidua*, Japanese larch *L. kaempferi* and a hybrid form *L. x eurolepis*) were also planted. As a result, the woodland cover of Scotland is now about 17% (Warren, 2002), comprising mainly conifer food resources novel to crossbills in Scotland.

This study set out to measure the habitat associations of Scottish crossbills across the current range of conifer types, and across the species’ range, comparing these with the habitat associations of common crossbills, which occur sympatrically (Knox, 1990b,c; Summers et al., 2002). This information will help in the conservation of the endemic Scottish crossbill through woodland management. We ignored parrot crossbills *Loxia pytyopsittacus* which also occur, but in only small numbers (Summers and Buckland, 2011). Characteristics of the cones (cone size and scale thickness) were examined because these affect the ability of crossbills to exploit cones (Benkman, 1987). We also discuss the possibility that crossbills are adapting to novel food supplies through changes to their bill morphology (Benkman, 2003).

2.3 Methods

2.3.1 Study area and sampling design

The study was carried out during January to April 2008, as part of the first national survey of the Scottish crossbill (Summers and Buckland, 2011) within c. 3500 km^2 of conifer woodland in mainland Scotland north of 56°50'N (i.e. within the main range of the Scottish crossbill; Summers et al., 2004).

The sampling design was based on 1-km Ordnance Survey grid squares that had conifer woodland at their centre, as defined by the 1999 National Inventory of Woodland and Trees (NIWT) (FC, 1999). Every fourth square was selected for survey, providing 889 points, of which 34 were excluded because they had no conifers within 50 m. Also, three points were not visited, leaving 852 survey points (Figure 1) (Summers and Buckland, 2011).

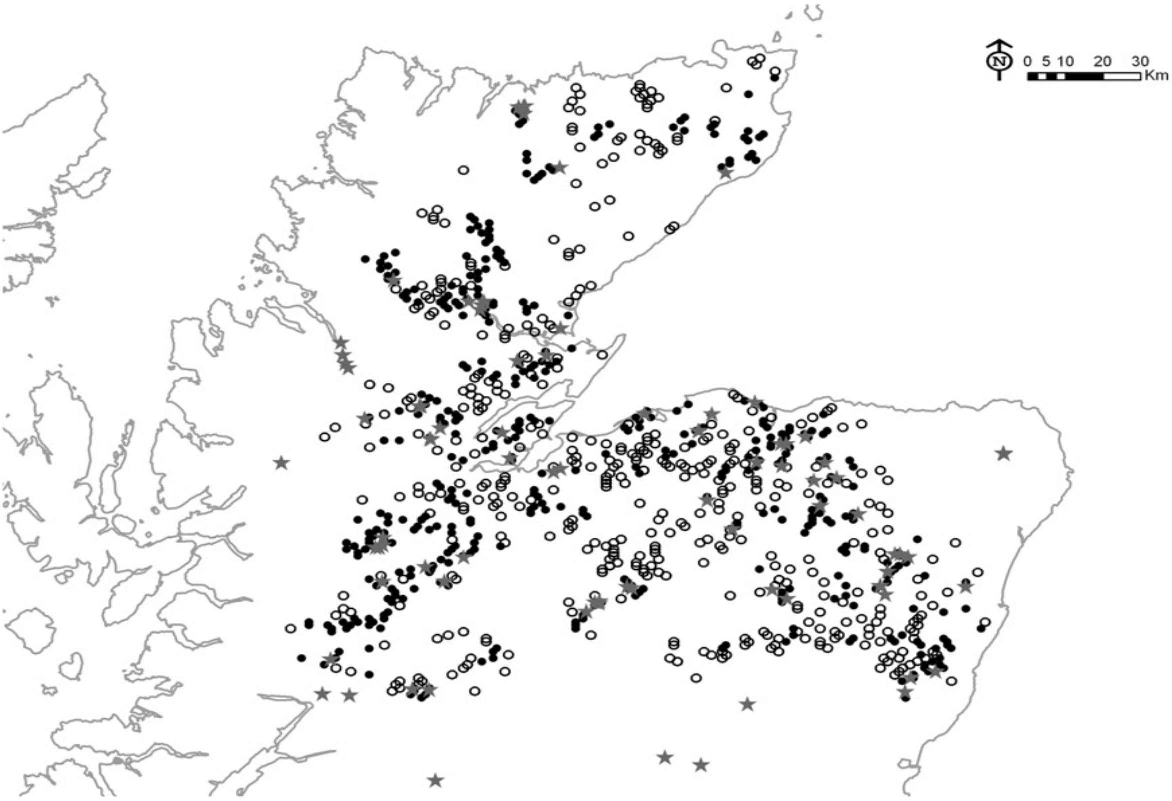


Figure 2.1 The distribution of sample points for crossbills in Highland Scotland. Filled circles refer to the Forestry Commission subset where a greater amount of habitat data were obtained around the points. The grey stars indicate the sites where cone monitoring was carried out prior to the crossbill survey.

The survey involved a single visit to the centre of each 1-km square where a crossbill excitement call was played from a compact disc player for at least ten minutes in the four cardinal directions from each survey point (2.5 min per direction). The exact positions of survey points were adjusted so that the observers stood in open spaces (rides etc.) rather than dense woodland in order to observe in-flying birds. To identify crossbill species, tape recordings of the calls were made and birds identified from sonograms (Summers et al., 2002; Summers and Buckland, 2011). No attempt was made to identify crossbills from the small differences in morphology (Knox, 1990a).

In order to relate crossbill presence/absence to habitat characteristics, the percentage cover of the different conifer species and the stand structures were determined from a sketch map of the area within 50 m of each survey point (0.8 ha). Observers also noted the presence/absence of cones on trees for each conifer species at the sample points. However, for those species that retain cones for many years (lodgepole pine and larches), it was difficult to be sure that cones from the current cohort were present, though there may have been residual seeds from previous cohorts. Conifer heights for each species and stand were allotted to the following five bands: less than 1 m, 1–5 m, 5–10 m, 10–15 m and over 15 m. Tree spacing was allotted to three bands: less than 2 m, 2– 5 m and over 5 m. For analysis, a height index was obtained by multiplying the percentage cover for 1–5 m conifers by one, 5– 10 m by two, 10–15 m by three and over 15 m by four. These four values were then added together. Trees less than 1 m high were ignored. A similar density index was obtained by combining the percentage cover of the three spacing bands, each weighted according to their spacing.

To describe the conifer species composition from a larger area of woodland, from which the crossbills were drawn, stock maps from the Forestry Commission's compartment data base were analysed. These provided areas of different tree species and their planting years within 25 ha around the sample points. This area was close to the effective sampling area for crossbills (21 ha, Summers and Buckland, 2011) and is the approximate foraging range for crossbills during the breeding season (RSPB unpubl. data). These subcompartment data were available for land only in Forestry Commission ownership and referred to 429 of the survey points (Figure 2.1). Only plantings before 1997 were included, thus excluding conifers that were probably not coning (Gordon and Faulkner, 1992).

The 2002 NIWT was used to obtain landscape parameters within 25 ha of the sample points: distance to the nearest conifer woodland edge, area of woodland and length of conifer woodland edge. Woodland edge was defined as the boundary, if it was greater than 50 m from another conifer woodland boundary in a perpendicular line from that boundary. A fragmentation score was determined by dividing the length of conifer woodland edge by the area of conifers in the sample.

Given that crossbills feed on the seeds from conifer cones (Benkman, 1987), stand use depends partly on the cone crop sizes of the different species (Reinikainen, 1937). In addition to noting the presence of cones during the survey of the crossbills, information on cone abundance was obtained from the Forest Research’s Forest Condition Monitoring (FCM) programme (Broome et al., 2007). At sites across northern Scotland (10 for Norway spruce, 14 for Sitka spruce, 18 for Scots pine, 40 for lodgepole pine and 20 for larches, Fig. 1), trained surveyors used a 4-point score (0 – zero, 1 – few, 2 – many and 3 – abundant) to assess the current year’s cone production from 12 selected trees from each site during the summer of 2007, six months prior to the crossbill survey. Historical data were also obtained, but only for Scots pine, Norway spruce and Sitka spruce (Broome et al., 2007). During summer, the cones are still green so can be readily distinguished from previous cohorts. Each score equates to an average cone density for a given conifer species and this weighted average was derived for each survey site to provide a value for each site (Broome and Poulsom, 2006). Median scores were then obtained for each conifer species based on the values for all sites.

Benkman (1993) argued that bill morphology (as seen in bill depth) is adapted to feeding on cones of particular conifers for seed consumption. Therefore, data on bill depths were obtained from North American crossbills that specialise on the non-native conifers grown in Scotland (Groth, 1993; Benkman, 1992; Benkman et al., 2009; Payne, 1987; Irwin, 2010), and compared with bill depths of western Palearctic crossbills (Knox, 1976).

2.3.2 Cone characteristics

Stands of lodgepole pine, Norway spruce and Sitka spruce were visited to collect five cones under the crowns of five arbitrarily chosen trees (25 cones per site). Cone lengths were measured with dial callipers to 1 mm. Data for Scots pine cones from semi-natural pinewoods and plantations had been obtained previously (Summers, 2002). These lengths provided the sizes of cones available to crossbills.

Cones (one per tree) of different sizes for each conifer were dried in an oven at 60 °C for two days so that the scales opened. The thickness of the tips of three scales in the mid part of the cone was measured with digital callipers to 0.01 mm. The tips of the callipers were inserted by 4 mm to make the measurement. The spines on lodgepole pine scales were avoided. The three values were averaged and related to the length of the cones.

2.3.3 Analysis

Logistic regression analyses were used to compare sample points with (scored as 1) and without (scored as 0) crossbills (Crawley, 1993). The following habitat measures provided the independent variables to test for the probability of occurrence of crossbills: percent cover by coning Scots pine, lodgepole pine, Norway spruce, Sitka spruce and larches, indices of stand density and tree height, distance to woodland edge, woodland area within 25 ha and the fragmentation index. Some of these predictor variables were inter-correlated (Table 2.1) and therefore taken into account when interpreting the results. Statistically significant associations were determined from stepwise regression. This method performs similarly to a range of other procedures (Murtaugh, 2009). The logit link function and binomial error distribution were assumed (Crawley, 1993) and models fitted in SAS (SAS Inst. 2000).

Analyses were performed for two sets of data and for each crossbill species. Firstly, and using all 852 data points, the presence/ absence of crossbills was related to the habitat variables around each survey point (0.8 ha). Conifers less than 1 m high and those without cones were excluded. In the second analysis, only the 429 data points from the FC sub-compartment data-base were used, and again the percentage cover of each coning conifer species within 25 ha were used as the independent variables, along with the landscape parameters and indices of height and density.

Table 2.1. A correlation matrix between the explanatory variables used in the analysis of all the data (n = 852). Significant correlation coefficients are in bold.

	Scots pine (%)	Lodgepole pine (%)	Sitka spruce (%)	Larch (%)	Norway spruce (%)	Area of woodland	Length of woodland edge	Frag. score	Dist. to woodland edge	Tree height index
Scots pine										
Lodgepole pine	**-0.36**									
Sitka spruce	**-0.34**	-0.16								
Larch	-0.08	-0.01	-0.07							
Norway spruce	-0.07	-0.11	-0.10	-0.16						
Area of woodland	-0.05	**0.23**	0.13	-0.04	-0.08					
Length of edge	0.09	**-0.23**	-0.10	0.03	0.07	**-0.78**				
Fragmentation score	0.07	**-0.20**	-0.12	0.01	0.05	**-0.88**	**0.80**			
Distance to edge	-0.08	**0.21**	0.08	-0.03	-0.07	**0.66**	**-0.69**	-0.55		
Height index	**0.43**	0.13	0.15	**0.20**	0.15	0.13	-0.08	-0.11	0.09	
Density index	0.11	**0.39**	**0.35**	0.09	0.03	**0.27**	**-0.28**	**-0.25**	**0.21**	**0.65**

2.4 Results

2.4.1 The conifer resource

The most abundant conifers were Sitka spruce, Scots pine, lodgepole pine and the larches (Figure 2.2). Japanese and hybrid larch were more abundant than European larch at the Forestry Commission (FC) points. Norway spruce, Douglas fir, western hemlock *Tsuga heterophylla* and Corsican pine *Pinus nigra* were scarce. The three main conifers (Scots pine, lodgepole pine and Sitka spruce) comprised 89% of the conifers at all points, and 88% in the FC subset. The main difference between all points and the FC subset was in the relative composition of the pines. The FC points had a greater percentage of lodgepole pines and smaller percentage of Scots pines, indicating that the private sector planted disproportionately more Scots pine.

In terms of conifer age, and hence coning potential, the FC points showed that there was a peak age of about 50–60 years for Scots pines (Figure 2.3). By contrast, the peak ages for lodgepole pines and Sitka spruces were younger (30–40 and 20–30 years, respectively) but, nevertheless, well into coning years (Gordon and Faulkner, 1992). The peak ages of the larches and Norway spruce were similar to the Scots pines. There were few young conifers.

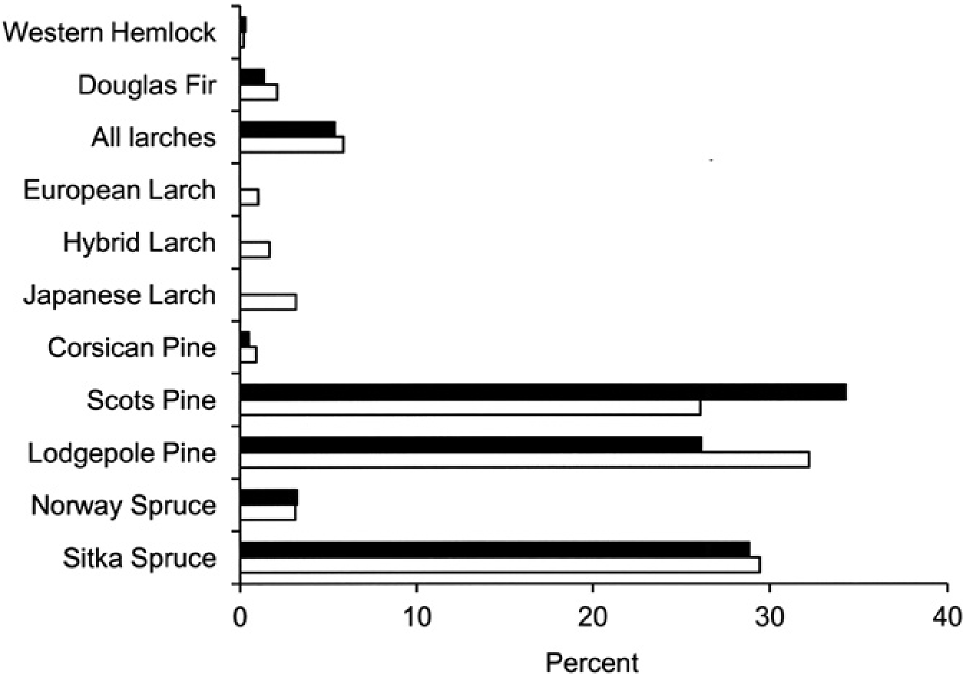


Figure 2.2 The percentage of areas of different conifers at all survey points (n = 852) (black bars) and at the Forestry Commission survey points (n = 429) (white bars) in Highland Scotland. The larches have also been split into three species for the latter data set.

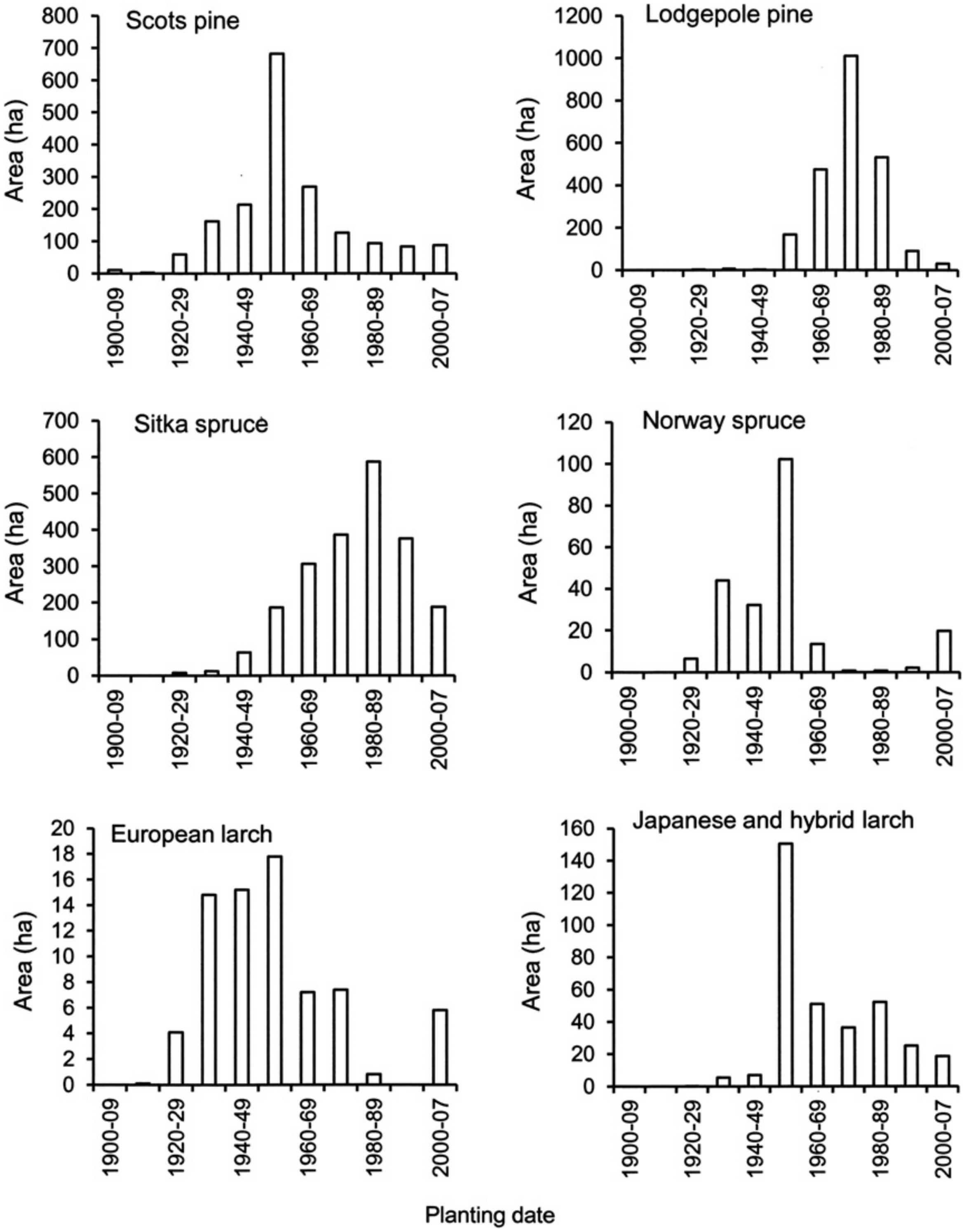


Figure 2.3 Planting years (in 10-year periods) for different conifers within 25 ha of the 429 Forestry Commission survey points in Highland Scotland.

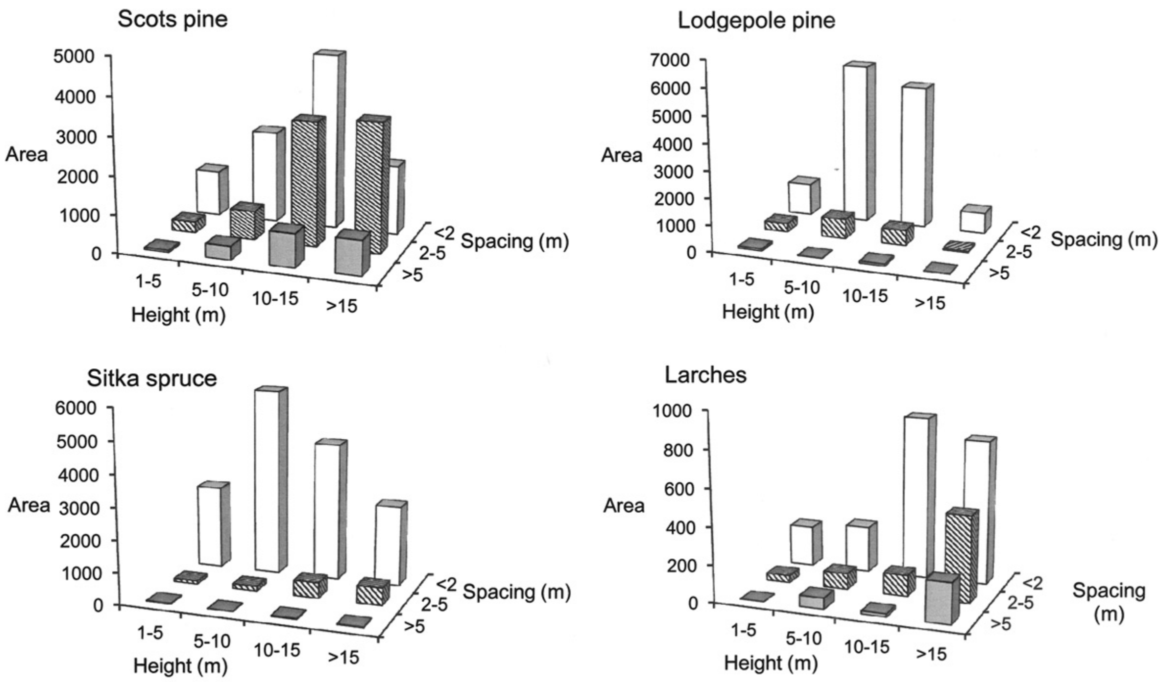


Figure 2.4 The structure (heights and density) of the different conifer stands at all survey points (n = 852) in Highland Scotland. The areas refer to the combined percentage covers around each point.

The structure of the woodlands, as described from all sample points reflected the age structure. Lodgepole pine and Sitka spruce woodland tended to be dense with medium or tall trees (Figure 2.4). Scots pine and larch woodland was often more open, reflecting thinning in the past.

The main conifers coned well in 2007, providing an abundant food supply during the survey in 2008 (Figure 2.5). Only the Scots pines had moderate coning relative to previous years. Although there were no data prior to 2007 for lodgepole pine and the larches, it was evident they coned well in 2007 relative to the other species. For example, the median value for the number of lodgepole pine cones per m^2 of canopy was twice that for Scots pine.

2.4.2 Associations between crossbills and habitat variables

Out of the 852 sample points, Scottish crossbills were identified at 144 and common crossbills at 276. Thirty-four points had both species. Crossbills were not identified at 64 points where they were present, due to lack of recorded calls.

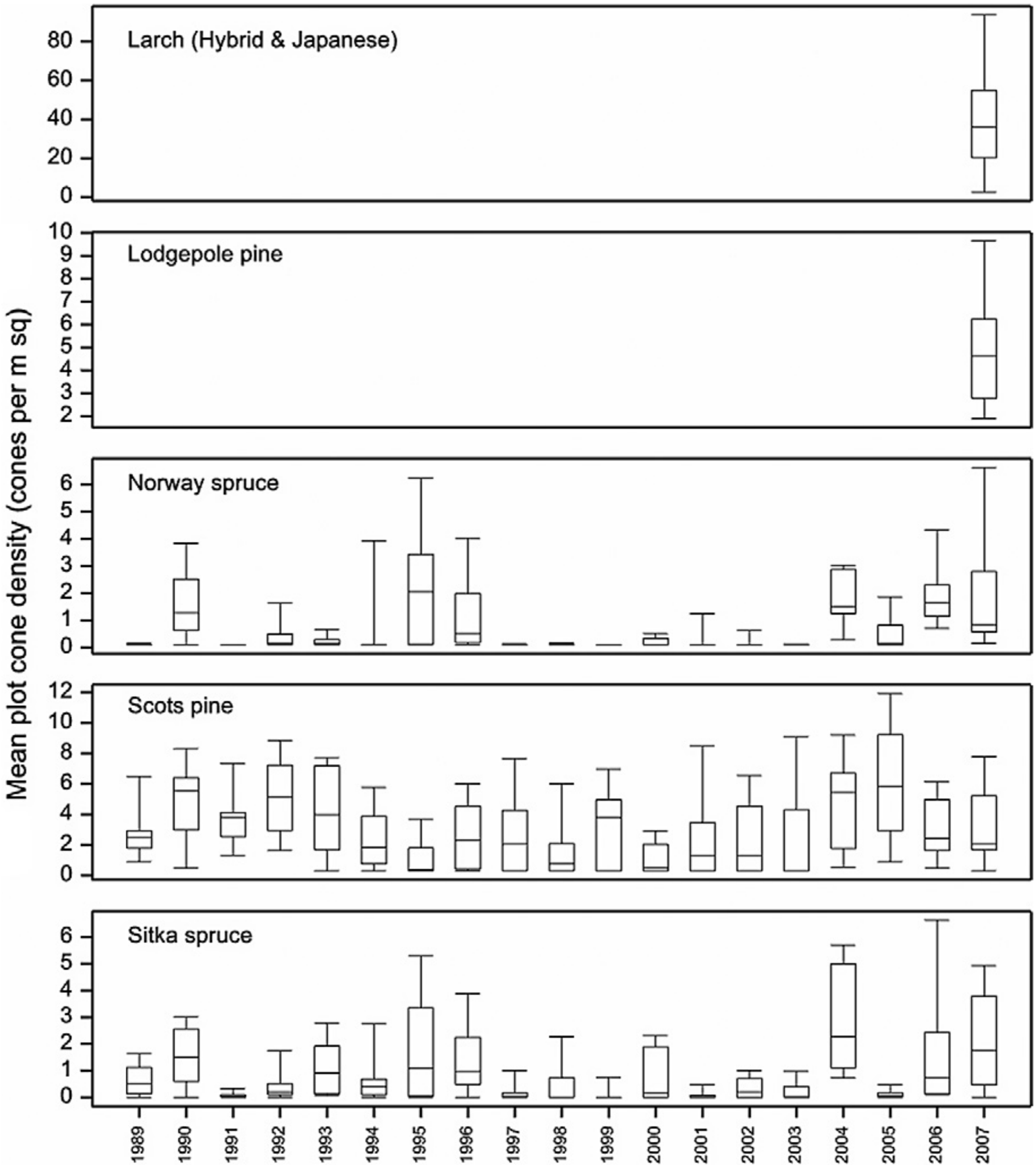


Figure 2.5 Cone indices (number of cones per square metre of tree canopy) for conifers in Highland Scotland described by box and whisker plots by year. The median value is shown by the middle horizontal line, the inter-quartile range by the boxes and ranges by the vertical lines.

In the analysis of the full data set and also the FC subset, Scottish crossbills were associated only with the amount of coning lodgepole pine (Table 2.2). The percentage cover by lodgepole pine was negatively correlated with Scots pine (Table 2.1), so there was a possibility that the association with lodgepole pine could be regarded as avoidance of Scots pine. However, an independent test with Scots pine alone failed to show a significant effect ($X^2 = 2.5$, $P = 0.11$). In the full data set, common crossbills were associated with coning Sitka spruce, lodgepole pine and to a small extent with larches (Table 2.2). Both percentage cover by lodgepole pine and Sitka spruce were negatively correlated with Scots pine (Table 2.1), suggesting a possible avoidance of Scots pine. For the FC subset, common crossbills were associated with just coning Sitka spruce and lodgepole pine (Table 2.2). Therefore, for both crossbill species, the additional information on the amounts of each conifer species in the larger area (25 ha *versus* 0.8 ha) made no difference to their associations. Back-transformation of the estimates for Scottish crossbills shows the relative strengths of the associations with lodgepole pine (Figure 2.6).

In terms of other woodland variables, Scottish crossbills tended to occur further from a woodland edge, but this variable was not significant (P = 0.082) when area of woodland (a non-significant variable) was included in the model. Common crossbills were associated with larger woods (Table 2.2).

Table 2.2 Maximum likelihood estimates from logistic regressions showing associations between crossbills and habitat variables in Highland Scotland. All parameters had 1 degree of freedom. Sample sizes were 852 for all survey points and 429 for the Forestry Commission points.

Parameter	Estimate	Standard error	χ^2	*P*
Scottish crossbill (all points)				
Intercept	-1.8197	0.1134	257.6	<0.001
Lodgepole pine (%)	0.0109	0.00273	15.9	<0.001
Scottish crossbill (FC points)				
Intercept	-1.7363	0.1654	110.2	<0.001
Lodgepole pine (%)	0.0133	0.0041	10.8	0.0010
Common crossbill (all points)				
Intercept	-2.3637	0.3302	51.3	<0.001
Sitka spruce (%)	0.0163	0.0027	35.5	<0.001
Lodgepole pine (%)	0.0120	0.00258	21.5	<0.001
Larches (%)	0.0141	0.00606	5.4	0.0203
Area of woodland	0.0497	0.0156	10.2	0.0014
Common crossbill (FC points)				
Intercept	-1.1540	0.1678	47.6	<0.001
Sitka spruce (%)	0.0191	0.0047	16.4	<0.001
Lodgepole pine (%)	0.0146	0.0037	15.7	<0.001

Table 2.3 Lengths (mm) of conifer cones in Highland Scotland. The data for Scots pine were from Summers (2002).

Species	Mean	Standard deviation	Range	Sample size	Number of sites
Scots pine (semi-natural)	36.1	5.9	20-61	932	35
Scots pine (plantation)	40.9	6.7	20-67	2747	95
Lodgepole pine	41.3	8.0	26-82	750	30
Norway spruce	115.7	17.1	64-164	350	14
Sitka spruce	69.2	10.7	42-99	750	30

2.4.3 Cone characteristics

Scots pine cones in plantations were similar in length to lodgepole pine cones, though the Scots pine cones in the semi-natural pinewoods were smaller than in plantations (Table 2.3). Norway cones were longer than Sitka spruce cones (Table 2.3).

The mid-cone scale thickness was greater in Scots pine than in lodgepole pine and increased in both as cone size increased (Figure 2.7), indicating that larger cones provide more protection to the seeds. The scale thicknesses of Scots pine and lodgepole pine cones that were 40 mm long would therefore be 2.10 mm and 1.77 mm, respectively (Figure 2.7). Thus, Scots pine cones had 19% thicker scales than lodgepole pine, for cones of the same length. The spruces have thinner scales than the pines and the scale thickness of Norway spruce cones was about three times greater than for Sitka spruce (Figure 2.7). There was no change in scale thickness in relation to cone length in the spruces (Figure 2.7), indicating that seed protection did not vary with cone size.

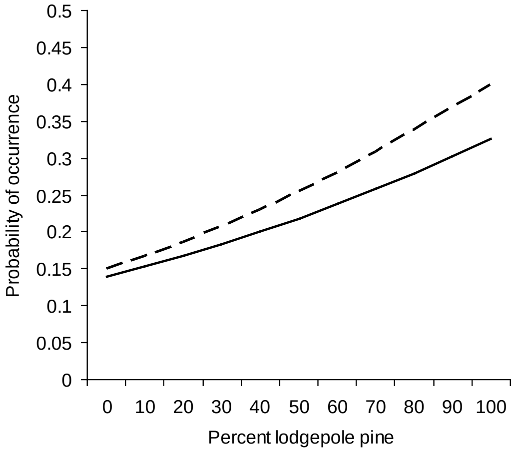


Figure 2.6 The modelled effect (from Table 2.2, solid line - all survey points, dashed line – Forestry Commission points) of the percentage of lodgepole pine on the probability of a survey point having Scottish crossbills.

2.4.4 Bill sizes of crossbills

Bill depths are generally smaller in the different taxa of North American crossbills than the western Palaearctic ones (Figure 2.8). Two of the North American crossbills with the large bills (*sticklandi* and *pusilla*) forage from the woody pine cones of *Pinus ponderosa* and *P. englemanni.* Notably, those crossbills that specialise on lodgepole pine (*pusilla, bendirei* and *sinesciuris*), and Sitka spruce (call type 10, Irwin, 2010) had smaller bill depths than even Palaearctic common crossbills (Knox, 1976; Groth, 1993; Benkman et al., 2009). Therefore, based on bill size, crossbills in Scotland are apparently not pre-adapted for foraging on either lodgepole pine or Sitka spruce (Benkman, 1993). However, if they were to adapt to those conifer species, one might expect directional selection for smaller bills if these are more efficient. This is unlikely to happen for the common crossbill because it is an invasive species and assumed to have only temporary residence in Britain before returning to continental Europe (Newton, 1972, 2006). Bill depths of Scottish crossbills could potentially decline as an adaptation to lodgepole pines. However, given the uncertainties of species identification in museum specimens, it was not possible to examine trends in size.

2.5 Discussion

The study showed that in winter/early spring 2008, Scottish crossbills were associated with the amount of coning lodgepole pines and common crossbills were associated with coning Sitka spruce, lodgepole pine and to a lesser extent with larches. Sitka and Norway spruces coned well in 2007/08, and Scots and lodgepole pines were also coning, so there was an abundance of food (Figure 2.5). Presence of common crossbills was also related to woodland area.

The association that common crossbills had for Sitka spruce is, initially, not surprising because common crossbills specialise on Norway spruce in northern continental Europe (Lack, 1944; Newton, 1972; Cramp and Perrins, 1994). Norway spruce is relatively uncommon in Highland Scotland (Figure 2.2), so Sitka spruce seems to be a suitable substitute. The cones of Sitka spruce have thin papery scales compared to the more leathery scales of Norway spruce, so it is probably easier to extract seeds from Sitka spruce than Norway spruce.

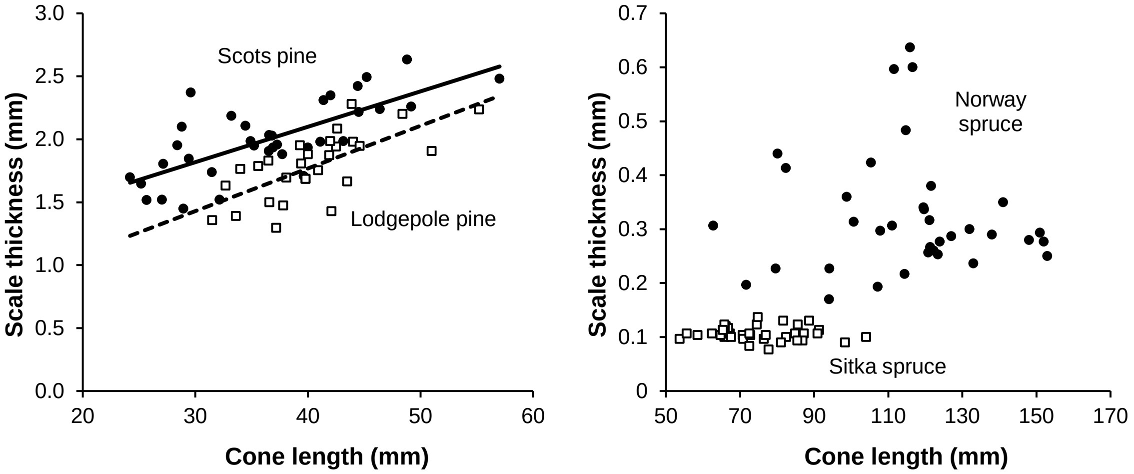


Figure 2.7 The relationship between mid-cone scale thickness and cone length for different conifers. The regression equations were; y = 0.974 (se = 0.0171) + 0.0281 (0.0046) x, for Scots pine (r = 0.73, P < 0.001, *n* = 35) and y = 0.413 (0.285) + 0.0339 (0.007) x, for lodgepole pine (r = 0.69, P < 0.001, *n* = 28). There was a significant difference between the intercepts for Scots pine and lodgepole pine ($F_{1,60}$ = 39.4, P < 0.001), but no significant difference in the slopes ($F_{1,59}$ = 0.45, P = 0.50). There were no relationships between scale thickness and cone length for Norway spruce (r = - 0.04, P > 0.1, mean scale thickness = 0.32 mm, sd = 0.11, *n* = 36) and Sitka spruce (r = - 0.07, P > 0.1, mean scale thickness = 0.11mm, sd = 0.013, *n* = 36).

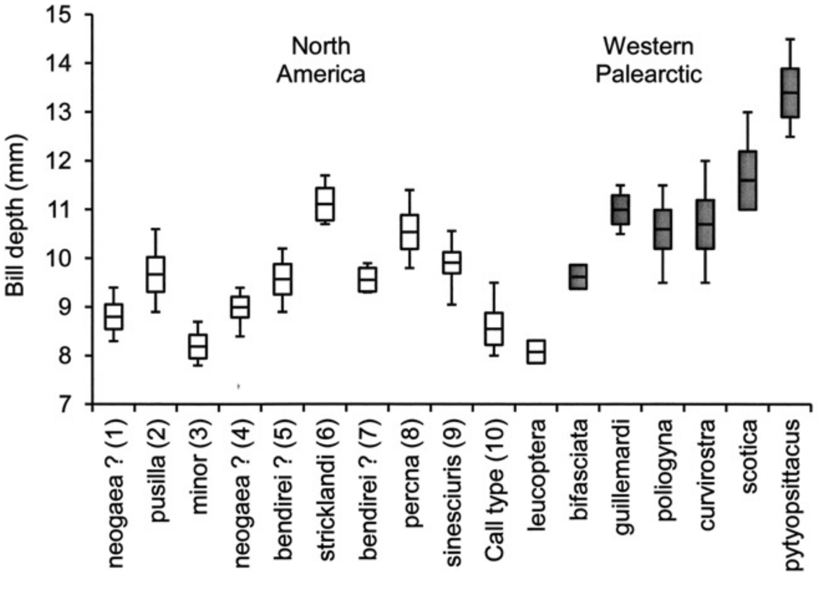


Figure 2.8 Mean bill depths of North American (open boxes) and western Palearctic male crossbill taxa (species or sub-species) (shaded boxes). The numbers in brackets for the North American taxa refer to the call types (Groth, 1993; Irwin, 2010). There is still some doubt about some of the associations between taxa and call types for North American crossbills. The boxes show one standard deviation either side of the mean, and the vertical lines show ranges. The data are from Knox (1976), Payne (1987), Benkman (1992), Groth (1993), Benkman et al. (2009) and Irwin (2010). Ranges were not cited for leucoptera and bifasciata.

However, the seeds of Sitka spruce are smaller than Norway spruce seeds (2.5 dry mg versus 5.5 mg; Marquiss and Rae, 1994) and although they provide a winter food, they may not provide a suitable food source for breeding. In a study in Scotland, it was notable that common crossbills did not breed when feeding on Sitka spruce in winter, and only attempted breeding when they switched to Scots pine seed, which became available when the cone scales opened in spring (Marquiss and Rae, 1994). The association that Scottish crossbills had for lodgepole pine is counter to the generally accepted assumption that the Scottish crossbill is adapted to Scots pine, having evolved within Scots pine forest after the last glaciation (Nethersole-Thompson, 1975; Murray, 1978). Its larger bill relative to common crossbills supports the idea that it is better adapted to opening the tough woody cones of Scots pine, compared to thinner-scaled Norway spruce cones that common crossbills feed from (Lack, 1944). However, a study of the diet in Deeside, showed that Scottish crossbills forage on larches in autumn and winter, and switch to Scots pine in spring (Marquiss and Rae, 2002). The importance of larch in Deeside may be due to the scarcity of lodgepole pine in this region. In our study, encompassing almost all of the range of Scottish crossbills, the association in late winter was with lodgepole pine. By having thinner scales than Scots pine cones (Figure 2.7), and opening earlier in winter, this food supply may be easier to exploit than Scots pine, at least until the Scots pine cones open in spring. The association that Scottish crossbills have with non-native larches led Marquiss and Rae (2002) to question whether the Scottish crossbill is a relict species adapted to the native Scots pine woods of Scotland. Rather, they suggested that it may have resulted from recent hybridisation between common and parrot crossbills. This intermediate-sized crossbill would then be able to exploit a mosaic of larch and semi-natural Scots pinewood (Marquiss and Rae, 2002). However, cross-breeding is uncommon amongst crossbills and has been recorded only between Scottish and parrot crossbills (Summers et al., 2007). There is also the issue about what crossbills are adapted to as opposed to what they will utilise. Each crossbill species/taxon often feeds from more than one conifer species, even though it may have evolved an optimal bill size or husking groove for a single conifer (Benkman, 1992, 1993). The size of the Scottish crossbill’s beak, though smaller than that of the parrot crossbill, is still large in comparison to most other crossbills (Figure 2.8), so Scottish crossbills could still be adapted to Scots pine.

One could argue that the association between Scottish crossbills and lodgepole pine is a recent adaptation to forage on this. However, lodgepole pine was introduced much later (1851) to Britain than larch (1629) (Preston et al., 2002), leaving a shorter time for the birds to adapt. In addition, the crossbills in North America that are adapted to lodgepole pines all have smaller bills than even common crossbills (Figure 2.8), so it seems unlikely that the Scottish crossbill has become a specialist on this introduced conifer. Perhaps Scottish crossbills utilised lodgepole pines because they were more profitable to feed on than Scots pine at the time of the survey. The same argument can be put forward for the common crossbill, which was associated with Sitka spruce rather than Norway spruce, its main food tree in northern Europe (Cramp and Perrins, 1994). The abundance of Sitka spruce and its thin scales made this more profitable during our study.

As well as tree species composition, an association was found with woodland characteristics. There was weak (not quite statistically significant) evidence that Scottish crossbills occurred further from the woodland edge, and common crossbills were in larger woods (Table 2.2). While the latter could be merely a function of more habitat equals more crossbills, edge avoidance is of ecological interest. Helle and Järvinen (1986) found edge avoidance (equivalent to interior preference) by common and parrot crossbills in Finnish forests, arguing that forest fragmentation and change in the tree age structure has been responsible for the declines of many forest birds in Finland.

In the year and area of our study all the common conifers coned well, though the coning by Scots pines was only moderate (Figure 2.5). Given the dynamic nature of coning (Hagner, 1965; Summers and Proctor, 2005; Broome et al., 2007, Figure 2.5), there needs to be further study of the crossbills in other seasons and years when the cones of the different species are in different stages of development and abundance. This would show if the association with particular conifers changes according to season and year. Coupled with such studies, experimental feeding studies are also needed to determine the profitability of feeding on cones of different conifers to establish the one to which they are adapted (Benkman, 1993). Only then, will we have a fuller understanding of the habitat requirements of the Scottish crossbill, and be able to guide habitat management for this endemic bird.

2.6 Acknowledgments

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Chapter Three: Can the site conditions required for successful natural regeneration of juniper (*Juniperus communis* L.) be determined from a single species survey?

An adapted version of this chapter has been published as:

Alice Broome and Kate Holl. 2017. Can the site conditions required for successful natural regeneration of juniper (*Juniperus communis* L.) be determined from a single species survey? *Plant Ecology and Diversity*, 10: 175-184.

Contributions: AB analysed data and wrote the manuscript, and KH commented on an earlier draft. AB also contributed to the original survey design and managed the field data collection occurring on the National Forest Estate.

3.1 Abstract

Ecological surveys often aim to inform biodiversity conservation policy and practice. Survey types differ; all require clear aims and a good design. A survey in Scotland was carried out to measure the distribution and health of juniper (*Juniperus communis*) and potential for its natural regeneration. To explore if one-off national surveys can inform conservation action, this study examined, as an example, the Scottish juniper data set to: (1) determine site conditions favourable for juniper regeneration, (2) provide recommendations for site management for regeneration. We investigated associations between site conditions and juniper occurrence with principal component analysis (PCA) and using species distribution modelling (SDM). To identify changes in site conditions over time, we compared degree of site suitability for natural regeneration (PCA distance) and population age structure. We found that twenty-one per cent of the sites showed juniper regeneration. Compared to all juniper sites, conditions at regenerating sites were different (e.g. climatically wetter, lower site fertility). Change over time in conditions was suggested by patterns in population age structure. We concluded that, following the establishment of a juniper population, site conditions may change, becoming unsuitable for natural regeneration. Historical site information to confirm this is however lacking and we could not answer fundamental questions about the causal mechanisms of the natural regeneration of juniper, and we question whether one-off survey data can inform conservation management.

3.2 Introduction

Surveillance and monitoring are important activities for governments who must meet targets set under Convention on Biological Diversity agreements. Globally, the sustained focus on monitoring effort over the last few decades highlights the importance of reviews/critiques provided in the scientific literature of the aims, approaches and appropriate monitoring methods (e.g. Legg and Nagy 2006; Hutto and Belote 2013; Pocock et al. 2015). Of the three categories of monitoring programmes recognised by Lindenmayer and Likens (2010), ‘mandated monitoring’ describes the type of monitoring carried out at the request of government or statutory authorities to report on trends in the status of species.

Although the scale of such programmes is usually large (occurring at the national level), they are often criticised due to their weak ability to determine on mechanisms of change. In contrast, ‘question-driven’ monitoring enforces a rigorous survey design allowing *a priori* predictions such as those concerning ecological processes to be tested but is often difficult to apply over large areas (Lindenmayer and Likens 2010). Repeated assessments are included in a monitoring programme to provide data on undesired changes of the system, and within an adaptive management framework, to assess success of management actions or the unintended ecological effects of management (Legg and Nagy 2006; Hutto and Belote 2013; Larson et al. 2013).

The national survey of juniper (*Juniperus communis* L. var. *communis* and var. *saxatilis* Pall.) (Sullivan 2003) in upland acid grassland/heathlands and pine-birch woodland habitats in Scotland (Thomas et al. 2007) is clearly a mandated survey. For this declining native conifer species, there is a statutory reporting requirement, as it is a protected species under country legislation (JNCC 2010) as well as being an important component of designated habitats as given in Annex 1 of the EU Habitats Directive (92/ 43/EEC 1992). Natural regeneration is the main measure proposed for the restoration of juniper required under international and country legislation (e.g. EC 2011). However, conservation research on juniper points to a mixed success of natural regeneration and has identified multiple factors influencing regeneration, including site conditions and manipulation of these by management. Therefore, learning more about the influence of these factors is necessary to support conservation action (Thomas et al. 2007). Surveys to provide this type of information may need to be designed specifically around the questions being asked so that variation or response of factor thought to be important can be detected by the sampling regime (Reynolds et al. 2011; Reid et al. 2013).

The national juniper survey (2002) set out to understand the existing distribution and general health of the species and, secondarily, the potential for it to regenerate naturally. Information on past distribution was used in the design of this one-off ‘mandatory’ survey to give an indication of trends in species distribution. Random stratified sampling selected field survey squares (100 km squares) according to Natural Heritage Zone (areas of differing landscape character) (SNH 2002) and historical juniper presence. Within the survey squares, all juniper populations were mapped and a nested subset of 1 km squares, centred on juniper populations, were randomly selected and surveyed. A population of juniper was defined as a group of bushes that can be clumped or scattered, at varying densities (e.g. 2 bushes encountered in 14 ha to 160 bushes ha^{-1}) and occupying areas of up to 80 ha (Vanden- Broeck et al. 2011). A comprehensive set of observations on juniper bushes and site factors thought to influence juniper (e.g. slope, aspect, ground vegetation, browsing animal presence, protection, management) were made (for full details see Sullivan 2003). In order to meet this secondary survey aim, there is an implicit requirement to understand the process of regeneration and the factors affecting it, to direct the collection of what Pocock et al. (2015) term ‘supplementary’ data. An evaluation of population viability was based on an assessment of the condition of the plants and their potential for regeneration, with the latter interpreted from observations of age and sex of bushes, and site conditions (including management) affecting natural regeneration. Occurrence of natural regeneration was indicated by the presence of bushes in the shortest/youngest morphological stage (‘pioneer’). Analysis was generally descriptive and consisted of summarising percentages of sites or plants exhibiting particular characteristics, but there were no formal tests of associations between site variables and regeneration. The survey data provided good information on the current extent and condition of juniper populations within Scotland (UK). However, we re-examined these one-off national survey data to assess their utility in answering other questions important to species conservation. Specifically:

(1) Can the site factors controlling natural regeneration and long-term continuation of the population be identified?

(2) Can this information be used to inform conservation action?

3.3 Materials and methods

Our re-examination used a subset of attributes from the survey by Sullivan (2003). For juniper bushes: population size and percentage of bushes in the five different morphological stages of bush development (‘ pioneer’, ‘ building’, ‘ mature’, ‘ old’, ‘ dead’ – descriptions in Table 3.1). For the site: location, elevation, slope angle, composition of the associated field layer (a list of three to five dominant or co-dominant species), and management attributes. Using Ecological Site Classification (ESC) (Pyatt et al. 2001), site location and elevation were used to obtain continentality class and to calculate accumulated temperature (AT – accumulated day-degrees >5°C), and moisture deficit (MD – accumulated monthly excess of potential evaporation over rainfall (mm)). Field layer plant species composition were used to estimate soil moisture regime based on the relationship between Hill-Ellenberg wetness score (Hill et al. 1999) and ESC soil moisture regime classes (SMRP.c, in eight classes, 1 = Very Dry, 8 = Very Wet), and soil fertility measures of Hill-Ellenberg ‘ reaction’ / pH (R) and Hill-Ellenberg nitrogen (N) values (both R and N are described as an index of 1–9, 1 = infertile site) (Hill et al. 1999).

Table 3.1 Descriptions of four of the five morphological growth stages (the fifth stage being ‘dead’) which juniper bushes were classed by during a survey of extent and condition of juniper (*Juniperus communis*) in Scotland.

Pioneer	Building	Mature	Old
Seedling/sapling stage. Smallbushes (average height 50 cm) but growing vigorously. Male/female cones rarely observed.	Moderate sized (average height 100 cm), vigorous, well branched bushes, with a full, dense canopy. Male/female cones frequently observed.	Full-grown bushes (average height 130 cm), canopy beginning to thin, growth rate decreasing. Male/female cones frequently observed.	Full-grown bushes (average height 200 cm) but canopy thin, dead branches, slow growth. Male/female cones frequently observed

Information on current land use (e.g. grazing) and management practice (e.g. livestock species, presence of other herbivores and information about the type and condition of fencing) was reviewed. Regardless of whether land was wooded or open, sites were grouped to create four types of land use: 1 = grazing: sheep–cattle– deer present; 2 = grazing: sheep– grouse management– deer excluded; 3 = grouse management– deer present; 4 = no grazers/ grouse management– deer excluded. Groupings reflect frequently occurring combinations which are likely to represent a gradient of impact on the habitat.

We used a principal component analysis (PCA) implemented in Canoco (ter-Braak and Smilauer 1998) to investigate relationships between sites with and without regeneration (as indicated by presence of pioneer growth stage bushes). The climatic variables of AT, MD, continentality, and site variables of R, N, SMRP.c and including slope and number of bushes (log transformed to reduce data dispersion) were included in the analysis. Data from 98 sites were included in the analysis. Locations of centroids of sites in the different land use types are shown on the PCA bi-plot along with the envelopes containing 90% of all the sites and 90% of sites where regeneration was recorded. The centre of the latter envelope was called the ‘ regeneration centroid’.

We calculated the ‘ PCA distance’ on the PCA bi-plot between the individual site locations and the regeneration centroid. We displayed age structure of juniper populations by PCA distance. We tested degree of clustering of each land use type around the regeneration centroid using a bootstrapping routine implemented in R 3.1.2 (RCT 2014) to generate one-sided 95% confidence thresholds for PCA distance for sites allocated to each land use type (Crawley 2005). Clustering would suggest an association between land use type and the environmental and other conditions related to juniper regeneration confounding the detection of land use type effect alone. Where independence between land use type and the other site variables associated with regeneration was justified and where sample sizes were adequate, i.e. more than five per category, association between land use type and regeneration was tested using a Fisher’ s exact test (GraphPad 2009).

As an alternative approach, we made use of a prominent SDM package, MaxEnt, as described in Elith et al. (2011). We used sites with pioneer bushes as ‘presence’ data and the full set of juniper locations as ‘background data’. After removal of highly correlated variables (correlation ≥ 0.6), seven variables were entered in to the model, these included land use type as the model allows for nonlinear and categorical variables. We used a fourfold cross validation, where presence data were partitioned (without replication) and used for model training and testing, to assess predictive model performance and estimate uncertainty around the relationship of the site variables with probability of pioneer bush presence.

3.4 Results

The analysis included 98 juniper sites sampled in open habitats (n = 54) and woodland habitats (n = 44); natural regeneration was recorded at 21 of these sites (n = 9 and n = 12, respectively).

Sites occupied by juniper were surveyed across the full range of continentality classes which occur in Scotland (except the most oceanic class where juniper was absent). Based on AT and MD values, most of the sites were within the cool wet climate zone of Britain, a further two are in the subalpine zone but the remainder have drier climates being in the cool moist or warm moist zones (Pyatt et al. 2001). Site fertility as indicated by the mean R and N values were in the range of 2– 6 (R) and 2– 5 (N), with soil nutrient regime from combined R + N of Very Poor and Poor with a few sites of Medium and Very Rich. The sites ranged in SMRP.c between Very Dry and Wet. Half of the sites had less than 10 bushes, a quarter between 10 and 100, the remainder between 100 and several thousand bushes, and three sites were estimated to have over 3000 bushes.

3.4.1 Principal component analysis

Site variables used in the PCA (Figure 3.1) explained the pattern in occurrence of juniper populations reasonably well, with axes 1 and 2 explaining 60% of the variation (axis 1 39%; axis 2 21%). Sites separated along PCA axis 1 according to their AT, MD, and their soil nutrient regime (R + N) and soil moisture regime (SMRP.c). Axis 2 separated sites with more oceanic climate (low continentality score) from those with more continental climate (high continentality score) and also sites with a few and many juniper bushes.

Sites with and without pioneer bushes overlapped in position on the PCA bi-plot; however, those with pioneer bushes were clustered indicating that natural regeneration occurs on sites with a restricted and overlapping range of the site conditions recorded for juniper sites in Scotland. The occurrence of pioneer bushes appeared to be positively associated with climatic wetness, coolness and continentality and with lower site fertility and wetter SMR. Sites with pioneer bushes were also those with larger population sizes.

All age classes of living juniper (‘pioneer’, ‘building’, ‘mature’, ‘old’) were recorded from the survey. The pattern in population age structure with PCA distance

(Figure 3.2) indicated that sites most similar in terms of site conditions to those appearing to support regeneration (short PCA distance), contained younger populations. In contrast, the five sites where site conditions were most unlike those apparently required to support natural regeneration only had ‘ mature’ and ‘ old’ bushes.

Of the sites grouped in the four land use types, type 1 (grazing: sheep– cattle– deer present) had the largest mean PCA distance and type 2 (grazing: sheep– grouse management– deer absent) the smallest, with types 3 (grouse management–deer present) and type 4 (no grazers/grouse management– deer absent) being intermediate (Table 3.2). None of the four groups of sites clustered ($P < 0.05$) around the regeneration centroid on the PCA bi-plot indicating that deployment of land use type was not strongly related to the combination of site conditions associated with juniper regeneration. Pioneer bushes were recorded from some of the sites in each of the four land use types (Table 3.2). Pioneer bush occurrence was lower than expected ($P < 0.05$) for land use type 1 compared to type 3. Less than 10% of the juniper populations growing on sites subject to land use type 1 contained pioneer bushes, whereas pioneer bushes were present at a third of the type 3 sites. Pioneer bushes were present on four out of the five type 2 sites, and half of the type 4 sites.

Table 3.2 Summary information for the juniper (*Juniperus communis*) sites managed under four land use types derived from survey data.

Land use type	Land use practice	Deer	Number of sites (N)	Mean distance in PCA units from regeneration centroid on PCA bi-plot	Bootstrapped lower confidence threshold ($P < 0.05$) for mean of sample size N	Number of sites with regeneration
1	Grazing: sheep, cattle	Present	50	2.23	1.61	4^a
2	Grazing: sheep Grouse management	Excluded	5	1.16	1.03	4^b
3	Grouse management	Present	39	1.66	1.56	11^a
4	No grazers/grouse management	Excluded	4	1.76	0.95	2^b

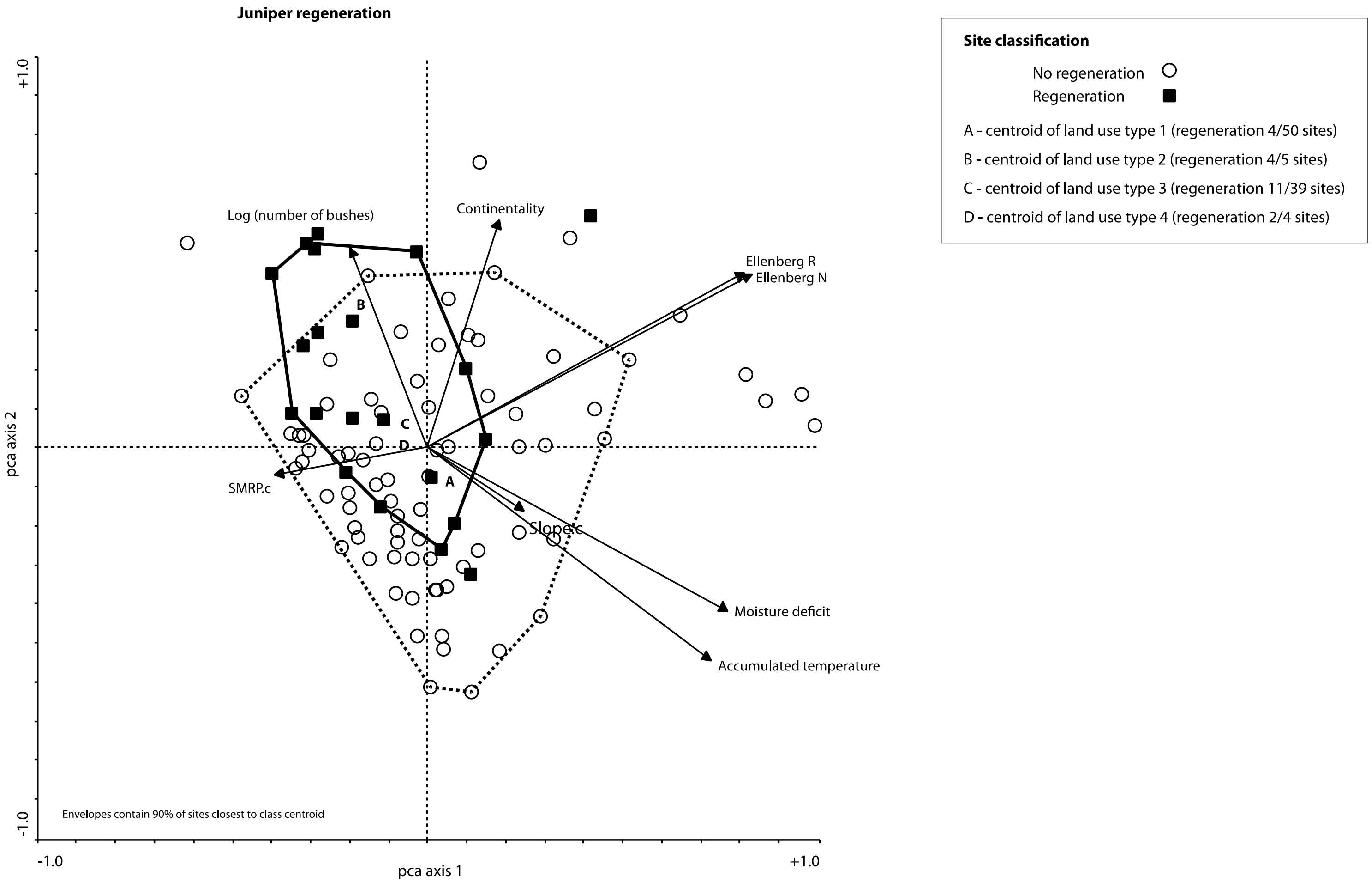

Figure 3.1 Principal component analysis bi-plot showing the distribution of climatic and other site variables at sites surveyed across Scotland with juniper (*Juniperus communis*) with (▪) and without (○) natural regeneration. Sites were allocated to one of four land use types the centroid of the sites grouped by land use are shown on the bi-plot as A, B, C or D.

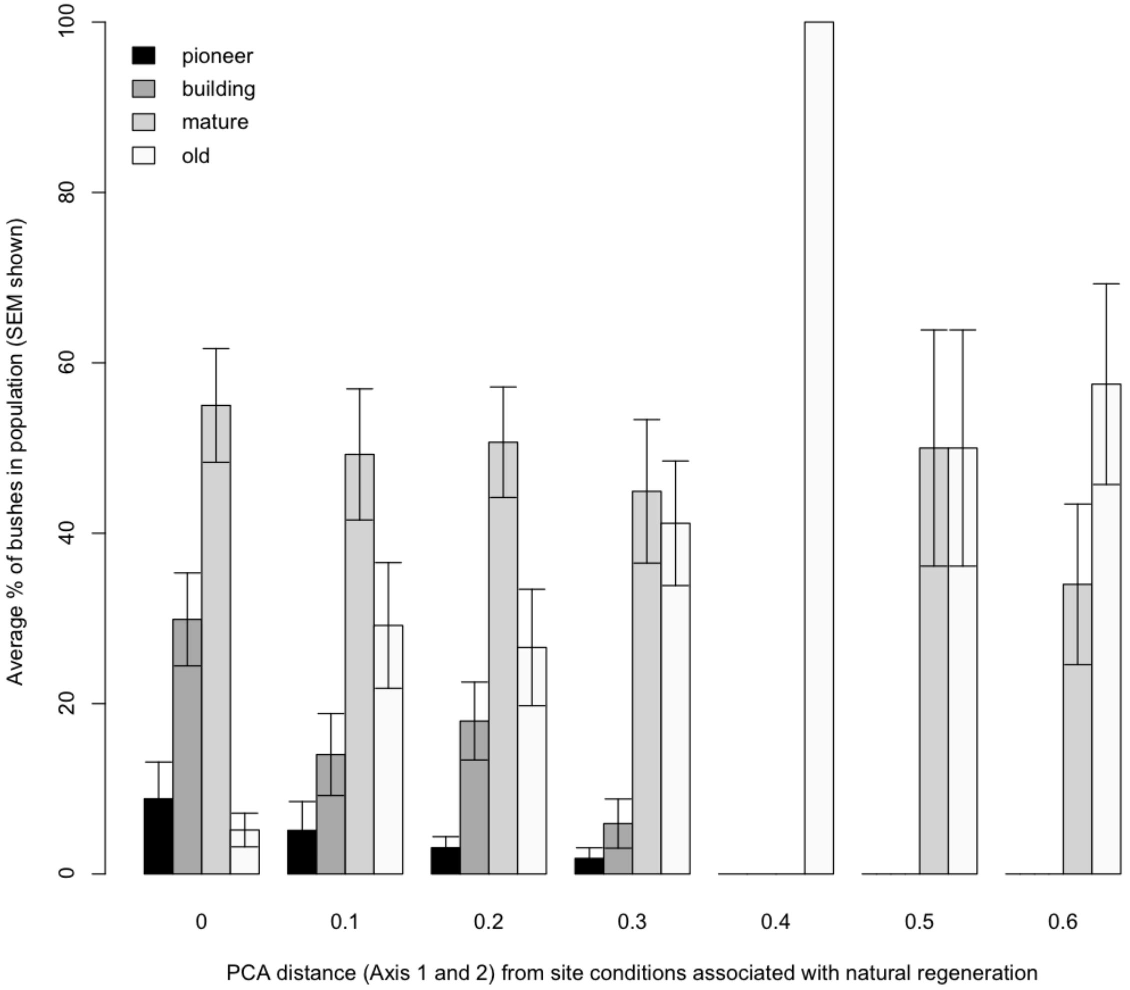

Figure 3.2 Age structure of juniper (*Juniperus communis*) populations and site conditions for natural regeneration. Age structure is based on recognising five morphological growth stages which roughly approximate to age in years: ‘Pioneer’ – up to 5; ‘Building’ – 5–20; ‘Mature’ – 20–80; ‘Old’ – >80 (maximum age around 200 years).

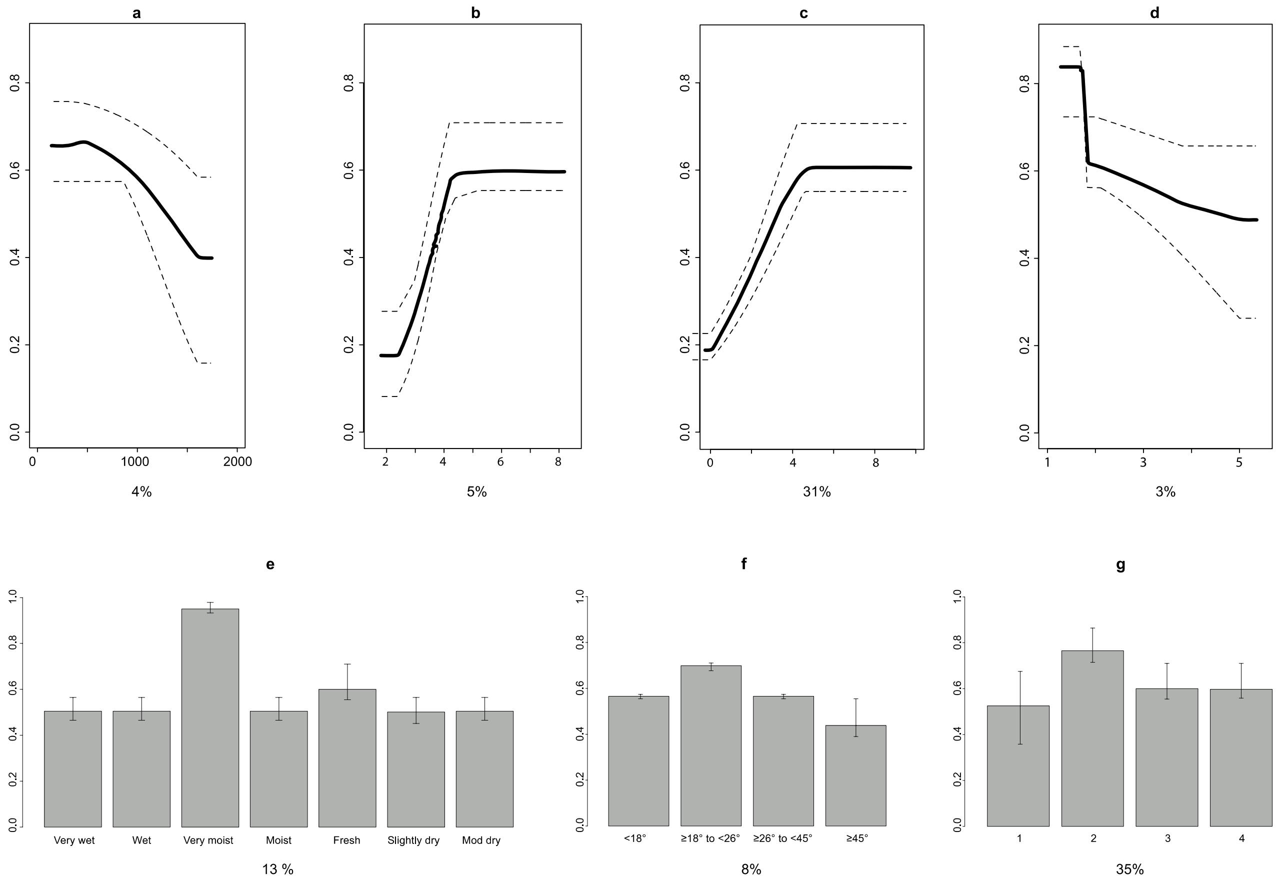

Figure 3.3 Partial dependence plots showing the marginal response of juniper (*Juniperus communis*) to the seven variables (i.e. constant values of the other variables), with variable importance below each graph. Juniper regeneration is measured by occurrence of pioneer stage bushes. (a) accumulated temperature (AT), (b) continentality, (c) log of juniper bush number, (d) Hill-Ellenberg (N), (e) soil moisture regime (SMRP.c), (f) slope, (g) land use type class. The y-axes indicated logistic output.

3.4.2 Maxent modeling

The model performed reasonably well with a cross-validated area under the curve of 0.77; all test‘ presence’ points were predicted to occur at sites classed by the model as suitable although in one of the four model iterations, this result could have occurred by chance (P = 0.11). The variables contributing the most to the model (more than 30% each) were land use type and bush number, but jackknife tests showed that bush number had a more important individual effect than land use type. The probability of pioneer bush occurrence was higher at sites with land use type 2 and with larger numbers of bushes (Figure 3.3). Of the remaining variables contributing to the model, probability of pioneer bush occurrence was greatest with SMRP.c ‘ Very Moist’, where maximum slope angle was between 18° and 26° and showed a relationship which was positive with continentality but negative with N and AT (Figure 3.3).

3.5 Discussion

This analysis of the Scottish juniper survey data shows that pioneer stage bushes, indicating recent natural regeneration, were not found on all the juniper sites. Sites with pioneer bushes appeared to have a restricted range of site conditions compared to all juniper sites covered in the survey. The associations between population age structure and the combination of site factors which relate to regeneration, as well as the lack of regeneration, suggests there has been a change in site conditions at the non-regenerating sites over time. The results from the two analysis approaches (PCA and SDM) highlight the influence of land use type on pioneer bush occurrence, indicating the apparent effects of sheep and stock grazing (negative) and grouse management with sheep grazing but absence of deer (positive). These findings could prove useful in informing conservation guidance.

3.5.1 Detecting natural regeneration

The presence of seedlings and young plants, provided they are old/robust enough to survive to maturity, are used to indicate that natural regeneration is occurring. For all plants, early stages of seedling growth are vulnerable to many pressures (e.g. herbivory, shading, drought). Tree seedlings are only considered as established and are counted as regeneration when they have survived for at least 3 years or have reached sapling stage (≥ 130 cm tall, <7 cm stem diameter at 130 cm from the ground) (Kerr et al. 2002). In other studies, juniper plants estimated to be ca. 5 years old and between 15 and 35 cm tall, with main stem widths of<0.75 cm and up to four side branches, were used to indicate natural regeneration (e.g. Ward 1973; Cooper et al. 2012). By using bushes described as 'pioneer' based on their morphology, this survey has identified established bushes of 3– 15 years old. These are likely to survive to maturity and therefore represent a measure of successful natural regeneration.

3.5.2 Site conditions associated with the natural regeneration of juniper

Juniper populations in Scotland vary in size and sites with juniper show a wide range of environmental and climatic conditions, but regeneration occurs at sites occupying only part of this range. Sites with larger populations were regenerating. Parent population size is important for population growth in woody species (Silvertown et al. 1993) and particularly so for dioecious species such as juniper. The relationship between population size and regeneration has been noted from surveys of juniper on many habitat types (e.g. Cooper et al. 2012) with population sizes of more than 100 bushes noted by Sullivan (2003) and those of more than 50 bushes associated with regeneration on upland grassland sites from other surveys in Scotland (BFT 1997; Mearns 2001). These reports are in accordance with our findings as our model suggests that maximum probability of pioneer bush presence occurs when the parent population reaches sizes of over 50 bushes. Lower minimum population sizes (20 when bushes grown from seed, 30 from cuttings) have been proposed on the basis of the extent of genetic variation measured in populations, for situations where regeneration is assisted by planting and planting material can be deliberately selected (BFT 1997; Broome 2003; Wilkins and Duckworth 2011). Sites with regeneration in the national Scottish survey tended to be wetter, more nutrient poor, cooler and tended to have a more continental climate. An SMRP.c of 'Very Moist', an Ellenberg N score of below 2 and a continentality score of above 4 being associated with highest probability of pioneer bush presence from our model. This concurs with site requirements for regeneration reported in the literature including a higher base saturation of soil for sites with regeneration compared to those without; relatively lower levels of nitrogen availability; greater availability of soil moisture, particularly where there is summer drought (García et al. 1999; Lucassen et al. 2011; Cooper et al. 2012).

3.5.3 Inferred change in site conditions over time

Our results suggest that sites with environmental and climatic characteristics least like those where regeneration was recorded may not have supported regeneration for many years. At these sites, we speculate that site conditions may have changed over the period since the last recruitment event of the surveyed population. Juniper is a long-lived species (maximum age ca. 200 years (Thomas et al. 2007)) and it is feasible that site conditions may change during the lifetime of an individual. There have been wide-scale changes in climate and in soil fertility over the last decades. Specifically, warming over the UK since 1960 with an increase of 1°C reported in the Central England Temperature and 0.8°C for Scotland (Jenkins et al. 2008), and increased atmospheric deposition of nitrogen and increased acidification of precipitation recorded over the same period across Europe (RoTAP 2012). In the UK, decline in plant species diversity in a range of habitats is considered to be due to the effects of nitrogen deposition reducing the frequency of species adapted to low nutrient conditions. Impacts affected sites from before the 1980s with little recovery from this pollutant being observed over last 20 years (RoTAP 2012). Juniper is apparently cold tolerant (survival at 150 day-degrees >5°C but no upper AT limit identified), and adapted to growth on low nutrient soil (Hill-Ellenberg indicator value of 3 for nitrogen) showing little growth response in fertiliser trials (Thomas et al. 2007). However, seed germination and establishment appears to require more precise conditions. Juniper regeneration may be reduced by warmer and shorter winters due to climate change as seeds require a long period of cold stratification to germinate and break dormancy (Bonner 2008; McCartan and Gosling 2013). Higher soil nutrient levels may also be detrimental as lower seedling survival has been recorded for juniper on soils with relatively higher levels of nitrogen and phosphorous (e.g. extractable nitrogen 3.4 $\mu g\ g^{-1}$ compared to 7 $\mu g\ g^{-1}$ dry mass) (Grubb et al. 1996). Seed production also seems more sensitive to varying environmental conditions. Studies in other parts of north-western Europe, where juniper populations are in decline (EC 2009), have linked low regeneration rates to acidification of sites due to atmospheric deposition and with climate warming;

both are considered to negatively affect juniper seed development and seed viability (Verheyen et al. 2009; Lucassen et al. 2011; Gruwez et al. 2014). Lack of regeneration at sites in Scotland may be a consequence of these changes, and whilst it is possible that seed viability remains adequate (Broome et al. 2017), our data suggest that site conditions for regeneration may no longer be suitable (e.g. some sites are too fertile and/or chilling requirements are not met).

3.5.4 Appropriate conservation management of sites with juniper

Habitat management is recognised as driving juniper population dynamics and the sensitivity of juniper regeneration to grazing and browsing levels is widely reported (Fitter and Jennings 1975; Thomas et al. 2007; Farjon 2013). The categories of land use type recognised in the survey attempted to reflect different levels of land use intensity that may be relevant to the regeneration of a woody shrub (e.g. access of, and type of browser or grazer) as well as the main differences in management practised (e.g. stock grazing or grouse management (SNH 2002)). Based on the PCA,we identified land use type 3 – grouse management but where deer were present as more appropriate for regeneration than land use type 1 – grazing with sheep and cattle, also where deer are present. This analysis involved us first confirming that site factors associated with juniper regeneration and the land use type of the site were not confounded (e.g. stock and sheep grazing taking place at warmer and more fertile sites). Although this was confirmed,we were unable to test all land use types as we were constrained by sample size. Using SDM, land use type was identified as the variable that contributed most to the model. Consistent with the PCA results, the model predicted the lowest probability of pioneer bush presence at sites subject to land use type 1. Additionally, the SDM algorithm, which was able to calculate a result from fewer input values, distinguished land use type 2 – grouse management with sheep grazing but where deer were absent as having the highest probability of supporting juniper regeneration. These inferences assume the land use type has remained constant at each site for the period of pioneer bush establishment but suggest that natural regeneration is associated with specific land use types.

3.5.5 Usefulness of national survey data in informing conservation action

In line with the recommendations of Lindenmayer and Likens (2010), the Scottish juniper survey had clear aims and a study design that supported the primary objective of ascertaining the distribution and general health of juniper. However, the analysis of the survey data by Sullivan (2003) provided an understanding of the size of juniper populations, area of its former range occupied and the variability in the viability of the populations. The inclusion of these attributes, the design of the survey and the descriptive approach of the analysis make this survey typical of vascular plant monitoring schemes occurring across Europe at this time (Kull et al. 2008).

A secondary aim of the survey by Sullivan (2003) was to assess the potential for regeneration of juniper at the surveyed sites. Whilst the Scottish juniper survey did generate a suite of field measurements which are grounded on an understanding of the ecology of the species and the environmental pressures thought to act upon it, the design of the sampling was not formulated to test expected effects of the different factors or processes. Instead, potential for sustained regeneration was inferred from the occurrence of natural regeneration and population size and apparent age structure (Sullivan 2003). Our re-examination of these data identifies soil and climatic factors which are associated with regeneration and the analysis of population age structure indicates a temporal effect underlying differences in site conditions. This suggests that many juniper sites in Scotland may not be viable in the future as they are becoming unsuitable for regeneration due to changes in site conditions and changes in population structure. More evidence on how soil and climate has changed at the sites along with how juniper populations have responded is needed to strengthen confidence in these conclusions. Similar concerns were raised by Kull et al. (2008) in their review of 96 vascular plant monitoring schemes/studies, who concluded that the effects of biogeographical factors on species could not be properly understood as schemes lacked assessments of dynamics and distribution of species. Several studies cited in Elith et al. (2011) have analysed survey data using SDM generated by the model MaxEnt to understand environmental correlates with species and some have investigated future responses to climate and land use change by forecasting species distributions. In the latter, the authors recognise the need for historical data on both species distributions and environmental conditions or that predictions should be validated through experiments to test physiological thresholds for species (Kharouba et al. 2009; Yates et al. 2010).

Whilst Sullivan (2003) gave prominence to land use practices influencing juniper distribution and abundance, there was no formal analysis of the effects of land use on regeneration. The survey was stratified by Natural Heritage Zone, and although Zones are partly shaped by the land uses practised (SNH 2002), the sample of different land use types was unbalanced. This made direct tests for association difficult although a strong probabilistic response to land use type was detected when data were analysed using more complex algorithms available within MaxEnt (Elith et al. 2011). Sullivan (2003) also advocated interventions to promote regeneration and reported the influence of browsing pressure and the apparent release from browsing in allowing regeneration to take place. However, lack of historical information about site management weakens these inferences. For example, we cannot tell for how long deer had been excluded from any particular site and whether their exclusion was concomitant with the regeneration of the pioneer juniper plants recorded there. When attempting to determine the impact incentivised management was having on native vegetation conservation, Reid et al. (2013) were unable to link responses to action due to the lack of detail on actions taken and timing of implementation. Similarly, Holland et al. (2012) although able to link the occurrence of the marsupial, *Phascogale tapoatafa*, to environmental variables at all 17 monitoring sites, found that lack of repeated annual monitoring meant that population trajectories could only be calculated for four sites, and argue that this level of survey effort is needed to fully understand the causal mechanisms of decline. Had the Scottish survey set out to test assumptions about management, detailed information on populations and management actions through time would have been needed. This highlights the lack of a ‘well-formulated conceptual model’, considered an important part of a well-designed monitoring programme, underlying the part of the survey concerned with potential for regeneration (Legg and Nagy 2006; Lindenmayer and Likens 2010; Reynolds et al. 2011). We suggest re-formulating the sampling design and including some experimental field manipulations (Reynolds et al.

2011). If treated as a pre-survey, the Scottish survey could be used as the basis for designing site sampling to take in to account the range of variation in factors (e.g. climate) experienced by juniper in Scotland. It would be useful to add any historical management records to the data set to identify the sites where management/land use has been consistent since the last survey. We recommend that any follow-up survey focuses on answering specific questions to help understand the mechanisms influencing juniper regeneration. The follow-up survey could ask whether populations are producing berries and if the seed is viable? For this, assessments would be needed of berry occurrence and seed viability (including within-berry seed predation) across the gradients of potential influence – climatic warmth and/or pollutant deposition rates, with sampling stratified by population size and site type (Verheyen et al. 2009; Lucassen et al. 2011; McCartan and Gosling 2013; Gruwez et al. 2014). Such a survey should be repeated annually for at least 4 years to account for cycles in seed production (Raatikainen and Tanska 1993; Ward 2010). The follow-up survey could ask whether suitable microsites are being provided at the juniper sites? Regeneration microsites have been described for different habitats and result from an interaction between site type and management/land use (Broome et al. 2017). A resurvey should include an assessment of microsite occurrence across the range of available site types and management/land use combinations. Experimental treatments could also be included to address other questions. For example, whether the predation of seedlings is influencing regeneration rates? For this, protection against small herbivores (e.g. mice and rabbits) could be installed at sites where viable seed is produced and apparently suitable microsite conditions occur (García 2001; Broome 2003). Juniper seed could also be sown and protected to augment this study. Such a set-up should be monitored annually for at least 5 years (Broome et al. 2017). Besides historical information management/land use, management could be tested more experimentally, e.g. to provide further insights in to the influence of management/land use on regeneration, management at a selection of sites could be experimentally manipulated, e.g. by removal or reinstating grazing, or protecting areas from deer. A monitoring programme that revisited sites every 1– 2 years for at least 5 years would be appropriate (Broome et al. 2017).

3.6 Conclusions

The survey data provided good information on the current extent and condition of juniper populations within Scotland (UK). Our analysis focuses on natural regeneration potential. Although our findings are only correlative, relationships between population size, current environmental site conditions (climate and soil) and natural regeneration appear clear and are consistent with those reported in the literature. From the survey data, we cannot determine reasons for changes in site conditions or the mechanisms by which different land use types affect regeneration potential of sites. However, we can use these data to describe the soil and climatic conditions suitable for regeneration and the land use types which are more likely to occur at regenerating sites. We tentatively conclude that (1) many juniper sites in Scotland may not persist in the future as they are becoming unsuitable for regeneration due to changes in site conditions, and (2) management may positively affect juniper regeneration on sites where the combination of climatic and soil conditions is favourable for regeneration, provided the parent population is sufficient (more than 50 for natural populations). More evidence on changes in site suitability and management history is needed to strengthen confidence in these conclusions, and to make best use of data collected in this survey to direct conservation efforts. Repeating this survey may provide some missing information about the conditions affecting regeneration. Recommendations on reformulating the sampling design (e.g. Legg and Nagy 2006; Reynolds et al. 2011) should be followed using the original survey data as a pre-survey guide. If recommendations of incorporating the principles of question-driven survey design into mandatory monitoring schemes had been followed, the utility of this survey to inform on appropriate site conditions for natural regeneration and for conservation management would have increased. For future studies, we make suggestions on how to incorporate questions in to a resurvey of juniper sites.

3.7 Acknowledgements

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Chapter Four: The effect of coppice management on moth assemblages in an English woodland

An adapted version of this chapter has been published as:

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Contributions: AB co-designed the survey with MP and SC. MP and SC conducted the field survey. AB and AP carried out data analysis. AB wrote the manuscript, and MP and SC commented on an earlier draft.

4.1 Abstract

Coppice woodlands in Britain may become the target of increased management due to the rise in demand for woodfuel. The biodiversity value of sweet chestnut (*Castanea sativa*) coppice and the effect of coppice management upon this has received limited study. Moths were the focus of this study in an actively coppiced sweet chestnut woodland in southern England. Coupes, with between one and 20 years of coppice regrowth, were systematically sampled for night flying micro- and macro-moths and coppice structure and ground vegetation were described. Using differences in moth assemblage, three stages of coppice development were distinguished: with one-four, five-nine and more than 10 years of coppice regrowth. Differences in moth assemblage related to habitat conditions within each coppice stage. The young coppice stage moth assemblage was characterised by species typically associated with open habitats; moths of the middle coppice stage assemblage fed on trees and were species typically associated with open woodland and scrub habitats; moths of the mature coppice stage assemblage were species typically associated with closed canopy woodland and contained specialist species whose larval food consists of material such as lichen and decaying leaves. All three coppice stages supported species of listed conservation status; the mature coppice stage contained a distinctive range of scarce and threatened species. The study showed that active coppicing promotes a change in moth assemblage but consequently will temporarily eliminate many species of mature stage coppice. Management which provides a range of coppice age classes within a woodland, appears key in promoting moth diversity.

4.2 Introduction

Woodlands provide a wide range of habitats and niches which are exploited by a large number of Lepidoptera species (Roberts 1996). Of over 800 species of macro-moths found in the British Isles (Skinner 2009), two-thirds occur regularly in woodlands (Waring 1989). Moths utilise a range of woodland habitats which include the canopy, understorey, forest edges and ride-sides. Moth species are associated with the foliage of trees, shrubs and herbs as well as the dead, decaying and fungus-infected timber found within woodlands. Some British tree species support a wide diversity of moths, for example both oak and birch are the foodplants for around 120 species (Young 1997), and 72 species have been reported as feeding on sweet chestnut (Parsons and Greatorex-Davies 2006; Parsons 2006).

Coppicing (the activity of felling close to ground level areas of woodland on a rotational basis of ca. 10–20 years) has traditionally been used as a silvicultural management system in many European deciduous forests. Areas of woodland subject to felling are termed ‘coupes’; all the woodland within an individual coppice coupe is coppiced in the same year as part of one operation (Harmer and Howe 2003).

The practice of coppicing started in the Neolithic period and was carried-out throughout European history, being widespread by medieval times (Szabo´ 2009; Farrell et al. 2000). Coppice systems have been described from northern and north-west Europe (e.g. Van Calster et al. 2008; Decocq 2000; Rydberg 2000; Dirkse and Martakis 1998; Rackham 1976), from central and eastern Europe (e.g. Szabo´ 2010; Coppini and Hermanin 2007; Sergio and Pedrini 2007; Benes et al. 2006; Vogt et al. 2006) and from the Mediterranean regions of Europe (e.g. Gondard et al. 2006). It has been suggested that the application of a coppicing regime to woodlands provides the early successional woodland and grassland habitats which are key for a significant proportion of woodland insects (Warren and Key 1991). The value of coppice management to Lepidoptera, lies in the production of a mosaic of habitats within an open, woodland system. These offer a variety of conditions across time and space including ground flora and canopy changes, and changes in the shelter and moisture aspects of the habitat (Bulman 2007; Waring and Haggett 1991). Such habitats are seen as vital for Lepidoptera (Warren and Key 1991) as 75% of the nationally scarce and threatened macro-moths in Britain are found in woodlands and are associated with transitional habitats such as clearings, rides, coppice and scrub (Waring 1989).

In Britain, sweet chestnut (*Castanea sativa*), hazel (*Corylus avellana*), and hornbeam (*Carpinus betulus*), are the main coppice species, often combined with an overstorey of standards, typically oak (*Quercus robur, Q. petraea*) (Evans 1992). Sweet chestnut is generally confined to the acid, freely draining and nutrient poor soils in the south-east of England; hazel is found more widely through Britain and although tolerant of a broader range of site conditions, is characteristic of the chalk downland of southern England (Harmer and Howe 2003). The coppice is generally cut on a 7–10 year cycle for hazel (Harmer 2004) and 12–16 year cycle for sweet chestnut (Rollinson and Evans 1987).

Coppicing was a standard method of woodland management in many areas of Britain for centuries, being the means of producing small round wood for a variety of uses including fuel wood, building and fencing materials, and charcoal production for the iron and glass industries (Howe 1991; Gardener 1993). Only recently, in the last 30–40 years, has coppice management been viewed as a specialist activity mainly conducted for nature conservation benefits (Rackham (1980) and Peterken (1981) cited in Mitchell (1992)). The area of coppice woodland under active management has greatly declined; in the 1947–1949 census, 140,000 hectares (ha) of actively managed coppiced woodland were reported (Anon 1952) compared to 24,000 ha from 1995 to 2000 records (Smith and Gilbert 2003) and this has resulted in large areas of abandoned coppice woodland. However, there is now an interest in low-quality wood products as bio-fuels (McKay 2006; Anon 2007a, b) and an emerging view that coppicing could once more be made profitable (Coppini and Hermanin 2007). This could lead to an upsurge in interest in coppice woodland management and a need for guidance on balancing conservation interests. Sweet chestnut is a rapidly growing species, and being non-native in Britain, is generally considered of lower biodiversity value than the native hazel woodlands (e.g. Fuller and Moreton 1987; Hill et al. 1990; Young 1997). Abandoned sweet chestnut coppice woodland is therefore more likely to be the target for management than abandoned coppice woodland of native species e.g. hazel, as it is more productive and its management will be perceived as being less constrained by biodiversity interests than that of native coppice woodlands. There are estimated to be 12,000 ha of sweet chestnut coppice woodland in England (Anon 2004) which could be returned to coppice management for bio-fuel production. The findings of our study will help underpin our understanding of the impact of this change in management on the woodland moth species in Britain.

A number of studies have shown a response of butterflies to woodland management, such as woodland glade creation and ride-widening (Hall and

Greatorex-Davies 1989) and reinstatement of coppice management (Warren 1987; Warren and Thomas 1992; Warren et al. 2001). In some instances, these have provided the basis for broad recommendations for appropriate rotation length and coupe sizes (Bulman 2007). There have been fewer studies on moth communities in coppice woodlands although this habitat was included in a study of moths in woodlands by Waring (1988). Our study, by concentrating on moth communities in managed sweet chestnut coppice woodland, provides new information on this topic. The specific aims of this study were to: 1) assess whether moth populations in sweet chestnut woodland are influenced by coppice management, 2) understand how differences in moth assemblage vary with the habitat; 3) consider the implications of the findings for conservation management of coppice woodlands for moth species.

4.3 Materials and methods

4.3.1 Study area

The study was conducted in Rewell Wood, West Sussex in Southern England (50.8720°N .5944°W). Rewell Wood is located in an area known as the High Weald, an area where the Weald Sands, surface (British Geological Survey 1995). Rewell Wood contains a variety of woodland habitats including approximately 200 ha of sweet chestnut coppice woodland of varying ages (Figure 4.1; Table 4.1). The site on which the coppice woodland occurs is fairly homogenous, being relatively flat with a slight south to south-east-facing slope and consisting of a single soil type. The coppice woodland is actively managed by Forestry Commission England on a cutting cycle of approximately 12–16 years, producing coupe sizes of between 0.25 and 4 ha. The eight coupes used in this study (Table 4.1) are dominated by a single storey of sweet chestnut with no standard trees, although silver birch (*Betula pendula*) and holly (*Ilex aquifolium*) are present, with birch being more frequently encountered than holly (Table 4.5).

4.3.2 Moth trapping

Trapping was carried out in coupes of 1–8 year old coppice regrowth, and in coupes that had not been cut for at least 12 years. Traps were positioned to ensure they were surrounded by coppice of uniform age and structure by being placed in the centre of the coupe, between 13 and 30 m from the coupe edge. Up to a maximum of eight coupes were surveyed simultaneously on the same night and a subset of six were surveyed each year during the 3 years of the study. Two rides were also surveyed (one trap per ride) in each of the 3 years (2002, 2003 and 2004) of the survey. Both rides were between woodland coupes. Moth trapping was conducted using 125 W mercury vapour ‘Robinson’ traps operated from dusk until dawn and powered by portable generators. This is a standardised procedure used widely in moth studies and one that has been subject to various calibration studies (e.g. Baker and Sadovy 1978). Trapping was carried out during weather conditions suitable for moth flight. For descriptions of light trap designs and a full discussion of techniques, see Fry and Waring (1996). Traps were operated on two nights in late June and early July in each of 2002, 2003 and 2004. A full species list (including micro-Lepidoptera) giving species name and Bradley Number (the unique species identity number in the checklist of Lepidoptera recorded from the British Isles (Bradley 2000)) was produced for each trap on each trapping occasion with counts of individual species recorded. Whether species were listed within the UK Biodiversity Action Plan (UK Biodiversity Reporting and Information Group 2007) was noted along with their National Status (Red Data Book, Nationally Scarce (Parsons 1984, 1993, 1995; Waring and Townsend 2009; Waring, unpublished). Data were converted into counts of individual species per trap.

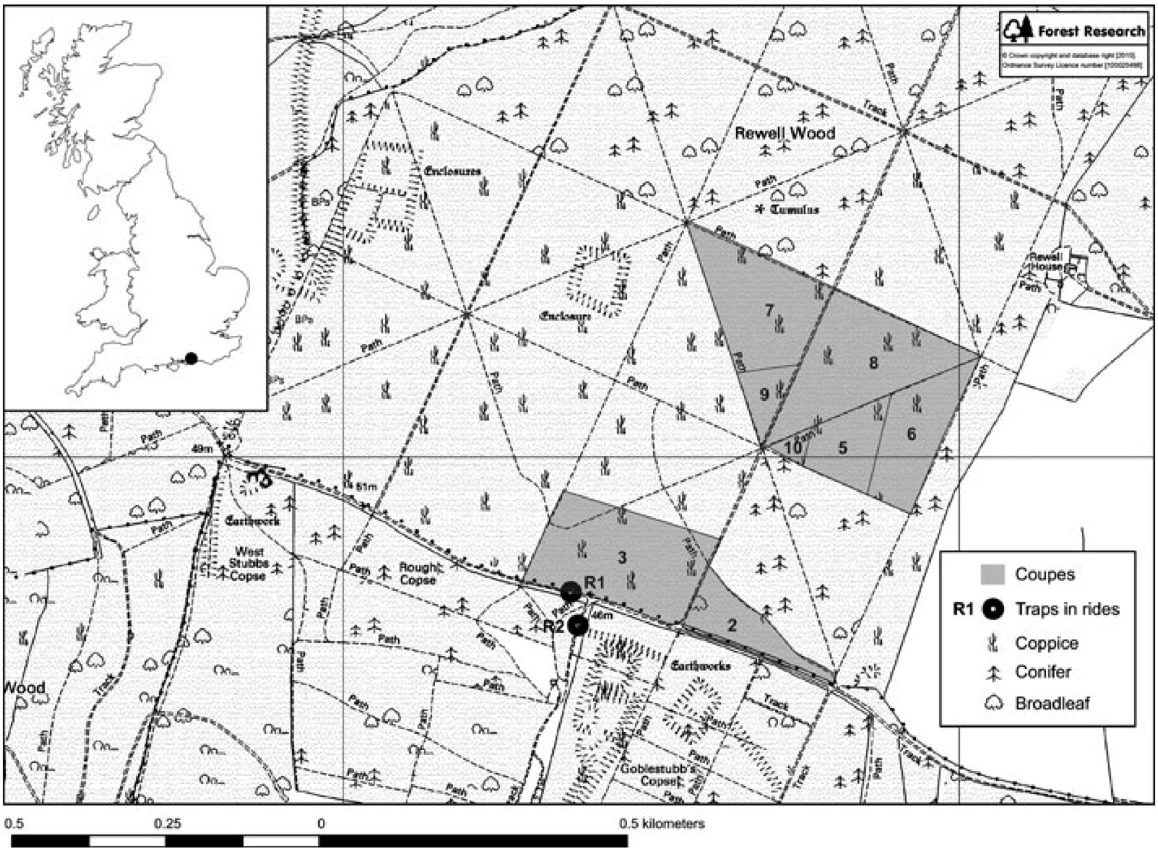

Figure 4.1 Map of Rewell Wood, West Sussex, showing layout of the coupes and location within Britain.

Table 4.1 Coppice age at time of night flying moth survey of 19 sweet chestnut (*Castanea sativa*).coupes in Rewell Wood, West Sussex. Vegetation in these coupes has been described in this and earlier studies

Coupe number	Year when last coppiced	Age (yrs) in;	Age (yrs) in:	Age (yrs) in:	Year of vegetation assessments	
		2002	2003	2004	20m x 20m survey	10m x 10m survey
2	2000	2	3	4	2001, 2002, 2003	2003
5	2000	2	3	4	2002, 2003	2003
6	2001	1	2	3	2002, 2003	2003
7	1996	6	7	8	2002, 2003	2003
9	1997	Not sampled	6	Not sampled	Not sampled	Not sampled
10	1998	Not sampled	5	Not sampled	2003	2003
3	1990	12	13	14	2001	2001
8	1984	18	19	20	2002	2002

4.3.3 Vegetation surveys

Vegetation surveys were undertaken over the period 2001 to 2003 in the coupes used for the moth trapping. Each coupe was assessed in at least 1 year (Table 4.1). Vegetation was described from 10 randomly located 20 x 20 m and one 10 x 10 m sample plot within each coupe and in the form of site notes listing the tree, shrub, climber and ground flora species encountered within the coupe (Clarke 2003). Detailed measurements of the coppice structure and condition were made in the 20 x 20 m sample plot following a modified Point-Centered Quarter Method (Ferris-Kaan and Patterson 1992—after Bonham 1989) whereby quadrats were located at random and their central points were used to identify the quarters lying either side of a north–south and east–west line starting from the central point. Species, height and maximum diameter were recorded for the coppice tree or stool nearest to the central point within each quarter. Presence or absence of canopy cover directly above the central point was recorded along with the tallest field or ground layer component (classed as being either bare ground, moss, leaf litter or vegetation) that was within 0.5 m of the ground, and thickness of the litter layer. The abundance of the trees and shrubs occurring within the 10 x 10 m sample plot was recorded using the DAFOR scale. This is a five point subjective scale that provides a method for assessing the percentage cover values for given species (dominant 91–100%, abundant 51–90%, frequent 21–50%, occasional 6–20%, rare\5%) (Hill et al. 2005).

4.3.4 Data analysis

Correspondence analysis (CA), implemented in Canoco for Windows Version 4.02 (ter Braak and Smilauer 1998), was used to examine relationships between moth assemblage and environmental variables. Variance of the moth assemblage caused by sampling in different years has been taken into account by treating ‘year’ as a co-variate in the analysis.

Moth abundance data, as average counts of individuals per trap over the 3 years of the study and maximum count for any one trap in the 3 years, have been presented for those species that demonstrate a particular association with one of the three age classes of coppice regrowth. Strength of association was interpreted from the location of the moth species in relation to coppice stage as indicated by the CA and the proportion of individuals adjusted for trapping effort, recorded in each coppice stage. Moth species habitat and larval foodplant preferences have been interpreted from the literature for this set of species.

Coppice structure measurements assessed in the 20 x 20 m plots from all coupes and all years have been pooled and are presented to show coppice growth and change in canopy and ground vegetation cover with coppice age.

A ground vegetation species list for each coupe was compiled using data recorded from the 10 x 10 m sample plots and from field notes. Where possible, only data from surveys in 2003 have been presented to minimise the effects of variation across years and in recorder effort. This is with the exception of data for trees and shrubs recorded for coupes 3 and 8 from 10 x 10 m quadrats (shown with a DAFOR scale score) which were surveyed in 2001 and 2002, respectively.

4.4 Results

4.4.1 Moth species and assemblages

The numbers of moth species recorded in each coupe varied across the 3 years of the study. Total numbers of moth species were greater in 2003 at 273 species compared to 2002 (194) and 2004 (199). The most abundant moth species were: mottled beauty (*Alcis repandata*), recorded in all years of the study with an average of 22 individuals per trap and maximum of 47 individuals in one trap; the micro-moth *Scoparia ambigualis*, recorded in all years, average of 20, maximum of 50; large yellow underwing (*Noctua pronuba*), recorded in two of the study years, average seven, maximum of 26.

A total of 43 species listed with a conservation status or listed in accordance with section 41 of the Natural Environment and Rural Communities Act 2006 (Natural England 2010) and within the UK Biodiversity Action Plan (BRIG 2007), were recorded in the study (Appendix 4.1). The highest diversity of these occurred in 2003; numbers of species trapped in the different aged coppice coupes were higher on average in the two coupes with coppice regrowth older than 10 years than in coupes with younger coppice regrowth (Table 4.2). The former UKBAP species, scarce Melville du jour (*Moma alpium*), was particularly associated with 5 year old coppice whereas the clay fan-foot (*Paracolax tristalis*), also a UKBAP species, was only recorded from 2 year old coppice, albeit in very low numbers.

Table 4.2 Numbers of scarcer moth species listed with a conservation status or listed in accordance with section 41 of the Natural Environment and Rural Communities Act 2006 (Natural England 2010) and within the UK Biodiversity Action Plan (UK Biodiversity Reporting and Information Group 2007), trapped in the eight sweet chestnut (*Castanea sativa*) coppice coupes in 2003

Coupe number	Coppice age in 2003 (in years)	Number of moth species
6	2	15
2	3	23
5	3	20
10	5	17
9	6	12
7	7	11
3	12	21
8	19	24

Moth data for coupes which had been sampled by trapping in all 3 years of the study were analysed using correspondence analysis (CA) (Figure 4.2). The two CA ordination axes explain 32% of the variance (19 and 13% for axes 1 and 2 respectively). Both axis 1 and 2 of the CA ordination explain the effects of coppice age. This is made clear when the coupes labeled by coppice age are shown on the CA plot (Figure 4.2a) where it can be seen that axis 1 relates to aging in coupes from pre- to post-canopy closure stages and axis 2 relates to aging within coupes at either pre-canopy or post-canopy closure stage. Three groups are evident: coupes containing coppice up to 4 years old, coupes containing coppice between four and 10 years old and coupes with coppice greater then 10 years old. This lack of overlap in the distribution of the variously aged coppice coupes in Figure 4.2a indicates that each coppice stage supports a different moth assemblage. Of the 293 species that were recorded during the course of the survey, 59 species were found with similar frequencies in the three age classes of coppice regrowth. Of the remainder, 110 species showed a particular preference for one of the age classes although 65 species were represented by one individual. Examples of the species that are distinctive to each of the assemblages are indicated on the CA (Figure 4.2b) and listed in Table 4.3. A summary of the total number of moths recorded from each coppice stage is given in Table 4.4.

Three coppice coupes comprise the early coppice stage, one the middle stage and two the late stage. Coupes are distributed on the CA (Figure.4.2) in order of increasing coppice age, in a clockwise direction, starting in the top right of the chart. Although the same sub-site appears within the same coppice stage grouping, its relative position on the chart, based on the moth trap results for each year, follows the clockwise progression. This indicates that there is a shift in moth species assemblage as the same coppice coupe ages over the 3 years of the study, and the shift is consistent with the change in moth assemblages seen between coppice stages.

The number of moth species encountered was slightly greater in the coupes of the oldest coppice stage: in 2003 there were 44 species per trap recorded in this stage compared with 26 and 31 species per trap respectively, for the coupes of the middle and youngest coppice stages (Table 4.4). Counts of individuals per trap follow the same pattern: in 2003 there were 342 individuals per trap in the oldest coppice, and 218 and 256 individuals per trap respectively in the coupes of the middle and youngest coppice stages (Table 4.4). The coupes of the middle coppice stage had the least number of unique species both in absolute number and on a per trap basis suggesting that this coppice stage had the least distinct assemblage.

The moth species representative of the assemblages (Table 4.3), show broad differences in habitat preferences as characterized from Emmet (1988), Parsons (2006), Skinner (2009) and Waring and Townsend (2009). A greater proportion of those representing the older coppice stage are associated with closed canopy woodland habitats whereas species representative of the middle stage coppice are mostly associated open woodland/shrub habitats; half of the species representing the young coppice stage are associated with open habitats e.g. grassland, the rest are associated with open woodland/shrub. A pattern in larval food preferences between the species in the different assemblages is also evident.

Herbs appear as the larval foodplants for 60% of the species representing the young coppice stage. For over half of the species representing the middle coppice stage, trees and shrubs are the preferred larval foodplants, for a third herbs are, and the remainder show no particular foodplant preferences. Lichens, fungi and dead and decaying material appears as a larval food for a third of the species associated with the mature coppice stage, and trees and shrubs for nearly 50% of the species.

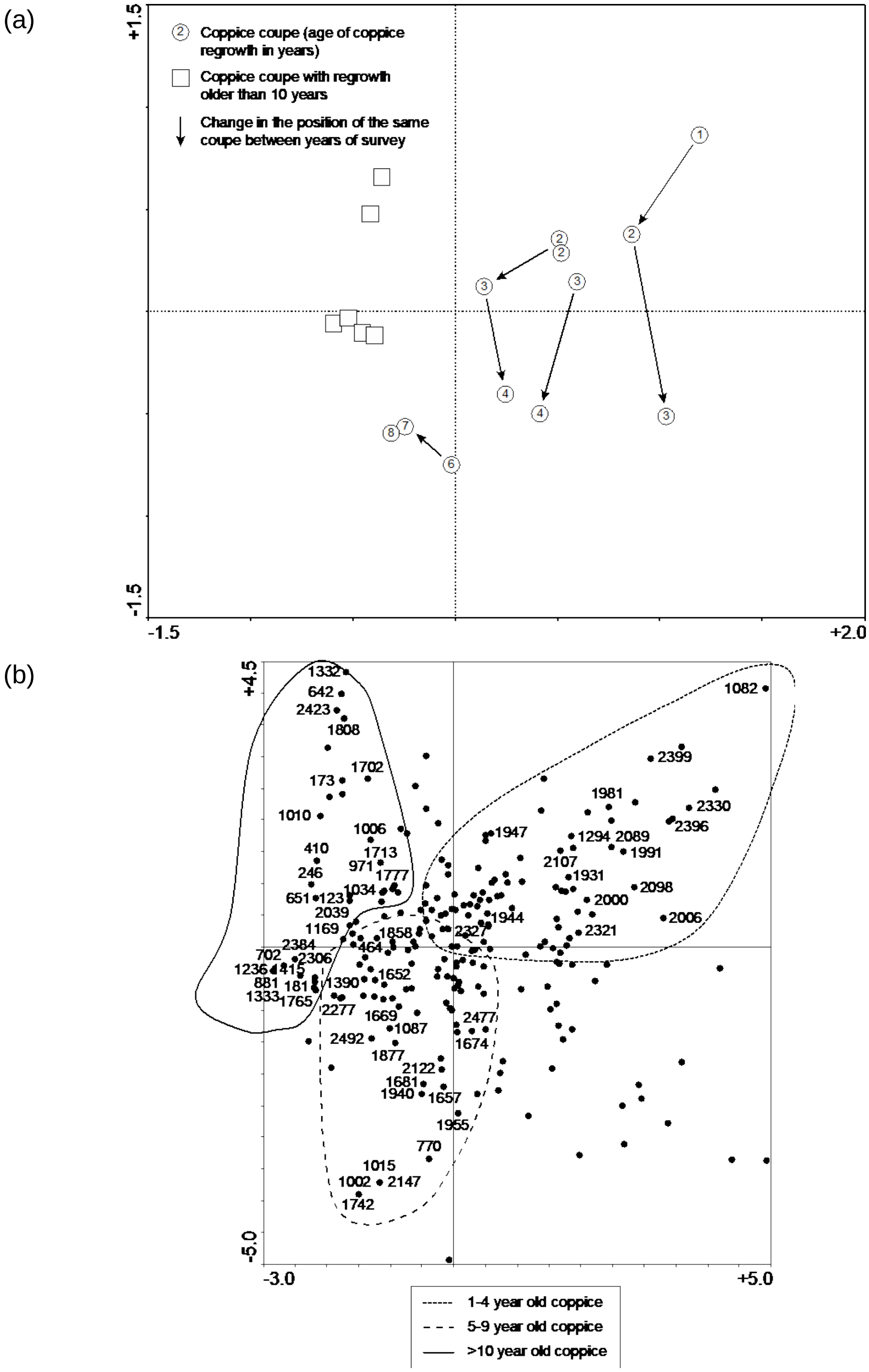

Figure 4.2 Correspondence analysis of the night-flying moth species sampled by light-trapping over a 3 year period (2002–2004), showing the grouping a) of coupes and age of coppice regrowth in the coupes and b) of moth species forming assemblages associated with the three different coppice development stages and with representative species labeled by Bradley number.

Table 4.3 Examples of moths associated with different stages of coppice development sampled in Rewell Wood as indicated by Correspondence Analysis. Larval foodplant (larval pabulum) and habitat preferences for the species are indicated.

a)Young Coppice Stage- (regrowth between one and four-years -old)

Bradley Number[1]	Species	Common name	Ave. Count[2]	Max. Count [3]	%[4]	Larval food[5]	Habitat[6]
2396	*Elaphria venustula*	Rosy Marbled	0.2	2	100	2	3
1082	*Hedya pruniana*	Plum Tortrix	0.1	1	100	1	np
2399	*Pyrrhia umbra*	Bordered Sallow	0.5	3	86	2	3
2089	*Agrotis exclamationis*	Heart & Dart	2.8	16	82	2	3
2330	*Apamea remissa*	Dusky Brocade	0.4	5	80	2	3
2006	*Pheosia gnoma*	Lesser Swallow Prominent	0.4	3	80	1	2
2000	*Notodonta dromedarius*	Iron Prominent	0.3	1	77	1	2
1991	*Deilephila elpenor*	Elephant Hawk-moth	0.9	8	77	2	3
2098	*Axylia putris*	The Flame	3.2	20	74	2	3
1981	*Laothoe populi*	Poplar Hawk-moth	0.5	3	73	1	2
1294	*Crambus pascuella*		0.2	3	73	2	np
2321	*Apamea monoglypha*	Dark Arches	3.8	15	70	2	3
1931	*Biston betularia*	Peppered Moth	1.4	7	60	1	2
2327	*Apamea epomidion*	Clouded Brindle	0.1	2	57	2	3
2107	*Noctua pronuba**	Large Yellow Underwing	9.3	52	45	2	3
1944	*Hypomecis punctinalis*	Pale Oak Beauty	1.7	17	43	1	2
1947	*Ectropis bistortata*	The Engrailed	0.4	2	38	1	2

b) Middle Coppice Stage- regrowth between five and nine–years-old

Bradley Number[1]	Species	Common name	Average Count[2]	Maximum Count [3]	%[4]	Larval food[5]	Habitat[6]
1742	*Camptogramma bilineata*	Yellow Shell	0.1	1	100	2	2
1015	*Eulia ministrana*		0.1	1	100	np	1
2147	*Hada plebeja*	Shears	0.1	1	100	2	2
1002	*Lozotaenia forsterana*		0.1	1	100	np	2
770	*Carpetolechia proximella*		4.7	18	81	1	2
1955	*Cabera pusaria*	Common White Wave	2.2	15	75	1	2
1940	*Deileptenia ribeata*	Satin Beauty	1.3	7	72	1	1
1087	*Orthotaenia undulana*		5.6	23	68	np	2
1877	*Hydrelia sylvata*	Waved Carpet	3.9	10	64	1	1
1390	*Udea prunalis*		0.4	2	64	np	2
464	*Plutella xylostella*	Diamond-back Moth	0.9	5	63	2	np
1858	*Chloroclystis v-ata*	V-Pug	1.3	6	57	1	2
2277	*Moma alpium*	Scarce Merveille du Jour	0.4	3	57	1	1
1669	*Hemithea aestivaria*	Common Emerald	0.8	3	53	1	2
2477	*Hypena proboscidalis*	The Snout	1.3	7	53	2	2
2122	*Diarsia brunnea*	Purple Clay	1.3	4	52	2	2
2492	*Herminia grisealis*	Small Fan-foot	1.5	5	48	1	2
1657	*Ochropacha duplaris*	Common Lutestring	1.8	7	48	1	2
1681	*Cyclophora linearia*	Clay Triple-lines	0.5	3	47	1	1
1674	*Jodis lactearia*	Little Emerald	1.4	5	46	1	2
1652	*Thyatira batis*	Peach Blossom	0.5	3	46	1	2

c) Mature Coppice Stage-regrowth more than 10-years-old.

Bradley Number[1]	Species	Common name	Average Count[2]	Maximum Count [3]	%[4]	Larval food[5]	Habitat[6]
702	*Agonopterix assimilella*		0.1	1	100	1	3
410	*Argyresthia brockeella*		0.3	1	100	1	np
642	*Batia unitella*		1.2	11	100	4	np
1765	*Cidaria fulvata*	Barred Yellow	0.2	1	100	1	2
1010	*Ditula angustiorana*		0.3	2	100	1	np
2384	*Hoplodrina ambigua*	Vine's Rustic	0.1	1	100	2	3
881	*Mompha terminella*		0.1	1	100	2	1
2423	*Nycteola revayana*	Oak Nycteoline	0.2	1	100	1	1
1415	*Orthopygia glaucinalis*		0.1	1	100	4	1
1236	*Pammene fasciana*		0.1	1	100	1	1
2306	*Phlogophora meticulosa*	Angle Shades	0.1	1	100	1	1
1333	*Scoparia pyralella*		0.1	1	100	4	np
1332	*Scoparia subfusca*		0.1	1	100	2	np
181	*Taleporia tubulosa*		0.2	1	100	4	1
246	*Tinea semifulvella*		0.3	1	100	4	np
651	*Oecophora bractella*		0.8	5	88	4	1
173	*Apoda limacodes*	Festoon	0.3	3	86	2	3
1702	*Idaea biselata*	Small Fan-footed Wave	1.8	12	85	2	1
1006	*Epagoge grotiana**		9.9	33	79	1	1
1777	*Hydriomena furcata*	July Highflyer	1.1	6	77	1	1
971	*Pandemis cinnamomeana*		1.8	6	77	1	1
1808	*Perizoma flavofasciata*	Sandy Carpet	0.3	3	77	2	2
1034	*Spatalistis bifasciana*		1.9	9	76	4	2
123	*Tischeria ekebladella*		0.5	4	76	1	1
1169	*Gypsonoma dealbana*		0.4	2	73	1	1
2039	*Atolmis rubricollis*	Red-necked Footman	0.7	5	68	3	1
1713	*Idaea aversata**	Riband Wave	7.2	22	65	2	2

1= Bradley number (Bradley, 2000);* one of the 15 most abundant species (total trap counts of >100 individuals) encountered in the study.
2, 3 & 4 = Trap records from the coppice sites for 2002 to 2004 have been used to provide average count per trap (Ave. Count), the maximum count in any one trap (Max. Count) and proportion of records of individuals of the species within the coppice stage compared to records of individuals of the species from all coppice stages (%) as weighted by trap number. [Note: To be included in the list, species had to be visible on the Correspondence Analysis within the region relating to the coppice stage, and had to have been recorded more frequently in the coppice stage given, than in the other two stages.].
5=Foodplant: 1=trees/shrubs, 2=herbs, 3=lichens, 4=decaying material and fungus.
6= Habitat: 1= closed canopy woodland, 2= open woodland/scrub, 3= open habitats e.g. grassland; np=no preference.

4.4.2 Habitat conditions characterising the coupe stages

Growth of coppice in the 7 years following coppicing and in the older coupes (12 and 18 years after coppicing) was characterised in terms of coppice height and coppice diameter (Figure 4.3a). Coppice height increased steadily with time elapsed since coppicing, reaching an average height of 10 m after 18 years. Coppice diameter (of live canopy) increased exponentially reaching a maximum width of three metres when the canopy closes at 5 years, with no change in width thereafter. Canopy cover reached 100% at 5 years (Figure 4.3b). All the coupes were dominated by sweet chestnut, either fully grown coppice or in the process of re-growing from cut coppice stools. Nine other species of trees, shrubs and shrubby climbers were recorded from the vegetation surveys. Of these, the most ubiquitous and frequently encountered were bramble (*Rubus fruticosus*), ivy (*Hedera helix*) and silver birch (*Betula pendula*), although the latter did not appear in the oldest coppice coupes. Honeysuckle (*Lonicera periclymenum*) was recorded in coupes across the full range of coppice ages. A full list of plant species recorded is given in Table 4.5. The requirements of the species that demonstrate a preference for a particular coppice stage, closely match the habitat provided by coupes sampled within this coppice stage (see Table 4.5).

Table 4.4 Numbers of moth species and numbers of individuals associated with three different stages of coppice development sampled in Rewell Wood. Trap records from the coppice sites for 2002 to 2004 have been used to provide average count per trap.

Young Coppice Stage- regrowth between one and four-years -old		Number of species		Number of individuals	
Example moths of coppice stage assemblage – as listed in Table 5.3		17		690	
Moths unique to coppice stage		51		104	
All moths recorded from coppice stage		233		2873	
All moths recorded from coppice stage by survey year and per trap:					
Survey year	Number of traps		Per trap		Per trap
2002	6	122	20.3	684.0	114.0
2003	6	186	31.0	1535.0	255.8
2004	6	132	22.0	654.0	109.0
Middle Coppice Stage- regrowth between five and nine–years-old		Number of species		Number of individuals	
Example moths of coppice stage assemblage – as listed in Table 5.3		21		564	
Moths unique to coppice stage		14		14	
All moths recorded from coppice stage		173		1832	
All moths recorded from coppice stage by survey year and per trap:					
Survey year	Number of traps		Per trap		Per trap
2002	2	52	26.0	323.0	161.5
2003	6	156	26.0	1310.0	218.3
2004	2	53	26.5	199.0	99.5
Mature Coppice Stage-regrowth more than 10-years-old.		Number of species		Number of individuals	
Example moths of coppice stage assemblage – as listed in Table 5.3		27		479	
Moths unique to coppice stage		31		60	
All moths recorded from coppice stage		218		3041	
All moths recorded from coppice stage by survey year and per trap:					
Survey year	Number of traps		Per trap		Per trap
2002	4	113	28.3	928.0	232.0
2003	4	176	44.0	1369.0	342.3
2004	4	118	29.5	744.0	186.0

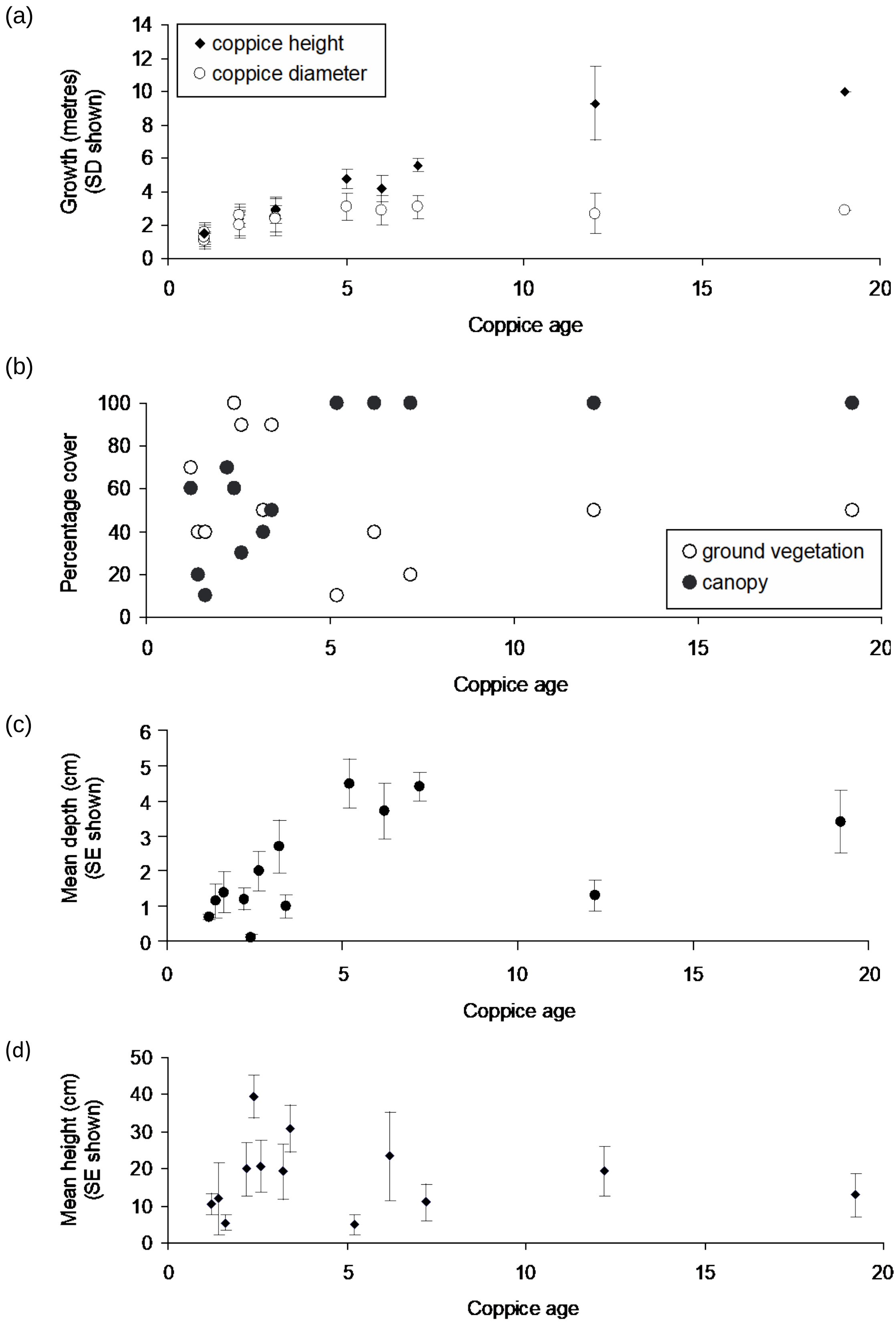

Figure 4.3 Change in habitat conditions described by coppice growth and structure and ground vegetation total % cover and height in coupes of different coppice ages assessed at Rewell Wood, West Sussex (all data from coupes and years have been pooled). a Coppice structure and growth, b vegetation cover and coppice age, c litter depth and coppice age, d vegetation height and coppice age.

Table 4.5 Tree, shrub, climber and ground flora species recorded during the vegetation surveys of coppice coupes at Rewell Wood, West Sussex. For species recorded from the survey using 10 x10m quadrats, abundance has been noted using the DAFOR[1]scale otherwise presence is indicated ('x') for species recorded in the site notes from 2003.

Coppice age in 2003 (in years)			2	3	3	5	6	7	12	19
Coupe			6	2	5	10	9	7	3	8
	Species	Common name								
Tree and Shrub species	*Castanea sativa*	Sweet chestnut	d	d	d	d	x	d	d	d
	Rubus fruticosus	Raspberry	o	f	f	f	x	f	a	a
	Betula pendula	Silver birch	o	a	f	r	x	o	x	
	Hedera helix	Ivy	x		x	f	x	f	x	d
	Lonicera periclymenum	Honeysuckle	x	x		r	x		f	o
	Ilex aquifolium	Holly		r	r				x	r
	Ulex europaeus	Gorse	r		r	x		x		
	Buddleia davidii	Buddleia		r					x	
	Ligustrum vulgare	Privet							a	
	Daphne laureola	Spurge-laurel		x						
Ground flora species	*Viola riviniana*	Common violet	x	x	x	x	x		x	x
	Pteridium aquilinum	Bracken	x	x	x	x		x	x	
	Teucrium scorodonia	Wood sage	x	x	x	x	x	x		
	Digitalis purpurea	Foxglove	x	x	x			x		
		Grass species	x		x			x	x	
	Eupatorium cannabinum	Hemp agrimony		x	x		x	x		
	Euphorbia amygdaloides	Wood spurge		x			x	x		
	Hyacinthoides non-scripta	Bluebell	x	x	x					
	Cirsium vulgare	Speat thistle		x	x					
	Epilobium sp	Willowherb	x					x		
	Glechoma hederacea	Ground ivy		x		x				
	Juncus spp	Rushes	x				x			
	Solanum dulcamara	Bittersweet	x		x					
	Adjuga reptans	Bugle				x				
	Carex spp	Sedges	x							
	Cirsium arvense	Creeping thistle	x							
	Cirsium palustre	Marsh thistle						x		
	Geranium robertianum	Herb robert	x							
	Rumex sp.	Dock							x	
	Scrophularia nodosa	Figwort		x						
	Senecio jacobaea	Ragwort		x						
	Urtica dioica	Nettle	x							
	Veronica officinalis	Common speedwell		x						
Total number of ground flora species			13	12	9	5	5	8	4	1

1= DAFOR scale (d= dominant 91-100%, a=abundant 51-90%, f=frequent 21-50%, o=occasional 6-20%, r=rare < 5%).

A total of 19 different herbs as well as bracken (*Pteridium aquilinum*) and species of sedges (*Carex* spp.) rushes (*Juncus* spp.) and grasses were recorded from the vegetation surveys (Table 4.5). Whereas the shrubs, trees and climbers were generally found in coupes with all ages of coppice regrowth, the ground flora species diversity tended to decline with age of coppice regrowth, returning to a woodland floor flora. The ground vegetation of coupes in the young coppice stage (1–4-year-old coppice regrowth) was the most diverse with a total of 16 species of herbs recorded as well as bracken, sedges, rushes and grasses. Coupes in the middle coppice stage (5–9-year-old coppice regrowth) contained a total of nine species of herbs as well as bracken, rushes and grasses. Besides bracken and grass, only two species of herbs were recorded from the coupes in the matures coppice stage (greater than 10-year-old coppice regrowth).

Percentage cover of ground vegetation (as opposed to bare ground, litter or moss) was highest in the first four years following coppicing and reaches around 40% cover in the mature coppice stage coupes; lowest occurrence of ground vegetation cover was in the coupes of between 5- and 9-year-old coppice regrowth (Figure 4.3b) which was also when litter was deepest (Figure 4.3c). Vegetation heights were variable at the different coppice ages (Figure 4.3d).

4.5 Discussion

In this study we set out to examine whether moth populations within a sweet chestnut coppice woodland were influenced by the age of coppice regrowth. Age of coppice regrowth was found to be the main factor shaping the assemblages of moth species and distinct assemblages were found for coupes in the young coppice stage (1–4-year-old coppice regrowth), in the middle coppice stage (5–9-year-old coppice regrowth), and in the mature coppice stage (greater than 10 year-old coppice regrowth). Changes in assemblage were indicated as the same coupe matured over time.

The effects of an established coppice cycle on the coppice and ground flora have been well studied (e.g. Barkham 1992, also see references in Hall and Greatorex-Davies 1989). Typically, vegetation of high species diversity establishes in newly coppiced areas. Shade tolerant, late successional species flourish and flower when the coppice is cut, and early successional or marginal species regenerate from the seed bank and surrounding habitats when the optimal microclimate prevails. With coppice regrowth, ground vegetation is reduced to the shade tolerant species. In this study, the canopy closure occurred after five years of coppice regrowth and the period of high vegetation species diversity relates to our young coppice stage. Habitat changes have been linked to changing environmental conditions within the coppice woodland. Soil moisture increases after coppicing but declines as the coppice regrows. The effects of water stress in dry years being more prominent and affecting root growth as well as leaf growth of perennial woodland herbs in coppice with regrowth of more than eight years, compared to coppice with between three and five years of regrowth (Cummings and Cook 1992). There are also changes in the amount of light (in the form of photosynthetically active radiation) reaching the woodland floor as the coppice matures. In sweet chestnut coppice with up to three years of regrowth, Mitchell (1992) showed that there was adequate light throughout the growing season to allow shade tolerant species to flower; for coppice with between three and six years regrowth, adequate light was only available in the spring months (February to May), and this was further reduced by one month (March–May) in coppice with more than seven years of regrowth (Mitchell 1992). Litter cover also increases as the coppice matures, with maximum litter depths recorded after five years of coppice regrowth. Litter has a negative effect on the establishment of many woodland species. It intercepts incident light and rain, and presents a physical barrier, impeding the growth of seeds, seedlings, and shoots (Facelli and Pickett 1991) and may control the ground layer vegetation in deciduous forests (Sydes and Grime 198l).

Waring (1988) in a study of moths in semi-natural woodland found that light trap catches of moths in a recently coppiced site contained significantly fewer individuals and fewer species over the year compared with sites in adjacent overgrown and abandoned coppice. We found average trap counts of individuals to be high in the mature coppice stage coupes where canopy had regrown to produce 100% cover but lower in the middle and late coppice stages. We also found the number of different moth species trapped was lower in the young and middle coppice stage compared to the mature coppice stage. These observed changes in moth species numbers and abundance are partially supported by Fuller and Warren, (1993) who report that both species richness and abundance of moths increased through the early years following coppicing, to peak after 2–3 years of regrowth. However, they also suggest that thereafter there is a decline in moth species numbers in over-mature and closed canopy coppice although this was not supported in our study. Studies of moth communities in deciduous forests in North America (Summerville et al. 2009) suggest that species richness increases over time following management intervention, returning to nearly pre-harvest levels within 25 years.

Our second aim was to determine whether differences in moth assemblage could be explained by associating habitat preferences of moth species with the habitat conditions created by the coppicing. We found differences in moth species assemblage could be related to variations in habitat provided within different coppice coupes. Moths that appeared within the young coppice stage assemblage tend to use herbs or grasses as their larval foodplants and are typically associated with grassland or other open habitat, often with some woodland/shrub cover, e.g. elephant hawk-moth (*Deilephila elpenor*) which feeds on willowherb and dark arches moth (*Apamea remissa*) which feeds on grasses (Waring and Townsend 2009). The young coppice stage coupes contained the highest proportion of grassland and had the greatest diversity of herbs (10–16 herb species listed). They were also the least shaded with the individual sweet chestnut stools at their smallest size (less than 4 m high with canopies less than 5 m wide which had not yet closed canopy). Two of the nationally scarce micro-moth species recorded during the course of our survey (Appendix 4.1) showed a preference for the younger coppice regrowth. These were the plume moth (*Capperia britanniodactyla*) and also the pyralid (*Anania verbascalis*); both of which are associated with the wood sage (*Teucrium scorodonia*) (Emmet 1988). Moth species in the middle coppice stage assemblage use trees and shrubs as their main larval foodplants and have an association with open woodland or scrub habitats, e.g. the peach blossom (*Thyatira batis*) feeding on bramble in areas of scrub, but a number of moths that use herbs, e.g. purple clay (*Diarsia brunnea*) which feeds on foxglove as well as other herbs are also contained in this group (Waring and Townsend 2009). At five years, the sweet chestnut coppice has closed canopy, reaching maximum coppice plant diameter however, at this coppice stage, a herb layer remains, with species such as foxglove and wood sage continuing to be present. This assemblage contained four of the scarcer moths listed in Appendix 4.1. The moth assemblage associated with the mature coppice stage consists mainly of woodland associates (Waring and Townsend

2009) which feed predominantly on trees. Some use herbaceous plants but a third are associated with lichens, fungus-infected wood and old, decaying leaves (Parsons 2006). This assemblage contains five of the scarcer moth species listed in Appendix 4.1. Some of these are the micro-moth species that feed on fungi and decaying leaves, e.g. *Oecophora bractella* and *Spatalistis bifasciana*. The red-necked footman (*Atolmis rubricollis*), which is a rare macro-moth, that also occurs in this assemblage is associated with lichens and algae in woodland situations (Skinner 2009). The presence of this moth which has such specialised requirements reflects the presence of appropriate niches provided within the mature, humid and shady conditions of the older coppice coupes. Sweet chestnut coppice at this stage reaches heights of 10 m; although some herb layer remains (40% cover), there are only a few ground flora species present.

Changes in assemblage were also seen at the same coupe over time and assemblage changes reflected alteration in habitat requirements as described above. For example, the assemblage from coupe 2 in 2002, when the coppice regrowth was two years old, contained species of open habitat and open woodland e.g. Bordered Sallow (*Pyrrhia umbra*) which includes restharrow (*Ononis repens*) as a larval foodplant and can be associated with grassland habitat (Waring and Townsend 2009); species making up the assemblage recorded in 2004 from the same coupe, provide examples typical of open and mature woodland e.g. clay triple-lines (*Cyclophora linearia*) feeding on beech in mature beech woodlands and The Snout (*Hypena proboscidalis*) feeding on nettle (*Urtica dioica*) in open woodland and scrub (Waring and Townsend 2009).

The change in habitat that accompanied the process of coppice regrowth in our study was similar to that observed in sweet chestnut woodlands in other parts of Britain. Canopy closure occurred five years after cutting (Mitchell 1992; Harmer and Howe 2003), vegetation of highest diversity in coupes with three years of regrowth, fewer plant species in coupes with five years of regrowth and only one ground flora species in coupes with 11 years of coppice regrowth as found by Mason and Macdonald (2002). As in the Mason and Macdonald (2002) study, we found the shade tolerant species wood sage, bramble and honeysuckle, present in coppice across the range of coppice ages; other ground flora species referred to as ‘marginal’ ‘casual’ or ‘shade evading’ by Mason and Macdonald (2002) were also represented in our study at an equivalent stage. Consequently, this would suggest that results from our study both in terms of habitat response and the associated moth response could be applicable to other sweet chestnut coppice woodlands in Britain.

The third aim of this study was to consider the implications of coppice management for moth species and to use the results of this survey to develop appropriate coppice management. The creation of a variety of habitats (structure and vegetation species composition) as a result of coppicing has been identified as an important way of increasing the moth diversity within woodland (Bulman 2007). The detailed knowledge available on the ecology of moth species that are found within coppice woodlands shows that different species thrive at each stage of the cycle, emphasising the value of rotational coppicing to moth diversity (Waring and Haggett 1991). Declines of certain moths such as the drab looper (*Minoa murinata*) (a UK BAP Priority species) has been attributed to the cessation of coppicing (UK Biodiversity Group 1999). Our results confirm that moth assemblages change as coppice regrowth proceeds, indicating that many moths have the capacity to colonise habitats as they become available. Amongst each of the assemblages associated with different stages of coppice development are a range of scarcer species, including several of conservation concern. For example, the waved carpet (a former UKBAP species (Parsons and Davis 2007)), is particularly associated with 5–9-year-old sweet chestnut coppice regrowth (Clarke 2003), and active coppicing will, therefore, clearly benefit such moth species (Wigglesworth et al. 2004). Our results also show that many species of high conservation status were present in the mature coppice stage coupes which also had the highest moth species diversity and abundance.

Waring (1988) concluded that overgrown coppice woodland was of considerable value to woodland moth populations when compared to recently cut coppice. Our study suggests that re-coppicing abandoned sites (which broadly equate to the coupes that had not been coppiced in the last 10 years in this study) should be approached with caution as they may contain a wide diversity of species and may harbour a large proportion of scarcer moth species. Although recently coppiced coupes support a diversity of moth species they tend to be species associated with open habitats that may be provided elsewhere. Such a conclusion appears at odds with advice widely given for management of woodland habitats for butterflies (e.g. Warren and Thomas 1992; Warren 1991; Bulman 2007) and the requirement to reinstate and maintain the coppice management thereafter. However, the apparent contradiction can be resolved if areas of un-managed and mature coppice are retained within actively managed coppice woodlands in order to maximise moth diversity and to provide a source for colonising new areas of suitable habitat. Further, we suggest some coupes of coppice should be allowed to mature beyond 15 years. This recommendation is supported by the work of Summerville and Crist (2008), who identify the importance of rare species in defining moth community composition in unmanaged woodland. They suggest that, unlike the dominant taxa which are relatively resilient to felling, rare moths show gradual recolonisation rates resulting in community recovery taking decades to complete.

The size of woodland that is coppiced is therefore important and small woodland blocks may not be appropriate subjects for coppice management if moth diversity is to be maintained, except, perhaps, as part of a mosaic of smaller woodlands within a wooded landscape. Further work is required to refine this guidance and clarify the importance of woodland scale and landscape context for optimising coppice management.

4.6 Conclusions

The influence of coppice age on moth assemblage was shown in this study of managed sweet chestnut coppice woodland. Here, the inference is that differences in assemblage results from the change in moth species which is driven by the availability of foodplants, changing from an assemblage of moth species dependent on ground flora in the newly cut coppice areas to one composed of species predominantly dependent on trees, shrubs and including species associated with deadwood fungi and leaf litter, in the mature coppice. Moth species with a conservation status (Red Data Book, Nationally Scarce or UKBAP Priority species (Appendix 1)) showed a preference for older coppice (greater than five and 10-year-old coppice regrowth), although there were also other scarce species associated with the early coppice stages.

Management of woodland by coppicing promotes a change in moth assemblage at the coupe level, providing a range of coppice age classes is present. Woodlands that have no history of coppicing or regular clearance should not be coppiced, as they are likely to contain a range of flora and fauna that require a continuity of woodland habitats rather than coppice related species (Waring and Haggett 1991). An important finding from our study is that old coppice provides an excellent moth habitat that offers appropriate conditions for a range of scarce and threatened species, many not found at other times during the coppice cycle. This is likely to be reflected in older coppice coupes at other sites. Felling of such areas may be detrimental in the short term and has been discouraged where coppice regrowth is more than 100-years-old (Waring and Haggett 1991). There is a need to ensure long-term annual continuity of older coppice to ensure this assemblage of moth species is represented. Therefore, quality and extent of coppice woodland along with the diversity of structure would appear to be key in promoting moth diversity, and options for extending coppice management cycles, and leaving coppice coupes unmanaged for longer than 15–20 years should be considered. Further work is required on understanding whether scale and location of coppice coupes for moth species can be optimised depending on the arrangement of coppice woodland in the landscape.

4.7 Acknowledgments

I thank the Forestry Commission for providing access to the study site and in particular Robert Thurlow and Stan Abbott. I am also grateful to Simon Curson, John Phillips and Sean Clancy for contributing information about the study site. I also thank Ralph Harmer, Joan Cottrell and Chris Quine who commented on earlier drafts.

Appendix 4.1 Scarcer night-flying moth species recorded from managed sweet chestnut coppice (one to 19 year old coppice coupes) in Rewell Wood, West Sussex between 2002 and 2004.

Bradley Number[1]	Species	Common name	UK BAP/ S41[2]	National Status[3]	Total count[4]
1382	*Anania verbascalis*			Nationally Notable B	9
1924	*Angerona prunaria*	Orange Moth		Local	22
1910	*Apeira syringaria*	Lilac Beauty		Local	2
2330	*Apamea remissa*	Dusky Brocade	yes		8
173	*Apoda limacodes*	Festoon		Nationally Notable B	5
2039	*Atolmis rubricollis*	Red-necked Footman		Local	12
1494	*Capperia britanniodactyla*			Nationally Notable	9
2387	*Caradrina morpheus*	Mottled Rustic	yes		2
2291	*Craniophora ligustri*	Coronet		Local	2
2040	*Cybosia mesomella*	Four-dotted Footman		Local	2
1681	*Cyclophora linearia*	Clay Triple-lines		Local	13
2123	*Diarsia rubi*	Small Square-spot	yes		1
2047	*Eilema complana*	Scarce Footman		Local	22
2043	*Eilema sororcula*	Orange Footman		Local	20
2396	*Elaphria venustula*	Rosy Marbled		Nationally Notable B	4
718	*Ethmia dodecea*			Nationally Notable B	10
1813	*Eupithecia haworthiata*	Haworth's Pug		Local	12
16	*Hepialus hecta*	Gold Swift		Local	1
14	*Hepialus humuli*	Ghost Moth	yes		12
2382	*Hoplodrina blanda*	Rustic	yes		3
1877	*Hydrelia sylvata*	Waved Carpet		Nationally Notable B	69
1978	*Hyloicus pinastri*	Pine Hawk-moth		Local	3
1943	*Hypomecis roboraria*	Great Oak Beauty		Nationally Notable B	9
1711	*Idaea trigeminata*	Treble Brown Spot		Local	4
1889	*Macaria notata*	Peacock Moth		Local	87
2155	*Melanchra persicariae*	Dot Moth	yes		10
1784	*Melanthia procellata*	Pretty Chalk Carpet	yes		6
2037	*Miltochrista miniata*	Rosy Footman		Local	60
2277	*Moma alpium*	Scarce Merveille du Jour		Rare (RDB)	8
881	*Mompha terminella*			Nationally Notable B	1
2038	*Nudaria mundana*	Muslin Footman		Local	2
651	*Oecophora bractella*			Rare (RDB) provisional	10
2494	*Paracolax tristalis*	Clay Fan-foot	yes	Nationally Notable B	1
1949	*Paradarisa consonaria*	Square Spot		Local	29
2268	*Parastichtis suspecta*	Suspected		Local	5
1904	*Plagodis dolabraria*	Scorched Wing		Local	66
2399	*Pyrrhia umbra*	Bordered Sallow		Local	10
2482	*Schrankia taenialis*	White-line Snout		Nationally Notable B	6
1034	*Spatalistis bifasciana*			Nationally Notable	30
2061	*Spilosoma luteum*	Buff Ermine	yes		73
769	*Teleiodes wagae*			Rare (RDB) provisional	4
1656	*Tetheella fluctuosa*	Satin Lutestring		Local	16
2069	*Tyria jacobaeae*	Cinnabar	yes		1

1= Bradley number (Bradley, 2000); 2= Species is listed within the UK Biodiversity Action Plan UKBAP) (UK Biodiversity Reporting and Information Group, 2007) and in accordance with section 41 of the Natural Environment and Rural Communities Act 2006 (Natural England, 2010); 3= National Status (Red Data Book (RDB), Nationally Scarce (Parsons 1984, 1993 & 1995; Waring & Townsend, 2009; Waring, unpublished); 4= total count of individual moths recorded from the coppice coupes between 2002 and 2004.

Chapter Five: Epiphytic lichens of Atlantic oakwood remnants can survive early stages of woodland restoration

An adapted version of this chapter has been sumitted to Annals of Forest Science as:

Lauren L. Inchboard, Kirsty J. Park, Richard Thompson, Mike Perks and Alice Broome. Epiphytic lichens of Atlantic oakwood remnants can survive early stages of woodland restoration.

Contributions: RT and MP designed the survey and conducted earlier field surveys. AB and LI conducted later field surveys, carried out data analysis and co-wrote the manuscript. KP commented on an earlier draft.

5.1 Abstract

Woodlands of long continuity are important for biodiversity and ancient semi-natural woodlands (ASNW) of Atlantic oakwood support rare and endangered species including a unique epiphytic lichen flora. Fragmented ASNW Atlantic oakwood sites have been historically planted with conifers to increase timber production. Restoration of 15% of degraded habitats by 2020 is an international policy objective aimed at conserving biodiversity and delivering ecosystem services and such Planted Ancient Woodland Sites (PAWS) are now being restored. However, there are concerns that the sudden removal of the dense conifer matrix surrounding remnant native trees PAWS, as effected during PAWS restoration, could change the environmental growing conditions for woodland epiphytes.

To guide forestry policy and practice we ask whether an unintended consequence of initiating habitat restoration aimed at maintaining habitat for epiphytic species, is the loss of the relict populations of epiphytes on ASNW remnant trees in the PAWS. In this study, ground flora composition was assessed immediately post conifer removal and nine years later along transects spanning the boundary between PAWS and ASNW/remnants. Dynamics and direction of change for the vegetation indicative of restoration progress were studied using indicator species occurrence and plant functional traits. Change in cover of lichen species was assessed by fixed-point photographs of trees supporting the target lichen species *Lobaria pulmonaria* and *L. virens* at the study site and chlorophyll fluorescence of these two species was used as a measure of lichen vitality.

Re-vegetation is predominantly by ASNW precursor vegetation species including three of the five desired species already present in the woodland. The ground flora functional traits profile in the felled area becomes more diverse and the frequency of tree seedlings and samplings increases. Lichen vitality is initially reduced by conifer removal but appears to recover. The *Lobarion* epiphyte community appears more stable in the ASNW than in the remnants where infrequently represented species are both lost and gained. The abundance of the main lichen species does not change.

As the observed vegetation changes indicate the site is recovering, this restoration approach is recommended for other similar Atlantic oakwood sites where epiphytic lichen conservation is an objective.

5.2 Introduction

International policy aimed at conserving biodiversity and enhancing the supply of ecosystem services is to restore 15% of degraded habitats by 2020 (Convention on Biological Diversity 2001). This is most efficiently achieved by focusing on priority habitats with currently inadequate conservation status (Benis et al. 2014). Restoration ecology concepts have continued to develop over the last 30 years and implementation of restoration projects are guided by clear principals (SER 2004; Shackelford et al. 2013). In outline, these principals include a strong motive for restoration e.g. meets a statutory requirement, clear goals of what is to be achieved with reference to the undamaged state of the target ecosystem, and knowledge of how to achieve and quantify restoration (Perring et al. 2015). Although this process of ecological restoration aims to assist the recovery of an ecosystem (SER 2004), the question remains whether degraded habitats can be restored without unintended consequences for the remnant ecosystem elements (e.g. Takekawa et al. 2015).

A review of 200 restoration projects worldwide found that a quarter were forest habitats (Hallett et al. 2013). Forests have been modified, with loss of natural forests and an expansion of plantations (FAO 2016). Human intervention is frequent in the histories of forests, as for example in the ancient semi-natural woodlands (ASNW) of Quercus and Fagus of western Europe, resulting in forest fragmentation and more recently infill planting with productive species (Bradshaw et al. 2015). In the same manner, the ASNW of Atlantic oakwood in the Britain has been highly modified. Forest policy dictated an increase of strategic timber resource in the 1960s resulting in many fragmented areas of ASNW being in-filled or replaced with non-native conifer species (Pryor et al. 2002). The resulting woodlands are termed PAWS (plantations on ancient woodland sites). Over time, detrimental impacts of such planting can result from over-shading of remnant woodland patches by mature conifers (Barbier et al. 2008) and changes in soil properties such as acidity (Laurent et al. 2015) and water retention (Barbier et al.

2009), thus affecting understorey development (Ferris et al. 2000; Bergès et al. 2017).

Restoration of Atlantic ASNW oakwood is a priority activity as the habitat is a European Union Habitats Directive Annex I habitat (91A0 “Old sessile oak with Ilex and Blechnum in British Isles”), and its conservation status currently ranges from unfavourable to bad (ec.europa.eu consulted January 2019; JNCC.defra.co.uk consulted January 2019). “Favourable condition” for priority woodland habitats in the UK is achieved when the canopy comprises 95% site native species (Brown et al. 2015). Therefore, in response to the maturation of many of the conifer crops on PAWS, recent forest policy has been to restore PAWS sites by removing the conifers (Brown et al. 2015). Ecological restoration management aims to restore the community and the necessary ecosystem components (Young 2000). Assessment of progress towards restoration often focuses on measures such as species diversity and/or plant-life groups, in place of other measures of site-level biodiversity or broader landscape or socio-economic effects (Brudvig 2011; Perring et al. 2015). Such species-based assemblages are often evaluated by the study of ground flora composition as vegetation composes a large part of the earth’s biomass and constitutes a major trophic layer (Young 2000). More recently, traits based approaches such as assessing communities based on species’ functions have been incorporated in to restoration assessments (Perring et al. 2015). Within PAWS, ground flora of ASNW Atlantic oakwood remnants provide the indicator species, measures of richness and profiles of traits against which progress of PAWS restoration towards Annex 1 Habitat 91A0 can be assessed (Perring et al. 2015).

Atlantic oakwood PAWS offer suitable subjects for habitat restoration considering there are clear motives and goals to reverse the habitat changes, and a facility (in the form of remnant areas) to assess restoration progress (SER 2004). However, the actions undertaken in restoration may be detrimental to some target species occupying the oakwood remnants which are a conservation priority. Internationally important lichen assemblages develop in 91A0 habitat (James et al. 1977), the richest being in the Scottish Highlands as indicated by diverse Lobarion communities. Of the 706 woodland lichen species present in the UK, 517 are reported only in Atlantic woodlands. Nineteen of the total 706 species are reported as being of UK international responsibility, often found upon remnant trees of Atlantic oakwoods (Coppins and Coppins 2005). Of the lichen species used to grade the ‘ancient woodland’ characteristics of deciduous woodlands in the British Isles (providing an Index of Ecological Continuity), a subset of 50 species form the Western Scotland community, particular to the mild, wet, Atlantic climate experienced along much of lowland and coastal western Scotland (Coppins and Coppins 2002). In a woodland ecosystem, removal of plantation trees (felling) can lead to sudden alterations in the water table, light availability and exposure, and therefore be detrimental to woodland ecosystems by impacting on both abiotic conditions and resource availability (Knapp et al. 2014). Thus, lichens may be detrimentally affected by restoration action. Lichens can only photosynthesise when they are wet but are generally able to resist damage from high light levels and temperatures when in a desiccated state (Green and Lange 1995). However, for epiphytic woodland species, damage can occur even when the thalli are dry (Gauslaa and Solhaug 1999). For these lichens e.g. in the genera Lobaria, Pseudocyphellaria and Sticta, reduced vitality would therefore be expected to occur with changes in microclimate at forest edges. Lobaria species have been used as the focal species in studies of lichen sensitivity to forest management changes with physiological responses manifesting more rapidly than changes in lichen abundance or presence (Renhorn et al. 1996; Palmqvist and Sundberg 2000).

In this study conifers were removed from an Atlantic ASNW in an attempt to restore the woodland. Following conifer removal, we used ground vegetation changes to assess restoration progress. We ask if early woodland restoration stages can be achieved without damaging the epiphytic lichen flora, which is a conservation priority. We anticipate that an unintended consequence of restoration management within the remnants of oak woodland will be initial physiological stress to epiphytic lichens immediately following conifer removal, and eventual loss of these species in years subsequent to the restoration actions. Our objectives were to quantify the effects of conifer removal on: (1) species-specific functional traits and composition of the ground flora (as indications of restoration success) and (2) epiphytic lichens on remnant native trees within a PAWs site (as measured by physiological stress / vitality to assess immediate response and long-term response and as measured by community composition and lichen species cover to assess long-term response).

5.3 Material and methods

5.3.1 Study site

The study site consists of a series of planted areas in a fragmented ASNW oak woodland in Glencripesdale National Nature Reserve on the shores of Loch Sunart, NW Scotland (56°40'N, 5°49'W) (Figure 5.1), mainly populated with Sitka spruce *Picea sitchensis,* dating from a 1971-1977 Forestry Commission plantation scheme. The clear-felling of conifers was carried out during the autumn of 2007 at which time the unthinned crop had achieved an average basal area of 62 m^2/ha. The site covers approximately 50 ha at elevations of less than 60 m above sea level. The remaining ASNW is mainly composed of Habitats Directive Annex I habitat (91A0 "*Old sessile oak with Ilex and Blechnum in British Isles"*) that typically occurs on impoverished acidic soils with an overstorey of *Quercus petraea*, *Q. robur*, *Betula pendula* and *B. pubescens* and an understorey containing *Ilex aquifolium* and *Corylus avellana.* The ground flora of these woodlands is strongly influenced by the oceanic climate leading to dominance by ferns, mosses, lichens and acidophilous grasses (Rodwell 2005). Mean monthly temperature (data for the period 2007 to 2016 from the nearest meteorological weather station: 56°45'N, 5°44'W) rarely exceeds 15°C or falls below 5°C and rainfall exceeds 100mm during nine months of the year, exceeding 200mm in three of these (Appendix 5.1 Figure 1). Compared to the climate of other oak woodland sites in Scotland (data also from the nearest meteorological weather stations) (Figure 5.1), Glencripesdale has one of the most oceanic climates, is at the higher end of the range for climatic warmth (yearly growing degrees) but has a median value for Heat/Moisture index. The range of values for these climate indices is however small and rarely are the values for Glencripesdale significantly different from those of the other oak woodland sites (Appendix 5.1 Table 1).

Figure 5.1 Location of Glencripesdale oak woodland and of the nine other Scottish oak woodlands to which its climatic data was compared (Figure 1, Appendix 5.1). Index of Ecological Continuity (IEC) grade is represented by symbols: dots for Western Scotland IEC, squares for Eastern Scotland IEC, triangles for New IEC.

5.3.2 Experimental design

The site is divided into three woodland types: 1) large areas of ancient semi-natural woodland, hereafter referred to as ASNW; 2) plantations of Sitka spruce (felled in autumn 2007), referred to as PAWS or former PAWS once the trees were felled and the areas were open; and 3) small patches of ancient semi-natural woodland named remnants (size range 0.01 - 0.03 ha) – sometimes consisting of only one tree surrounded by conifer plantation within the PAWS. Ground flora assessments were carried out to compare communities in the PAWS (bare after autumn 2007) and communities within the remnants and the ASNW. The impact of conifer removal on epiphytic lichens was assessed on trees within the remnants facing the PAWS (exposed after autumn 2007) by comparison to those inside the ASNW (Figure 5.2).

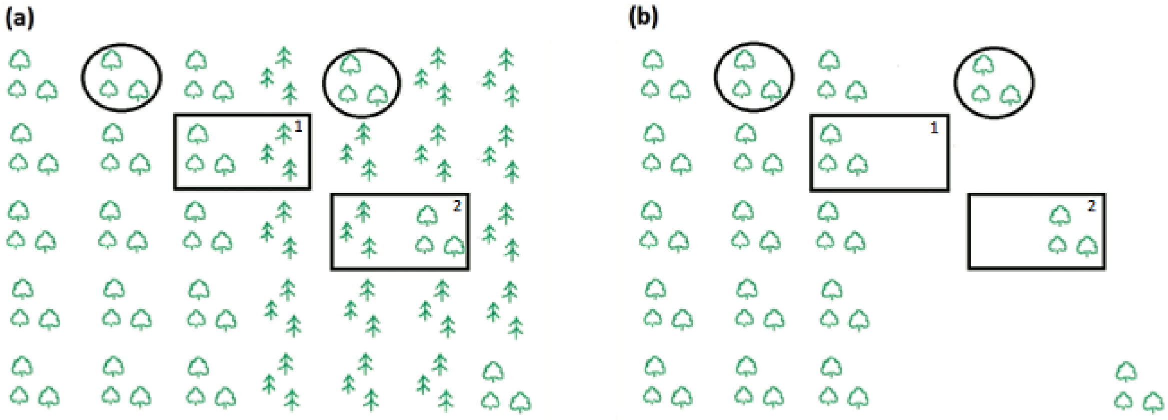

Figure 5.2 ASNW/PAWS/remnant matrix and experiment design: neighbouring ASNW and PAWS with remnants of ASNW within the PAWS, before (a) and after (b) felling. Rectangles depict ground flora assessment sites composed of transects running either from ASNW into PAWS (1) or from remnant into PAWS (2); circles depict lichen assessment sites.

5.3.3 Ground flora assessment

The ground flora was assessed in six plots by estimating total percentage cover of all species of vascular plants, mosses, lichens and liverworts as well as of inert matter (bare ground and litter/brash), in 12 quadrats (0.5m x 0.5m) per plot. These were arranged as four quadrats positioned along each of three parallel transects running from the ASNW or remnant into the PAWS at 6m (Q0) distance inside the ASNW/remnant from ASNW/remnant - PAWS boundary (ecotone) and 3m (Q9), 6m (Q12) and 9m (Q15) into the PAWS from the boundary. Assessments were made prior to conifer removal (2005), immediately after conifer removal (2008) and again in 2016. The locations of the transects were recorded via GPS and delimited with marker pegs. The sampling in 2005 followed a similar design as outlined above but had 12 plots each with two transects spanning the ASNW/remnant and PAWS each with 10 quadrats spaced at 2 m intervals (for details see Thompson and Hope 2005).

5.3.4 Lichen assessment

Prior to conifer removal, 26 trees supporting Lobarion lichen communities were selected, 15 in the remnants (10 acidic-barked trees (oak) and 5 higher pH bark trees (hazel or ash)) and 11 within the ASNW (6 and 5, respectively) (see Thompson and Hope 2005). The trees hosted on occasion other native epiphyte species.

Chlorophyll fluorescence (CF) yield was measured for *Lobaria pulmonaria* and *L. virens*, each on two thalli located on the low stems or branches of ten of the remnant trees and five of the ASNW trees. Chlorophyll fluorescence is a rapid, non-destructive ecophysiological tool that allows measurements of photosynthetic capacity and light utilisation to be made in situ which can detect reductions in plant vitality before any visible signs are evident (van Kooten and Snel 1990) and is commonly used as a proxy measure of lichen vitality (MacKenzie et al. 2001). Measurements were taken in the spring, summer and autumn in the year prior to and following conifer removal to assess short-term changes, and in the autumn nine years after conifer removal to assess long-term changes. CF measurements were taken at ambient temperatures using a pulse amplitude moderated (PAM) chlorophyll fluorimeter (Walz MiniPAM, Wlaz GmBH, Effeltrich, Germany), details are presented in Appendix 5.2.

Lichen community composition and growth were assessed using fixed-point photographs pre-conifer removal in 2007 and in 2016, nine years after conifer removal. Forty communities were initially photographed from the 26 lichen assessment trees, 25 communities on remnant trees and 15 on ASNW trees. A PVC 0.04m^2 frame was fixed around each lichen community with three plastic nails set into the bark; for smaller lichen samples a half-frame measuring 0.02m^2 was used. The samples were taken at surveyor height (between 52 cm and 273 cm from base of tree) and photographed with a 10 megapixel digital field camera. Setting up a tripod was not deemed feasible on the steep slopes and the lighting could not be homogenized, but these adjustments were not considered necessary for the assessment of lichen surface area. The frame was removed to be used on another tree, but the nails were left in situ for the next survey in 2016. Twenty-two of the former forty communities were relocated and photographed in 2016, split equally between the remnants and the ASNW trees. The photographs were corrected for parallax with the Windows utility Perspective Image Correction and processed with Trimble's ©E-cognition in order to extract the surface areas of the different lichen species; details are presented in Appendix 5.2.

5.4 Data analysis

5.4.1 Evaluating restoration success through ground flora species and functional trait composition

In order to evaluate the restoration success, we assessed changes in ground flora, using both species- and functional trait-based approaches.

Evaluating change in ground flora community

We determined pre- and post-felling occurrences of all species present in PAWS and ASNW/remnants quadrats. Of these species, we counted the occurrences of tree seedlings and saplings and of species indicative of site potential for native woodland establishment and development. The latter correspond to *precursor vegetation* and *desired invaders* as defined by Rodwell and Patterson (1994) in the National Vegetation Classification (NVC) woodland types (W7, W9, W11 and W17) that constitute the native woodland matrix at the study site. *Precursor species* represent open land vegetation able to become components of corresponding woodland, and the *desired invaders* are woodland specialists that arrive once the canopy is established (Rodwell and Patterson 1994).

Evaluating change in functional traits

The Ellenberg resource intake classification and Grime strategies were used to describe the functional traits of each species occurring in the study site (Grime 1977; Ellenberg et al. 1992). Vascular plants were attributed revised Ellenberg values for British plants (Hill 1999) for light, moisture and nitrogen. These are not available for bryophytes, for which the original Ellenberg values for European plants were used (Ellenberg et al. 1992). The Ellenberg values for light and nitrogen requirements range from 1 to 9, and for moisture from 1 to 10, with a higher value indicating a stronger demand for resources. We calculated three weighted Ellenberg values per quadrat, approximating an overall requirement in light, moisture and nitrogen. For this calculation, inert matter was attributed an Ellenberg value of zero.

$$E_{weighted} = \sum_{0}^{E_{max}} \frac{E_i * Cover_{Species\ E_i}}{Total_{Cover}}$$

Grime strategies (Grime 1977) are only available for vascular plants, which were classified as ruderal, stress-tolerant, competitive or as adopting a mix of two or three strategies (thus named ‘strategic’), resulting in a total of seven Grime categories being used to characterise the ground flora; for the analysis, the label “No_CSR” was attributed to bryophytes.

Each quadrat, defined by a position on the transect relative to the ecotone (Q0 for ASNW; Q9, Q12, Q15 for PAWS) and a measurement year (2008/2016), was assigned a percentage of presence per Grime strategy and three weighted Ellenberg values (for light, moisture and nitrogen). These data are hereafter referred to as *functional trait data*.

Baseline vegetation quadrat data pre-felling (from 2005) were described by the percentages of cover of each Grime strategy and Ellenberg value; results are presented descriptively in Appendix 5.3.

Principal components analysis

The functional trait data described previously were analysed using principal component analysis (PCA) to determine the functional response to the conifer removal in the PAWS. The variables and quadrats are presented graphically in resulting factorial plane PC1 x PC2 and correlations and loadings were extracted for the most informative variables.

5.4.2 Evaluating the impact of clear-felling on lichen survival

Assessment of lichen vitality

As there is seasonality in chlorophyll fluorescence (CF) yield in lichens (MacKenzie et al., 2001; and confirmed by our own data) we compared measurements taken in only the autumn of each assessment year. Further, as CF yield in lichens is sensitive to temperature (Palmqvist and Sundberg 2000) only pairwise comparisons of yield should be made at each assessment time i.e. relative differences in CF yield between lichens in remnants and ASNW compared. A total of 52 readings, equally split between *L. pulmonaria* and *L. virens*, were taken at each of the three time points (n=32 remnants, n=20 ASNW), from the same sample of 15 trees. Means and dispersion of yield values were calculated for *L. pulmonaria* and *L. virens* by treatment (ASNW and remnant) and time point.

Assessment of changes in lichen cover and species richness

Difference in cover between 2007 and 2016 was calculated for each lichen in each frame. Sample sizes were insufficient to conduct statistical tests, so for each species occurring in more than 5 frames, a 95% confidence interval for mean difference of cover was estimated through bootstrapping with n=100 resamples. These confidence intervals were compared between ASNW and remnants for each lichen species.

All analyses were conducted with R 2.14.1 and implemented with R Studio 2.14.1 (R Core Team 2018). The package FactoMineR was used to calculate the principal components (Lê et al. 2008).

5.5 Results

5.5.1 Evaluation of change in ground vegetation and functional-trait composition

Ground flora species richness

In the year immediately following conifer removal, species richness of ground flora was lower in the former PAWS than in the ASNW/remnants (Table 5.1). Species richness increased in both former PAWs and ASNW/remnant quadrats between 2008 and 2016, with a 53 to 61% increase in species richness in the former PAWS and a 25% increase in the ASNW/remnants. The species richness in the former PAWS was close to that of the ASNW/remnants in 2016. Lower species richness recorded in the former PAWS in 2008 may not have been completely due to the impact of the felling operations as in the baseline (pre-conifer removal) survey of 2005, twice as many species (100) were recorded in the ASNW/remnants (120 quadrats) compared to the PAWS (55 species in 110 quadrats).

Table 5.1 Total species richness in quadrats 3m into the ASNW/remnants (Q0), and 3m (Q9), 6m (Q12) and 9m (Q15) into the former PAWS, with increase calculated as a percentage.

	2008	2016	Increase (%)
Q0 (n=18)	33	44	25
Q9 (n=18)	19	41	54
Q12 (n=18)	15	38	61
Q15 (n=18)	16	36	56

Natural regeneration

Tree seedlings and saplings were found within 17% of both former PAWS and ASNW/remnant quadrats one growing season following conifer removal, of which two thirds were native species in the PAWS, and all were native species in the ASNW/remnants. In 2016, tree seedlings and saplings were recorded in 67% (59% with site native species) of the quadrats in the former PAWS and 33% (22%) of the quadrats in the ASNW/remnants. Corresponding areas assessed in the baseline survey carried out prior to conifer removal had a frequency of seedlings of 2.7% and 3.3% in the PAWS and ASNW/remnants, respectively. Regenerating native species included (in descending order of frequency) *Betula pubesences/ B. pendula, Alnus glutinosa, Quercus petraea, Ilex aquifolium and Corylus avellana.*

Ground flora precursor and invader species

Twenty-five recorded ground flora species were listed as *desired invaders* and a further 39 species were identified as *precursor vegetation* in at least one of the four woodland types proposed by Rodwell and Patterson (1994) present at the study site. Eighteen of the 64 species were present immediately after felling and nine years following felling; nine species in the in the ASNW/remnants, two in the former PAWS and a further seven in both woodland types. The species are an equal mixture of *desired invaders* and *precursor species* and all occurred at low frequencies except for *Oxalis acetosella* which occurred in more than 30% of the quadrats (Table 5.2). Changes were seen in the ground flora nine year following felling, with seven species previously only recorded in ASNW/remnants appearing in the former PAWS (two of which are *desired invaders - Dryopteris dilatata* and *Lysimachia nemorum*), and new records of a further seven species (three in the ASNW/remnants, one in the former PAWS, and the reminder recorded in both areas). Three of the new species were *desired invaders* (*Dryopteris filx-mas; Geum urbanum; Hyacinthoides non-scripta*); the latter two of these were only recorded in the ASNW/remnants.

Table 5.2 Quadrat frequency of desired invader (Inv) and precursor (Pre) ground flora species in 2008 and 2016, in ASNW and former PAWS. Each and invader and precursor species is indicated to be present in at least one woodland type found in our site. (o) indicates absence, (x) indicates presence, and (xx) indicates a high frequency of presence (defined as recorded in more than 30 % of quadrats)..

Precursor or Invader by woodland type:					**2008**		**2016**	
W7	**W9**	**W11**	**W17**	**Ground flora species**	**ASNW**	**Former PAWS**	**ASNW**	**Former PAWS**
	Pre	Pre	Pre	*Agrostis capillaris*	x	x	x	x
Pre	Pre	Pre	Pre	*Anthoxanthum odoratum*	x	o	x	x
		Pre	Pre	*Blechnum spicant*	o	x	x	x
			Pre	*Calluna vulgaris*	o	o	x	o
Inv				*Chrysosplenium oppositifolium*	x	o	x	o
Pre				*Cirsium palustre*	x	o	o	x
Pre	Pre			*Deschampsia cespitosa*	o	o	x	xx
			Pre	*Deschampsia flexuosa*	o	o	x	x
Inv		Pre	Inv	*Dryopteris dilatata*	x	o	x	x
	Inv			*Dryopteris filix-mas*	o	o	o	x
		Pre	Pre	*Galium saxatile*	x	o	x	x
	Inv			*Geranium robertianum*	x	o	x	o
	Inv			*Geum urbanum*	o	o	x	o
	Pre	Pre		*Holcus lanatus*	x	o	xx	xx
Inv	Pre	Inv		*Holcus mollis*	x	x	o	x
	Inv	Inv		*Hyacinthoides non-scripta*	o	o	x	o
Pre				*Juncus effuses*	x	x	x	x
Inv	Inv			*Lysimachia nemorum*	x	o	x	x
Inv	Inv	Inv	Inv	*Oxalis acetosella*	xx	xx	xx	xx
Pre	Pre			*Poa trivialis*	x	x	x	x
		Pre	Pre	*Potentilla erecta*	o	o	x	x
	Pre	Inv		*Primula vulgaris*	x	x	x	x
		Pre	Inv	*Pteridium aquilinum*	x	x	x	x
Pre				*Ranunculus repens*	x	o	xx	x
	Pre			*Veronica chamaedrys*	x	x	x	o
Pre	Pre	Pre		*Viola riviniana*	x	x	x	x

Interpretation of ground flora community composition using species-specific functional traits

PC1 and PC2 jointly explained only 49.52% of the variance of the functional trait data, composed of variables present in Figure 5.3a. The most important variable correlations (presented with loadings) on PC1 (37.38% of total variance) were 0.99 (0.45), 0.98 (0.46), 0.95 (0.45) and -0.99 (-0.47) for the weighted Ellenberg values for light, moisture and nitrogen values, and the cover of inert matter, respectively*.* On PC2 (12.14% of variance), the variables [percentage cover of] stress-tolerant, no CSR, strategic and competitive [species] had correlations (and loadings) of 0.73 (0.61), 0.68 (0.56), -0.37 (-0.31), -0.35 (-0.30), respectively.

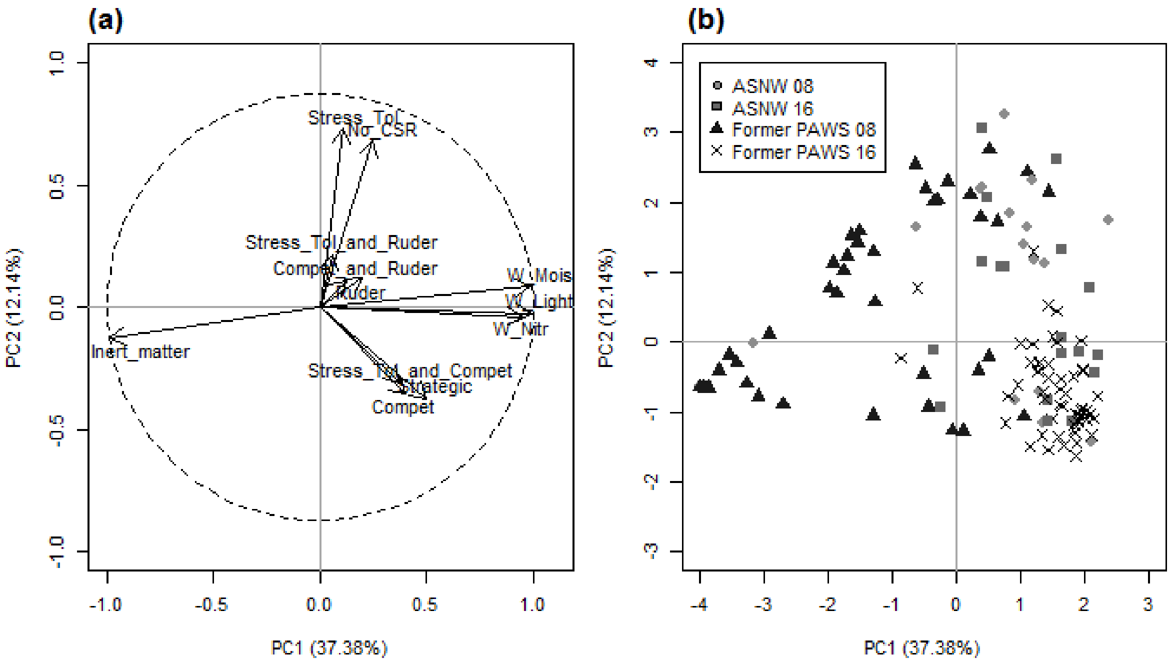

Figure 5.3 Principal Components Analysis (PCA) conducted on functional trait data: (a) correlation circle of the twelve variables; (b) scatter plot of quadrats represented according to categorical variables location (ASNW vs former PAWS) and year (2008 vs 2016), both in PC1xPC2 (49.52% of total variance).'No_CSR' is the Grime strategy assigned to lichens and mosses.

The separation of quadrats depending on categorical variables *location* and *year* is observable in Figure 5.3b. The quadrats in the recently felled 2008 PAWS (triangles) are separated from the other quadrats along PC1 (Figure 5.3b). In Figure 5.3a we remark that the variable *inert matter* is the only negative correlation on the first axis, opposed to the positive correlations of all the other variables. This indicates how inert matter was still present in large amounts during the immediate post-felling assessment.

Felled 2016 PAWS quadrats (crosses) are separated from those of 2008 and 2016 ASNW/remnant quadrats (circles and squares, respectively) on the second axis, though PC2 only accounts for 12.14% of total variance (Figure 5.3b). Variable-wise, Grime strategies are separated on the second axis with stress tolerant and ruderal covers opposed to the cover of competitive and strategic species. Whereas the ANSW/remnant quadrats of both assessments contain vegetation of various strategies, the 2008 former PAWS quadrats are characterised by an important amount of inert matter and stress tolerant species and 2016 former PAWS quadrats contain primarily competitive species.

5.5.2 Impact of clear-felling on epiphytic lichens

Chlorophyll fluorescence (CF) data

Even though the remnant trees were surrounded by the conifer matrix pre-felling, CF yield from lichens on the remnant trees were similar to that from lichens on the ASNW trees at this time (Figure 5.4). In the autumn following felling, CF yield was a third lower in the lichens sampled on the remnant trees relative to the ASNW control trees. Nine years following felling, CF yield was again comparable between lichens on remnant and ASNW trees. This response was consistent for the two lichen species, but *L. virens* generally showed greater variability in CF yield than *L. pulmonaria* (Figure 5.4).

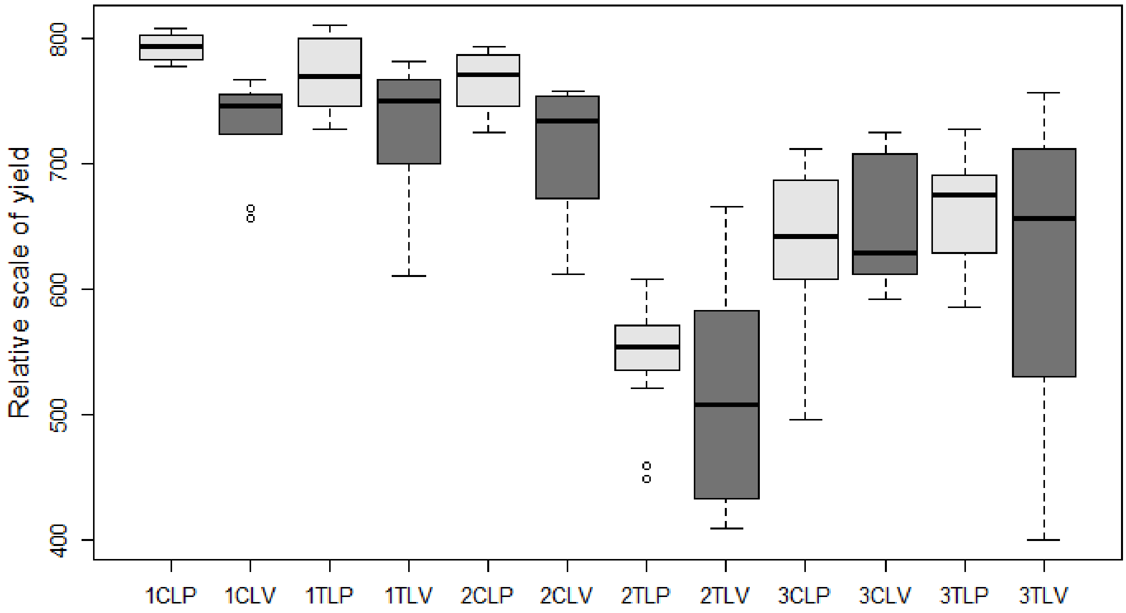

Figure 5.4 Chlorophyll fluorescence measured in two Lobarion lichen species (Lobaria pulmonaria - LP, L. virens – LV) on remnant native trees facing former PAWS (Treatment –T) and areas of ASNW (Control –C), assessed the autumn prior to (1), following (2) and nine years (3) after PAWS restoration by winter felling of the conifer matrix.

Photographic data

The 40 samples photographed pre-felling comprised: 22 communities containing *L. virens,* of which seven were in the ASNW and 15 in remnants; 17 communities containing *L. pulmonaria*, ASNW (10) and remnants (7); one community containing both *Lobarion* species simultaneously in the ASNW. Additionally, seven communities contained *Degelia atlantica,* ASNW (4) and remnants (3), and a further seven lichen species were detected with smaller frequencies.

In 2016, it was possible to locate 22 of the original 40 trees on which samples had been photographed; these were split equally between the remnants and the ASNW. The change in cover for each species of lichen between 2007 and 2016 is presented in Table 5.3. *Lobarion pulmonaria* remained in 10 frames but disappeared from two, one in the ASNW and one in the remnant. The remnant frame in question was relatively exposed, close to the loch shore facing the prevailing winds; nevertheless *L. scrobiculata* in the same frame did not disappear. *Lobarion scrobiculata* appeared in one and remained in another frame in the ASNW samples but disappeared from the two frames in the sample of remnants. *Lobarion virens* was present in 11 frames, appearing in three frames and disappearing from one in the remnants. We relocated only three frames containing *Degelia atlantica*, and this species remained in two frames but had been lost from one frame in ASNW. Of the infrequently occurring lichen species, *Platismatia glauca* and *Lichenoconium usneae* disappeared, and *Ochrolechia androgyna* and *Stricta limbata* had reduced cover, each time in one frame only.

Table 5.3 Change in percentage of cover for each species of lichen between 2007 and 2016 in each of the framed photograph samples (percentage of the frame rounded to nearest unit), over nine years in remnants and in ANSW. Darker shading indicates greater decreases in lichen cover; (o) = lichens which disappear i.e. present in 2007 and completely absent in 2016 from the sampled frames; (*) = lichens which appear i.e. absent in 2007 and present in 2016 in the sampled frames.

	Photo number	Squamules of *Cladonia spp*	*Degelia atlantica*	*Hypotrachyna sinuosa*	*Ochrolechia androgyna*	*Platismatia glauca*	*Lobaria pulmonaria*	*Lobaria scrobiculata*	*Stricta limbata*	*Lichenoconium usneae*	*Lobaria virens*
Remnant	**1**	+3									**-40**
	2										**-65***
	3										+27
	4										+9
	5										+21
	6						**-45**	-1°		-1°	+21*
	7	+1	+2				+29	-4°			-8
	8	+11*									**-43°**
	9	-1					-19°		-1		+8*
	10				-5	-10°	+1				
	11	-1					**-39**				
ASNW	**1**	+3	-21°		-8°		-4	+6*			
	2						-6°	-1			
	3		+6				+12				
	4						**+43**				
	5										
	6			-8	-1	13	-11				
	7										
	8	-1									-8
	9	-4					+25				
	10				+3	-3	-1				+7
	11	+2			+3						+5

Bootstrapping of change in cover was conducted for mosses and lichens, and then specifically for *L. pulmonaria*, *L. virens* and the squamules of unidentified species of Cladonia with 100 resamples. Note: the ANSW samples for change in *L. virens* cover were insufficient to carry out bootstrapping, so the measured values of change are shown as points.

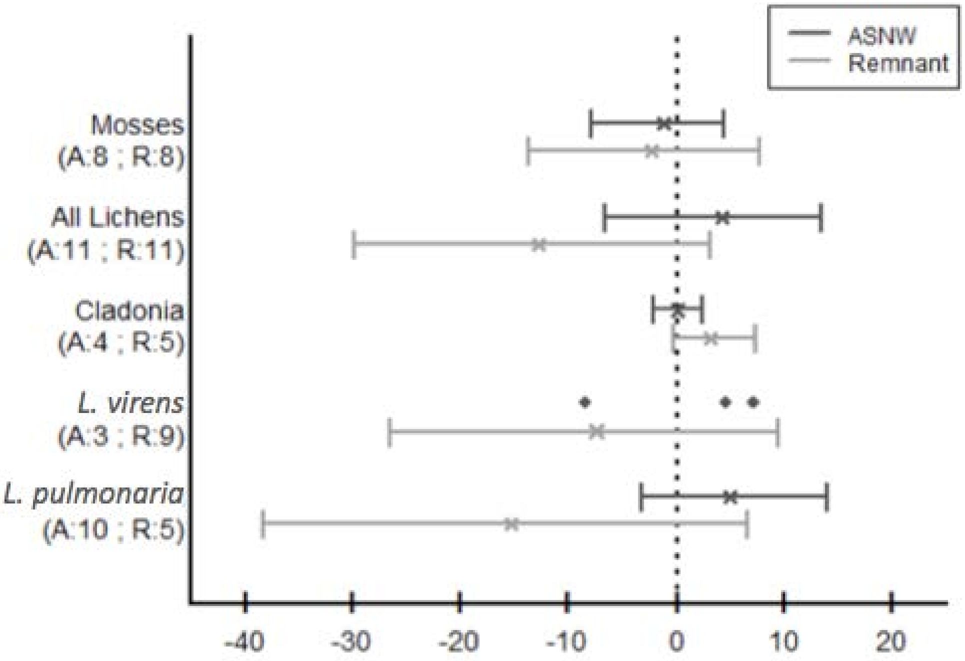

Figure 5.5 Bootstrapped confidence intervals (95%) for mean change in epiphyte cover as percentage of frame area between 2007 and 2016 in ASNW and remnants, estimated with 100 resamples. Number of frames for considered species in ASNW (A) and remnants (R) is indicated. Measured values are given as points where there were an insufficient number of values (<5) to perform bootstrapping.

All bootstrapped confidence intervals for remnant and ASNW samples overlap, indicating little change in lichen cover on remnant trees in response to conifer removal. Confidence intervals are large for the remnant samples indicating a strong disparity in change between samples, but no trend to decrease in cover caused by the conifer removal could be inferred from bootstrapping.

5.6 Discussion

5.6.1 Overview

Baseline survey, prior to felling the non-native conifer matrix, indicated there was very little ground flora present in the PAWS and what was present was similar to that of the ASNW/remnants. Following conifer removal, a substantial amount of litter was left behind, often covering the whole survey area. Re-vegetation of the former PAWS area occurs but vegetation does not closely resemble that within the remnants. However, native woodland *precursor* and *desired invader* species are represented, and a higher frequency of tree saplings was detected post-felling in the former PAWS compared to the ASNW/remnants. Lichen vitality is reduced following conifer removal in the remnants relative to the ASNW but recovery is observed after nine years. No long-term impact on lichen abundance or community composition was determined from the photo analysis. However, the loss or gain of a few infrequently represented species was observed in the remnants after conifer removal compared to the ASNW suggesting the epiphyte community assemblage appeared to be more constant in the ASNW than in the remnants.

5.6.2 Ground vegetation response measures of restoration success and timeframe of restoration

Habitat restoration is considered successful not only when a characteristic assemblage of the relevant species is present but also when continued development and resilience to perturbation is indicated (SER 2004; Shackelford et al. 2013). However, restoration success is frequently assessed using plant species diversity and rarely are measures of growth form and growth traits determined to elucidate succession and community function (Grime 1977; Polley et al. 2005; Pfestorf et al. 2013; Kirby et al. 2017). We utilised ground vegetation assessments in former PAWS following clearfelling compared to the reference sites of ASNW/remnants to assess progress towards ecosystem restoration.

Evaluation of change in ground vegetation functional-trait composition

Nine years after felling, vegetation in the former PAWS is characterised by species with greater variety of functional traits, including competitive species, with different resource requirements to that occurring in the adjacent

ASNW/remnants. Kirby (1988) observed three phases during restoration of ASNW: an initial increase of richness, a decrease during the dense thicket stage and a further increase in the long-term. We suspect that at our study site the former PAWS, having gained between 53% to 61% species richness per quadrat since the felling, is still in the first stage of restoration, whereas the smaller 25% increase in species richness in ASNW/remnant quadrats indicate a slower dynamic corresponding to the third phase.

Presence of characteristic assemblage of species compared to the reference ecosystem

Nine years after felling, the former PAWS had developed a typical assemblage of *precursor* and *desired invader* species matching the ground flora of the reference ecosystem (*i.e.* adjacent ASNW/remnants). Kirby et al. (2017) reported that restoration of mixed Norway spruce-oak resulted in a ground flora which resembled that of the oak woodland, with restoration being encouraged by the close proximity of clear-felled areas to existing oak rows facilitating species survival and dispersal after thinning. At our study site ground flora composition was assessed in the former PAWS at distances up to 9m from the PAW - ASNW/remnant ecotone.

Continued development of ecosystem

Using species-specific functional traits extracted from literature we show that there has been a change in ground flora composition in the former PAWS with respect to representative functional groups. This suggested there would be continued development of functional diversity within the ground flora in the future. At the end of our study, ground flora assemblages were dominated by competitive and strategic species with high requirements in nitrogen and light; the ground flora appeared to be responding to change in habitat conditions as the community was formerly composed of stress tolerant species. The clear-felling event, producing a large amount of litter, was not detrimental to the stress-tolerant species. We infer that these disappeared as increased access to light through absence of canopy cover and to a more abundant resource of nitrogen through decomposition of litter, favoured more competitive species. Previous studies show that clear-felling initially provokes vigorous plant growth, with an abundance of grasses on abandoned grassland invaded by conifers (Paul and

Ledgard 2009), or bracken and bramble in lowland oak woodlands (Harmer et al. 2005) but results in reduced plant diversity, particularly of woodland specialists (Brown et al. 2015). In the years following this study, we anticipate the development of an overstorey will start to drive the community towards one composed of more “stress-tolerant” species (Grime 1977). However, although there was greater functional richness within the former PAWS leading to increased diversity of ecological function, the abundance of competitive species may limit resource partitioning which could ultimately diminish final species diversity and resemblance of the restored ecosystem to the adjacent ASNW. Polley et al. (2005) also used functional diversity as a measure of restoration success, and found functional diversity to be higher in relic rather than restored tallgrass prairies. The response of ground vegetation to clear-felling is nevertheless likely to vary according to initial composition and local-site factors (Knapp et al. 2014).

Ecosystem is self-supporting and resilient to perturbation

Results from this study suggested that regeneration of former native woodland flora is occurring, indicating the resilience of the ecosystem. The rate of natural regeneration of trees is constant in the ASNW/remnants and increasing in the former PAWS. Recovery of woodlands is sensitive to the way in which harvesting is performed and results concerning recovery depend on the time over which it is assessed. Paul and Ledgard (2009) showed that increases in herbaceous vegetation were proportional to thinning, and the intensity of thinning rates affected the response in functional groups in longer-term assessments.

5.6.3 Lichen response

Chlorophyll fluorescence

Immediate changes in microclimate following conifer removal were sufficient to affect the vitality of the epiphytic lichens on the remnant native broadleaves and this concurs with findings of previous studies (Gauslaa and Solhaug 1996; Gaio-Oliveira et al. 2004). However, it appears that the *Lobarion* species at our study site, like those adapted to deciduous woodlands elsewhere, can tolerate increased exposure to light as the effects of the restoration treatments on lichen vitality were no longer evident after nine years (MacKenzie et al. 2001; Gaio-Oliveira et al. 2004). Such physiological changes have been recorded as happening within as little as 13 months after the conifer removal (Gauslaa and Solhaug 1999).

Change in lichen cover

Change in lichen cover was not significant. However, our lichen assessments were conducted solely on remnant trees of site native species, and, as no systematic study of lichen species distribution before felling was conducted, cannot infer that conifer removal did not detrimentally affect the survival of lichen communities due to loss of coniferous substrate. In conifer dominated stands, some authors have reported little difference in epiphytic lichen species richness between ASNW and adjacent plantations or between native and non-native trees in conifer systems (Coote et al. 2012; Bäcklund et al. 2016), so it is possible lichens were lost in the PAWS. In contrast, Jüriado *et al.* (2008) showed that substrate type and tree species have a crucial effect on lichen diversity which outweighs the effect of environmental conditions in unperturbed sites. Renhorn *et al.* (1996) reports *Lobaria pulmonaria* as being unaffected by its positioning *i.e.* forest edge compared to forest centre, in spite of the negative effects they anticipated due to altered microclimate and mechanical damage. In our study, some trees were not found for the photographic survey nine years after felling, and we do not know whether trees were lost at random or due to a form of bias such as an unfavourable immediate environment which could also have reduced lichen abundance or survival. These study limitations need to be borne in mind when interpreting the lichen response to PAWS restoration. However, from this study we can confirm that the ASNW areas and remnants at our study site continued to provide suitable host tree species. This is important as it is the native broadleaved trees and not the non-native conifers which need to be present for favourable condition to be achieved for this priority woodland type (Brown et al. 2015). Furthermore, the prospect for restoration and continuity of epiphyte assemblages appears good, as regeneration within the clearfelled areas is predominantly of site-native broadleaves and is close to ASNW/remnants. Such proximity between potential/future host trees has shown to increase lichen diversity and abundance when comparing semi-natural pine and oak woodlands with adjacent planted stands (Humphrey et al. 2002) as it favours propagule dispersal, essential for maintaining lichen diversity (Ellis 2012).

5.7 Conclusion

Whilst this restoration assessment covered a relatively short timescale when compared to the natural regeneration cycle of an oak forest, our results are encouraging for restoration by removal of planted non-native conifers from mixed native woodland. Our study provides evidence that epiphytic lichen communities can withstand environmental changes caused by PAWS restoration in the first nine years following intervention. With continued woodland restoration, conditions for epiphyte lichen survival should remain favourable (e.g. Palmer et al. 2005). However, a balance needs to be struck whereby there is sufficient regeneration but high densities of saplings, which could pose a threat to epiphytes through shading, do not result (Leppik et al. 2011). Densities of sheep and red deer (which are ubiquitous throughout these habitats) will need to be carefully managed to allow continued regeneration, perhaps balanced with some judicious thinning to prevent overstocking of the woodland (Harmer et al. 2010). This study was conducted at one site which may limit how far the results can be extrapolated. Nonetheless, the study site has high oceanicity which is a defining feature of the European Atlantic Region as a whole and one which shapes lichen assemblage composition. There are 59,000 ha of PAWS in Scotland, a large proportion of which falls within the European Atlantic Region in the West Highlands (FC 2013). Securing ancient woodland remnants and restoration of the matrix to native woodland will reap benefits to biodiversity in the long-term and help in achieving goals set for habitat restoration in the Convention on Biological Diversity (Convention on Biological Diversity 2001; Benis et al. 2014)

5.8 Acknowledgements

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Appendix 5.1 Climatic data for Scottish oak woodlands.

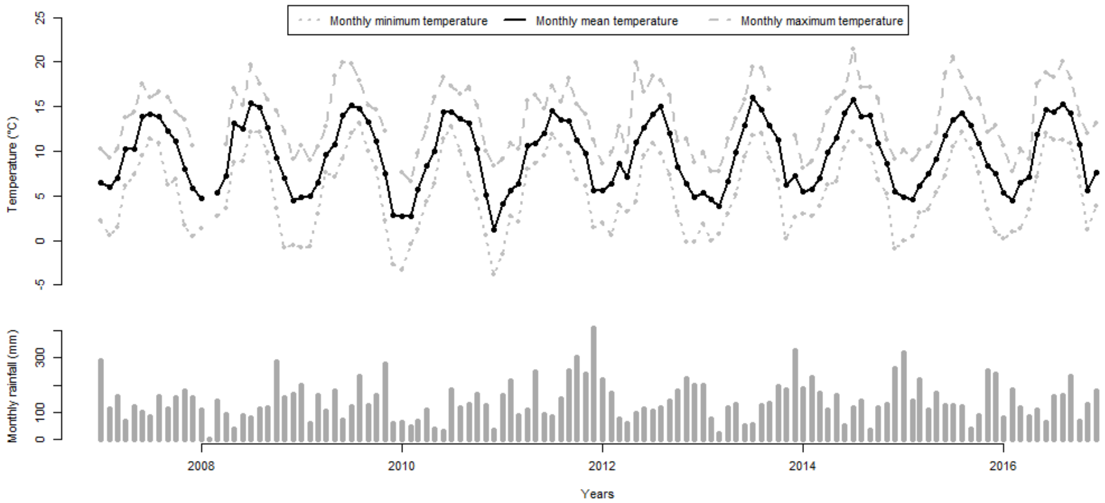

Figure 1 Minimum, mean and maximum monthly temperatures and total monthly precipitations for the Glencripesdale site (Dunstaffnage meterological station) from 2007 to 2016 covering the years of the Planted Ancient Woodland Site restoration study from pre-conifer removal to nine years after conifer removal. Glencripesdale occurs within the area of the British Isles where the *West Scotland Index of Ecological Continuity* (WSIEC) for ancient deciduous woodlands applies (Coppins and Coppins 2002); the *Eastern Scotland Index of Ecological Continuity* (ESIEC) and the *New Index of Ecological Continuity* (NIEC) applies to oak woodlands in other parts of Scotland (Table 1)

Table 1 Values and standard errors of Continentality (°C), Heat Moisture Index and Yearly Growing Degrees (sum of degrees above 5°C), and calculated on climatic data ranging from 2007 to 2016 for10 Scottish oak woodland sites including our study site. The letters indicate groups of mean values that differ at a 5% level determined by Tukey's Post Hoc test.

Oak Woodland	Met Station	Continentaily (°C)	Heat Moisture Index	Yearly Growing Degrees (°C)
Loch Maree	Poolewe	11.2a (±0.8)	11.9c (±0.8)	1437ab (±100)
Alvie	Aviemore	13.2a (±0.6)	18.3de (±0.8)	1331ab (±100)
Dinnet	Aboyne	13.2a (±0.6)	22.1f (±0.8)	1331ab (±100)
Comrie	Drummond Castle	12.3a (±0.8)	14.8cd (±0.8)	1025a (±100)
Glencripisdale	Dunstaffnage	10.9a (±0.7)	12c (±0.8)	1775bc (±100)
Firkin wood	Benmore	12a (±0.7)	7.1a (±0.8)	1631bc (±100)
Mugdock	Mugdock Park	12.8a (±0.8)	11.3bc (±0.8)	1091a (±100)
Wood of Cree	Portpatrick	10.6a (±0.8)	19.2ef (±0.9)	1931c (±112)
Glen Nant	Inverinan Beg	12.8a (±0.8)	7.6ab (±0.9)	1464abc (±112)
Ledmore Wood	Urquhart	11.9a (±1.1)	22.5ef (±1.2)	1379abc (±159)

Three climatic indices were calculated for 10 oak woodland sites, including Glencripesdale, in order to determine how we can extrapolate the results of our study site to other oak woodlands. Its mean continentalism is comparable to all the other woodlands considered. Its mean heat moisture index was significantly different to that of five other sites which had either very high or very low values for this index. Finally, the amount of yearly growing degrees (for all days of mean temperature above 5°C, the sum of the degrees above 5°C) at Glencripesdale was only significantly different to the values of two sites, values which were very low. We consider that between 2007 and 2016 Glencripesdale presented a median climate and, on the basis of climate data, our results can be extrapolated to most Scottish oak woodlands.

References
Coppins AM, Coppins BJ (2002) Indices of ecological continuity for woodland epiphytic lichen habitats in the British Isles. British Lichen Society London

Appendix 5.2 Technical details on lichen data collection and processing

Chlorophyll fluorescence measures and calculation

Parameter settings of the pulse amplitude moderated (PAM) chlorophyll fluorimeter in this study used a controlled illumination protocol after dark adaptation of the thalli. The application of basic fluorimetry of dark-adapted samples (Fv/Fm) has been published for Lobaria pulmonaria (Palmqvist and Sundberg, 2000). In this investigation we employed more complex assessments of light utilisation by the Lobarion lichen species on remnants in PAWS and ASNW trees offering various microsites. After dark-adapting the lichen thalli for 30 min, maximal photochemical utilisation (ΦPSII), after 90 seconds exposure to 400 μmol m^{-2} s^{-1} of constant illumination, was recorded. Quantum efficiencies of photosystem II photochemistry parameter, measured under illuminated conditions, were calculated following van Kooten and Snel (1990), where $\Phi PSII = Fv' / Fm' * qp$.

Lichen cover image processing

Trimble's ©E-cognition carries out object-based classification as opposed to pixel-based and is mostly used in the analysis of high resolution spatial imagery (Darwish et al. 2003; Liu and Xia 2010; Myint et al. 2011). Each photo was primarily subjected to a personalised multi-resolution segmentation, for which ©E-cognition is renowned, in order to extract the individual elements as objects. These were classified by the software using a rule set which was constructed using various object features related to colour, shape and texture. A kappa-coefficient for agreement and an estimate of classification accuracy were calculated per class per photo by comparing the automatic and manual classification of objects sampled at random. These were extracted along with the total surface area per class. The classification was only accepted if the overall kappa-coefficient exceeded 0.7 and if the class-specific kappa-coefficient exceeded 0.6. Differences in cover were calculated between 2008 and 2016 for each lichen in each frame and expressed as a percentage of frame cover. Absolute differences lower than 3% are recorded but arbitrarily not considered of importance, as variability of the photographed area due to tree growth and segmentation error could not be completely removed.

References

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Palmqvist K, Sundberg B (2000) Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. Plant Cell Environ 23:1–14. doi: 10.1046/j.1365-3040.2000.00529.x

Appendix 5.3 Baseline vegetation pre-felling: distribution of species-specific functional traits along the PAWS to ASNW transect

Baseline vegetation data was composed of ten quadrats set along a 20m transect ranging between PAWS and ASNW (see Thompson and Hope 2008).
Mean percentages of quadrat cover for each Grime strategy are shown per quadrat in Sup. Figure 3. Quadrats in the PAWS contained mostly *inert matter*, mainly litter, and the species that were encountered were mostly stress tolerant. A diverse range of plant strategies is displayed within the ASNW/remnants (e.g. strategic, ruderal competitor, stress tolerant competitor) but an important amount of *inert matter* was also present. Quantities of *inert matter* seemed to increase along the transect from deep in the PAWS to deep in the ASNW.

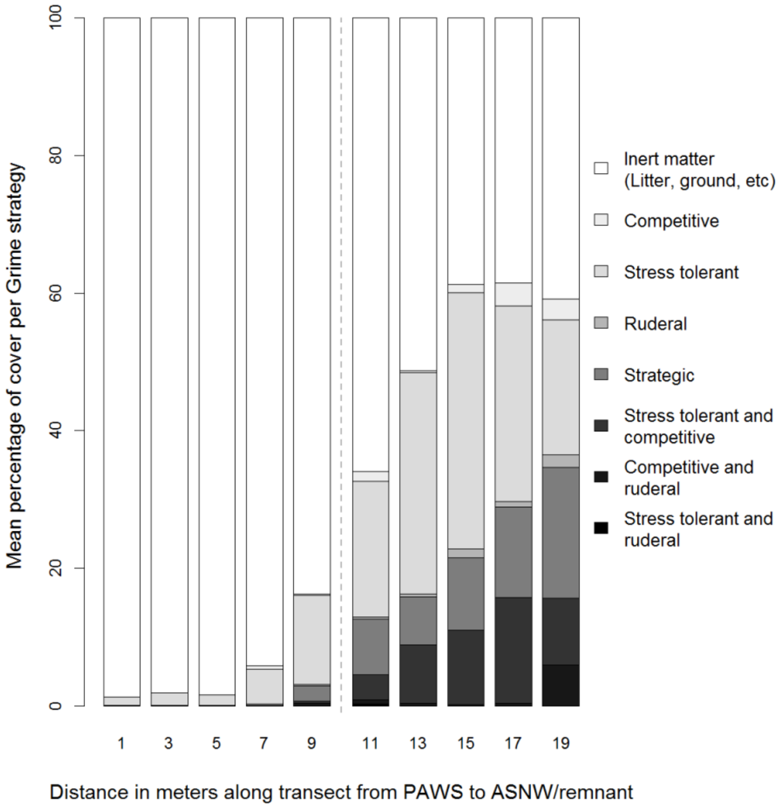

Figure 1 Mean percentages of quadrat cover per Grime strategy along the transect from PAWS to ASNW/remnant before clear-felling, inert matter included. Dotted line represents the boundary between the PAWS and the ASNW/remnant

Chapter Six: Implications of lowland broadleaved woodland management for the conservation of target bird species

An adapted version of this chapter has been published as:

Alice Broome, Robert J Fuller, Paul E. Bellamy, Marcus P. Eichhorn, Robin M. A. Gill, Ralph Harmer, Gary Kerr, Gavin M. Siriwardena, 2017. Implications of lowland broadleaved woodland management for the conservation of target bird species. Forestry Commission Research Note 028, Forestry Commission, Edinburgh.

Contributions: AB synthesized the findings from a three year Defra and Forestry Commission funded research contract (WC0793/CR0485) with the aim of reporting the work and its outcomes in a format that was accessible to the forestry sector in Britain. RFJ led the research undertaken by the members of the research consortium, who are also listed as authors of Chapter 6. The contract report* published by Defra, provides a full account of the work along with a list of the authors and their contributions.

NB: Being written as a sector Research Note, the style of Chapter 6 differs from that of the other data Chapters in this thesis.

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*Fuller, R.J., Bellamy, P.E., Broome, A., Calladine, J., Eichhorn, M.P., Gill, R.M. and Siriwardena, G.M. (2014). Effects of woodland structure on woodland bird populations with particular reference to woodland management and deer browsing (WC0793/CR0485). Defra, London.

6.1 Abstract

This research consisted of a literature review and field study which investigated woodland management for birds within lowland broadleaved woodlands in Britain. The research considered the effect of woodland management (silvicultural intervention and control of deer browsing) on vegetation structure, and the relationships between vegetation structure and woodland birds. Based on habitat–bird relationships, a classification of six woodland stand structures (A–F) related to their value to birds, and a framework to help understand and manage woodland development to deliver these structures was created. The field study, which was conducted in England and Wales, showed that woodlands are predominantly mature or late thicket stands, with low structural heterogeneity (type E – closed canopy, few strata), and silvicultural interventions are primarily mid to late rotational thinning. Such interventions lead to a uniform stand structure and reduced stem and understorey density. High deer browsing pressure also reduces understorey density. Study results showed these vegetation structures to be less favourable to the target bird species which were instead found to be associating with the structures predicted from the literature as being favourable. This suggests that vegetation structures for birds can be described, and if provided, bird populations could be enhanced. The frequently occurring woodland structure type E is of least value to woodland birds. Woodland managers are encouraged to move type E stands towards other types to help meet bird conservation objectives.

6.2 Introduction

Woodlands support a range of different bird communities, which vary according to woodland type and geographical location. Trends in breeding bird populations are used as one of the key indicators (the ‘bird index’) of the state of the UK’s biodiversity and woodland bird populations remain of conservation concern and a policy priority. The woodland bird index fell by nearly 20% between 1970 and 2012, with declines especially pronounced for birds in southern broadleaved woods, but with an opposite trend seen in Scottish populations since 1994 (Balmer et al, 2013; SNH, 2015). There is particular conservation concern for a number of bird species, including 17 species which are the focus of the present study: Nightjar, Lesser spotted woodpecker, Willow tit, Marsh tit, Wood warbler, Willow warbler, Garden warbler, Song thrush, Spotted flycatcher, Nightingale, Pied flycatcher, Redstart, Dunnock, Tree pipit, Lesser redpoll, Bullfinch and Hawfinch. Several factors may drive the declines (Fuller et al, 2005), including pressures on birds during migration or when on wintering grounds outside the UK. Within the UK, climate change and impacts on land use outside woodlands may be affecting food resources, while increased predation pressure and competition between species may also be occurring. In woodlands, there have been changes in vegetation structure in recent decades, with a large proportion of lowland broadleaved woodlands becoming shadier due to canopy closure and many woods being increasingly heavily browsed by deer (Mason, 2007).

Vegetation structure can be altered by woodland management, both by the timing and type of silvicultural interventions applied and by management of deer browsing pressure. Based on our understanding of the resource requirements of the target bird species (Table 6.1), structural changes to vegetation could alter habitat suitability for birds, including many understoreydependent birds, for example by altering the foliage within 2 m of the ground, an area that provides nest sites, food and cover.

A review of European literature showed that the relationships between woodland management and target bird species have been relatively well studied in coppice systems, but information is sparser on the influence of woodland management on the target bird species in high forest systems (Table 6.2). The review also showed that, although early stages of growth in rotationally managed woodland may be valuable to several bird species, conventional stand thinning may have little positive effect on habitat suitability. There is strong evidence for the impact of deer on vegetation: deer browsing reduces vegetation in the low shrub layer (below 2 m), reduces the herbaceous component of the field layer and leads to an increase in coarse grasses and sedges (Gill and Fuller, 2007; Cooke and Farrell, 2001; Gill et al., 1996). Impacts on young coppice regrowth are particularly marked. However, there is a lack of knowledge about the direct effects of deer browsing on woodland birds in high forest systems and the links between habitat change and bird species response requires further study.

Table 6.1 Summary of resource requirements for 17 target bird species (migrant species indicated in bold). These relate to nesting, feeding and territory requirements as well as broader habitat associations and behaviour likely to be relevant in determining responses to changes in woodland structure. Principal food outside breeding season refers mainly to the UK rather than in migrants' wintering grounds. This summary is based on published information (for details see Fuller et al., 2014, Appendix 1).

		Nightjar	**Nightingale**	**Wood warbler**	**Willow warbler**	**Tree pipit**	**Garden warbler**	Song thrush	Dunnock	Lesser redpoll	Bullfinch	Lesser spotted woodpecker	Willow tit	Marsh tit	**Spotted flycatcher**	**Pied flycatcher**	**Redstart**	Hawfinch
Broadleaved	Woodland type		X	X			X					X	X	X		X		X
Conifer										X								
Young	Stage of woodland develop-ment	X	X ?		X	X	X	X	X	X			X					
Mature				X								X		X	X	X	X	X ?
Varied											X							
Dense lower shrub layer	Wood - land structure		X				X	X	X		X							
Dense upper shrub layer					X								X	X				
Sparse understorey				X		X										X	X	
Open canopy					X	X									X		X	
Closed canopy				X														
Large trees												X			X			X
Open space		X				X												
Unknown																		
Ground or near-ground	Nest site location	X	X	X	X	X												
Tall field layer or shrub layer							X	X	X	X	X							
Canopy or tree cavities												X	X	X	X	X	X	X
Ground	Main foraging sites		X			X		X	X	X							X	X
Shrub layer							X						X					
Canopy				X	X					X		X						X
Aerial		X													X			
Varied											X			X		X		
Inverte-brates	Main food in breeding season	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Seeds											X							X
Buds and flowers											X							X
Inverte-brates	Main food outside breeding season																	
Seeds									X	X	X		X	X				X
Fruit			X				X	X							X			

Table 6.2 Effects of woodland management on birds based on a review of European literature. (Evidence - studies which between them fulfill most of the listed criteria).

Silvicultural system	Intervention	Stand stage / conditions	Habitat response	Target bird species benefited	Evidence*
Coppice	Harvesting on a short rotation	Stem initiation / prior to coppice regrowth	Temporary open ground increase	Tree pipit	STRONG
		Stem exclusion / young woodland growth stages	Dense low/ young woody vegetation provided	Nightingale, Willow Warbler, Garden Warbler, Dunnock, Song Thrush, Bullfinch	
Clearfell	Harvesting and restocking	Early stem initiation / post-harvesting	Temporary open ground increase	Tree pipit, Nightjar	STRONG (but from conifer systems) WEAK (for variation of scale of intervention)
		Late stem initiation to stem exclusion	Dense low shrubby vegetation (bramble and birch + crop trees) – increase	Willow Warbler, Garden Warbler, Dunnock, Song Thrush, Lesser Redpoll, Bullfinch	
	Thinning c. 30–40% canopy	Stem exclusion to understorey re-initiation	Shrub layer – no change / decrease Damaged and dead trees – decrease	No change in bird populations / lower numbers of ground- and shrub-nesting species compared to unthinned stands	MEDIUM
Low-impact silvicultural systems	Variable density thinning (<40% of canopy removed)	Stem exclusion to understorey re-initiation	Shrub layer – no change Mature trees – little change	Dunnock, Song Thrush	WEAK
	Variable density thinning (>80% of canopy removed)	Stem exclusion to understorey re-initiation	Dense low shrubby vegetation – increase Mature trees – little change	Bullfinch, Hawfinch, Lesser Redpoll, Garden Warbler	
Restoration of planted ancient woodland sites	Thinning to remove non-native trees (when low % non-native trees)	Stem exclusion to understorey re-initiation	Dense low shrubby vegetation – no change Mature trees – little change	Dunnock, Bullfinch, Song Thrush	WEAK
	Thinning to remove non-native trees (when high % non-native trees)	Stem exclusion to understorey re-initiation	Temporary open ground – increase Dense low shrubby vegetation – increase	Tree Pipit, Willow Warbler, Garden Warbler, Dunnock, Song Thrush, Bullfinch	

STRONG EVIDENCE –	MEDIUM EVIDENCE – (may also include some of the criteria for strong evidence).	WEAK EVIDENCE –(may include some of the criteria for medium evidence but none for strong).
1. Studies which include comparisons between different stand types. 2. Based on several sources, the results of which concur. 3. Most studies from UK.	6. Based on few studies. 7. Results may include inference from studies of other forest types,	9. Information is based on anecdotal information. 10. Results from different studies are contradictory.

4. Studies have recorded impacts on vegetation structure and birds. 5. Studies with good replication of sites and/or studied over suitable timescales.	e.g. boreal and Mediterranean forests. 8. Few studies include effects on birds, with further inference drawn from vegetation effects.	11. Little or no direct evidence for birds with inference drawn from effects on woodland structure. 12. Based on a single study that does not include replication or suitable comparisons.

The research aimed to address knowledge gaps in those forest systems where the 17 target bird species are showing the greatest declines, by conducting (1) a field study in high forest, lowland broadleaved woodlands in England and Wales to test relationships between - a) woodland management (both silviculture and deer) and woodland structure - b) birds and woodland vegetation structure features, and (2) a synthesis of knowledge on the resource requirements of woodland bird species and woodland habitat features to identify woodland structures likely to support the full range of woodland bird species.

6.3 Lowland broadleaved woodland study

6.3.1 Design and survey methods

We established a selection of study areas where the effects of recent silvicultural intervention could be examined within woodlands of varying deer densities.

The field study was conducted on a sample of 300 woodland plots, selected as representative of woods in two regions of lowland Britain – southern England and the Welsh Marches (Figure 6.1). Based on prior knowledge of the status of deer in each study region, there was considered to be a gradient of deer density from ‘High’ to ‘Low’ in the two study regions (Figure 6.1). Roughly half of the plots within each region had been subject to silvicultural interventions in the last 20 years. Plots were not stratified by stand stage/structure. Study plots were chosen to be internally homogeneous with respect to the application of silvicultural interventions and broad structure. Their median area was 3.31 ha. All 300 plots (150 in each region) were subject to an extensive survey of birds and habitat, and a subset of 40 plots (20 in each region) were intensively surveyed for deer population density and vegetation structure.

For the extensive (300 plot) survey, birds were assessed using a four-visit territory mapping method (Hewson et al, 2007). Vegetation structure and composition was assessed using a suite of quantitative and qualitative measures in a Rapid Vegetation Assessment (RVA) (for details see Fuller et al, 2014, Appendix 3).

In the subset of 40 plots, deer population density was estimated by distance sampling, based on observations of deer made at night using thermal imaging (Gill et al., 1997). Half of the plots were in areas considered a priori as ‘High’ deer density and half were in areas considered a priori as ‘Low’ deer density. Vegetation structure was assessed by ground-based laser scanning (for details see Fuller et al., 2014, Appendix 4). This method creates a three-dimensional reconstruction of the woodlands, documenting foliage density and stem material across the entire vertical span of the canopy.

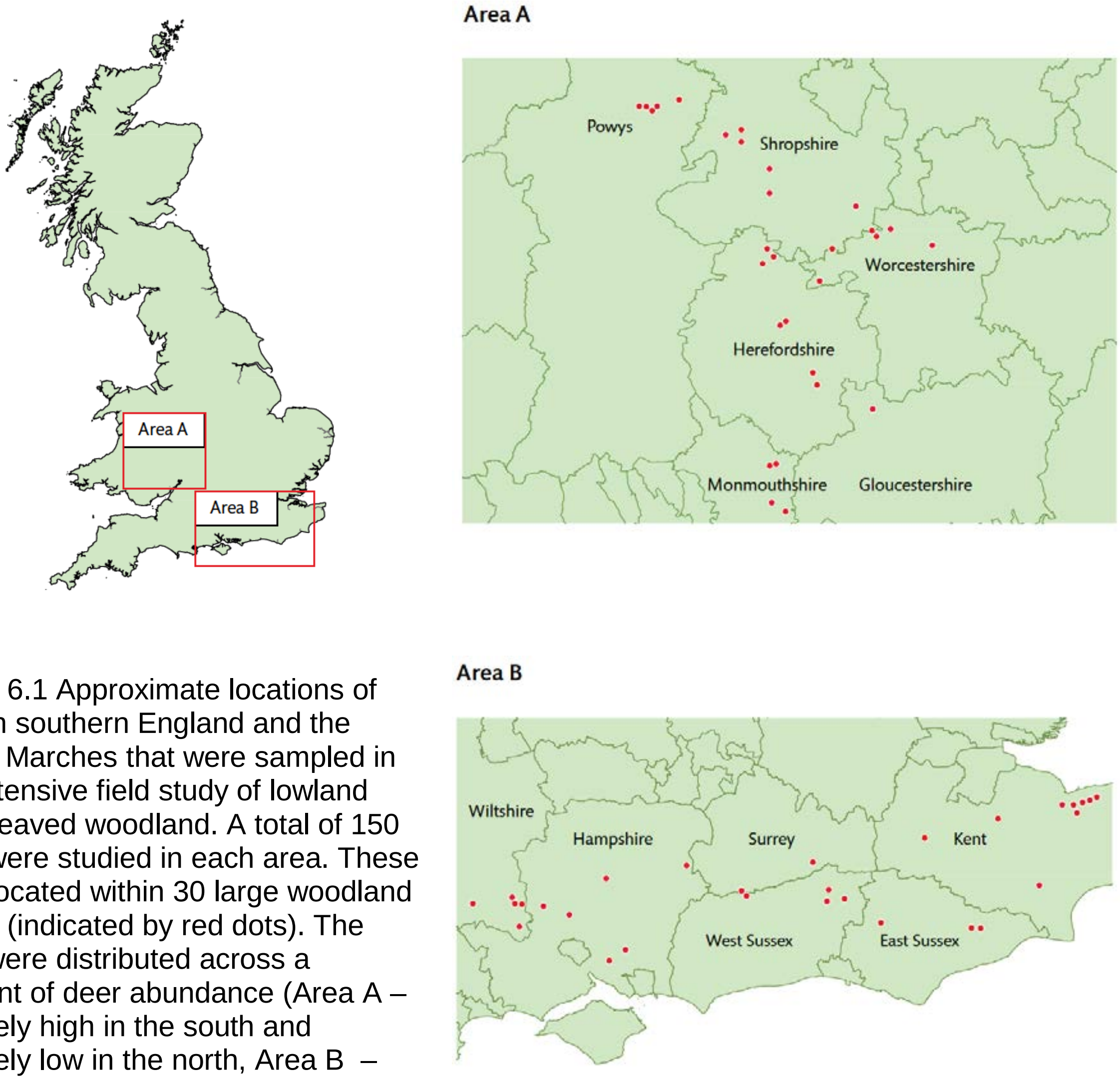


Figure 6.1 Approximate locations of sites in southern England and the Welsh Marches that were sampled in the extensive field study of lowland broadleaved woodland. A total of 150 plots were studied in each area. These were located within 30 large woodland blocks (indicated by red dots). The sites were distributed across a gradient of deer abundance (Area A – relatively high in the south and relatively low in the north, Area B – relatively high in the west and relatively low in the east).

6.3.2 Results of the field study

Stand structures

Overall, 81% of the plots were classified as mature or late thicket stands. Other stand types, particularly the younger stages, were relatively rare in these long rotation high forest broadleaved systems. Only 21 plots (12 in the south and 9 in the Marches) were classed as recent plantations and 35 plots (20 in the south and 15 in the Marches) as recent natural regeneration. Overall, 25% of the plots were within PAWS restoration sites, with similar numbers in each region. The most commonly applied interventions appeared to be mid to late rotation thinning, rather than end of rotation harvesting and restocking. Consequently, only a restricted range of the full variety of stand structures possible within a high forest system were available for this study.

Bird species

Forty-nine bird species were recorded in the study plots in sufficient numbers to enable their analysis. Blackbird, Blue tit, Great tit, Robin, Woodpigeon and Wren were recorded from almost all the plots. Of the target species, Song thrush and Marsh tit were the most frequently recorded, occurring in half or more of the study plots. Dunnock, Spotted flycatcher and Bullfinch were the next most abundant (recorded in a quarter to a third of the plots), followed by Willow warbler, Garden warbler, Redstart and Pied flycatcher (10–25% of plots). The least frequent target species were Wood warbler, Lesser spotted woodpecker, Tree pipit, Nightingale, Lesser redpoll, Nightjar, Willow tit and Hawfinch, the latter four being encountered too infrequently for inclusion in the analysis.

Deer species encountered during the field survey were mostly roe and fallow deer, with muntjac deer being recorded in much smaller numbers. No red or sika deer were seen.

Effects of woodland management

Woodland management is here taken to mean silvicultural intervention and control of deer browsing. The effects on woodland habitat structure attributable to silvicultural intervention were investigated through a number of tests of association using data from the extensive (300 plot) and intensive (40 plot) surveys.

Associations between woodland habitat structure and silvicultural intervention were found from the extensive survey data but were not clear from the intensive survey. Plots with recent silvicultural interventions appeared more uniform in structure, with a reduced stem number and understorey cover, and a tree canopy that contained less birch compared to the plots without recent silvicultural intervention.

The effects of deer on vegetation were considered for the 40 intensive survey plots only (20 ‘High’ and 20 ‘Low’ deer density class), as deer density class was validated by population density estimates for these plots. Strong associations were found for the effects of deer density on vegetation with reduced foliage and stem density, and reduced understorey cover recorded where deer density was higher.

Bird abundance and habitat features

Tests for the relationships between habitat features and abundance or presence–absence of individual bird species encountered in the extensive survey were conducted in two different ways:

1. Empirical habitat–bird relationships: analyses conducted using only the data collected in the field study.

2. Hypothesis testing of habitat–bird relationships: habitat– bird relationships indicated from the literature review (Table 6.1) were tested using the field study data.

Empirical habitat–bird relationships

Separate analyses were undertaken for individual species. The important structural habitat features for target species for whichvalid models could be constructed are summarised in Tables 6.3 and 6.4. Table 6.3 shows that the combinations of habitat features were highly species-specific. For example, both Bullfinch and Marsh tit abundance was positively associated with tree height and understorey cover occurring between 2 m and 4 m above the ground, and negatively associated with understorey cover below 2 m, but showed contrasting response to grass cover.

Table 6.4 indicates which structural habitat features were the most important across all bird species examined. Stem diversity (of trees) was the most frequently important feature, having a model weight greater than 0.5 for 17 species (65% of the total examined), for which 13 relationships were positive. Other significant habitat features (i.e. having a model weight greater than 0.5) and relating to ten or more of the bird species were: basal area, semi-woody cover, understorey cover and density, grass cover, canopy cover and bare ground. Associations between these structural habitat features and birds were more frequently positive than negative, with the exception of understorey cover at less than 2 m, grass cover and bareground, which were consistently negatively associated. Relationships of bird species with plant composition were also highly individual.

Table 6.3 An overview of positive (+) or negative (−) effects of structural habitat features based on multivariate model weights for the target species for which there were sufficient data for analysis. Dots mean no effects were detected. Data were collected in a field study in lowland broadleaved woodlands in England and Wales.

Habitat feature[1]	Bullfinch	Dunnock	Garden warbler	Marsh tit	Spotted flycatcher	Song thrush	Willow warbler
Understorey cover <2 m	−	.	.	−	.	.	+
Understorey cover 2–4 m	+	−	.	+	−	.	.
Understorey density at 0.5 m	.	.	+	.	.	−	.
Understorey density at 1.5 m	.	.	+	+	.	.	.
Canopy cover	.	.	.	.	+	−	.
Tree height	+	.	.	+	.	.	.
Semi-woody cover	.	.	−	+	.	+	.
Bracken cover	.	+	−	.	.	−	.
Grass cover	−	−	−	+	−	−	.
Herb cover	.	.	−	.	+	.	.
Bare ground	−	.	−	.	.	−	.
Number of stems	+	.	.	.	.	+	.
Stem diversity	−	.	.	.	−	−	.
Basal area	.	+	.	.	.	−	−

[1] 'Understorey cover' refers to the density of vegetation when viewed from above whereas Understorey density' is assessed horizontally.

Table 6.4 Numbers of bird species for which associations with individual structural habitat features (variables) were identified. Relationships could be either positive or negative. Importance of the relationship for each species was determined by a summed variable-specific model weight of greater than 0.5 indicating the relationship was significant. The total number of bird species examined was 26. Data were collected in a field study in lowland broadleaved woodlands in England and Wales.

Habitat feature[1]	**Number of species with weight >0.5:**		
	All	**Negative only**	**Positive only**
Stem size diversity	17	4	13
Basal area	14	4	10
Semi-woody cover in field layer	13	3	10
Understorey cover occurring <2 m above ground	12	8	4
Understorey density at 1.5 m above ground	12	2	10
Grass cover	12	9	3
Canopy cover	11	3	8
Bare ground	10	8	2
Tree height	9	1	8
Herb cover	9	5	4
Understorey cover occurring between 2 m and 4 m above ground	8	3	5
Understorey density at 0.5 m above ground	8	5	3
Bracken cover	8	6	2
Number of stems	6	3	3

[1] 'Understorey cover' refers to the density of vegetation when viewed from above whereas 'Understorey density' refers to the density of vegetation when it is assessed horizontally.

Hypothesis testing of habitat–bird relationships

Of particular interest are associations between different habitat features and birds where prior knowledge can be used to hypothesise about possible relationships. These hypotheses were established on the basis of the results of the species requirements review (Table 6.1). Tests of single habitat features (the predictor variables) were conducted for hypotheses, where the data allowed successful model fitting (Table 6.5). For example, Song thrush abundance is hypothesised to increase or presence to be more likely with an increase in bare ground and with an increase in cover of shrub layer (at 0.5–4 m above ground level).

Table 6.5 Target bird species[1] for which negative (–) or **positive (+)** effects[2] of increasing amounts of habitat features were detected consistently across study regions (Welsh Marches and southern England). Habitat features are those which were hypothesised to affect habitat suitability for the selected species based on existing knowledge. Support (or not) of the hypothesis is indicated.

Habitat attribute	Species number[3]	Hypothesis supported[4]	Hypothesis not supported[5]	Variable response hypothesised[6]
Tree size (basal area) and height	10	**Spotted flycatcher(+)** Garden warbler(–) Nightingale(–) Willow warbler(–)		**Blackcap(+)**
Number of tree stems	1			
Shrub and tree diversity	2	**Bullfinch(+)**		
Birch cover	1	**Willow warbler(+)**		
Oak cover	4			
Canopy cover	13	Dunnock(–) Garden warbler(–) Willow warbler(–)		**Spotted flycatcher(+)** Blackcap(–)
Understorey cover 0.5 m to 2 m	4	**Dunnock(+)** **Garden warbler(+)**		
Understorey cover 0.5 m to 4 m	9	**Blackcap(+)** **Song thrush(+)** **Willow warbler(+)** Tree pipit(–)		
Bare ground	6	Wren(–)	Pied flycatcher(–)	

[1] In addition to the target species, Blackcap and Wren were included because these relatively common species are likely to be sensitive to understorey structure and may therefore provide useful insights.

[2] Bird species are listed where significant P<0.05 and near-significant P<0.07 relationship was detected.

[3] Number of bird species hypothesised to be affected (positively or negatively, linearly or non-linearly) by habitat attribute.

[4] Species for which significant relationship was in direction hypothesised.

[5] Species for which significant relationship was in opposite direction to that hypothesised.

[6] Species whose abundance/presence was hypothesised to vary as habitat attribute increased but which showed a significant positive or negative response.

Effects were only detected for half of the associations hypothesised to occur between birds and habitat features (Table 6.5). Lack of support does not necessarily mean that the hypothesis is inappropriate, because there may have been insufficient variation in the habitat feature concerned or insufficient numbers of birds to undertake an adequate test. Where effects were seen, three-quarters were in the expected direction, i.e. supporting the hypothesis. Hypotheses for shrub cover in the height range 0.5–4 m, shrub and tree diversity, and tree size and height were most strongly supported. As predicted, Dunnock, Garden warbler, Blackcap, Song thrush and Willow warbler were all associated with higher levels of understorey cover while Tree pipit avoided such areas. The hypothesised negative effects of tree size, tree height and canopy cover appeared to be supported for a number of species and most of the species associated with more complex understorey vegetation also avoided closed canopy areas.

6.4 Resource requirements and woodland features for the target bird species

6.4.1 Methods

Links were made between birds and woodland habitat features that would deliver resource requirements of the target bird species. This information was used to define the set of 'characteristic stand structures' occurring in lowland broadleaved woodlands and their value to the target bird species. The habitat features were derived from the habitat–bird models using the field study data. For completeness (and to represent lowland broadleaved woodlands more widely in Britain), these were supplemented from the literature by habitat–bird data for woodland structures not encountered in our field study.

The characteristic stand structures have been set in context of the stand development stages that woodland is expected to pass through (Harmer et al, 2010). This interpretation incorporates stocking density gradient, and also the likely impact of deer on achieving stand structures. Management recommedations for delivering the different stand structures have been proposed with reference to a stand's likely development trajectory.

6.4.2 Results

Characteristic stand structures for woodland birds

Six characteristic stand structures were defined and are referred to as:

A – dense low shrub layer

B – dense high shrub layer

C – open understorey

D – open canopy

E – closed canopy, few strata

F – closed canopy, multiple strata.

Figure 2 provides a visual and text summary of the key features of these six structures. The text summary contains:

- Resource definition available to the bird species in the breeding season, e.g. low complex dense vegetation of shrubs and woody plant structures typically within 2 m of the ground (resource definitions were produced from a synthesis of the available literature on bird ecology).
- Bird species and the level of association with the set of listed resources, e.g. Bullfinch, Lesser redpoll, Marsh tit, Willow tit – weak/moderate association (levels of association with resources were produced from a synthesis of the available literature on bird ecology).
- Stand features reflecting the key, and most biologically meaningful, variables identified in the statistical models (see 'Lowland broadleaved woodland field study' section) which correlate with the associated bird species, e.g. high numbers of small stems (stand features are based on the field study data).

The silvicultural notes (Figure 6.2) and Table 6.6 provide the context of the stand development stage, the influences of stocking density and capture management recommendations. Stand structures of type A (dense low shrub layer) and type B (dense high shrub layer) are developed in young stands at stem initiation stage but type A can be maintained through later stages of stand development with management, if stand basal area is low enough (<10 m^2/ha). Structure C (open understorey structure) can develop in stands with high basal area (>20 m^2/ ha) in stem exclusion and understorey re-initiation stages and in old-growth stands, and only in these stages in stands with lower basal area when grazed or heavily browsed. Structure D is found in typical wood pasture where grazing is necessary to maintain open conditions. Stand type E is individually of least value for woodland birds and is a widespread and typical structure in much current lowland broadleaved woodland. Many of the 300 stands examined in the field survey approximated stand type E or that of stand type C, although with rather more understorey vegetation in many cases. Structure F (closed canopy, multiple strata) is only found in stands with medium and high basal areas and during the late understorey re-initiation and old-growth management phases of development. Such structures are likely to arise when using methods of continuous cover forestry. Between them, characteristic stand structures A–F should provide breeding season resources for all the target species and most other species of woodland birds.

Table 6.6 Occurrence of the six characteristic stand types in different stages of stand development.

	Stage of stand development				
Stocking	**Stem initiation**		**Stem exclusion**	**Understorey re-initiation**	**Old-growth**
	Early	**Late**			
Low Basal area <10 m^2/ha		A → B[1]	A[2] B(early) (C)	A[2] B (C) D[3] G(late)	A B (C) D[3] G
Medium Basal area 10–20 m^2/ha		A → B[1]	B(early) (C) E[4]	(C) E[4](early) F(late) G(late)	B (C) F G
High Basal area >20 m^2/ha		A → B[1]	B(early) C E[4]	C E[4](early) F(late) G(late)	B C F G

Six characteristic stand types are:
A – dense low shrub layer, B – dense high shrub layer, C – open understorey, D – open canopy, E – closed canopy, few strata, F – closed canopy, multiple strata.
Stem exclusion includes pole stage; Old-growth – death of overstorey trees and replacement of these with younger trees developing from the understorey. (early) / (late) – only occurs early or late in the stage of stand development. (C) – will only occur when grazed or heavily browsed. G – cavities within stems/trunks etc. although not a stand structure type it is an important structural resource. 1 – If the shrubs in stand type A are all low growing, such as bramble, then will not develop into B. 2 – Suitable management to regenerate the understorey will be needed to maintain this structure.
3 – Wood pasture with open canopy structure not represented in survey.
4 – Stand type E does not appear to favour target woodland bird species.

Figure 6.2 Characteristic stand structure types (A–F).

A. Dense low shrub layer

Resource definition: Low complex dense vegetation of shrubs and woody plant structures typically within 2 m of the ground.
Strong association: Dunnock, Garden warbler, Nightingale, Song thrush, Willow warbler.
Weak/moderate association: Bullfinch, Lesser redpoll, Marsh tit, Willow tit.
Stand features:

- High density of low understorey <2 m (ideally stands where horizontal visibility below 1.5 m is <6 m)
- High numbers of small stems
- Low tree height and low diversity of stem sizes
- High ground cover possibly including high bramble cover.

Silvicultural notes

This type of stand structure typically develops following canopy disturbance, usually after clear felling at the end of a rotation or when group felling takes place. It is a short-lived stand structure comprising shrubs and small regenerating trees. It forms part of the stand initiation phase of stand development, but it may occur during later stages if basal area is low. Unless actively managed to restrict height growth it will develop into stand structure B.

A. Dense high shrub layer

Resource definition: Complex dense vegetation structures in the upper shrub layer typically 2–5 m above the ground.
Strong association: Bullfinch, Marsh tit, Song thrush, Willow tit.
Weak/moderate association*:* Hawfinch.
Stand features:

- High understorey cover up to 4 m above ground (ideally >60% cover)
- High density of stems
- Broken canopy (canopy cover no more than 80%)
- Low bracken cover
- Some grass cover
- High hazel cover.

Silvicultural notes

This stand structure develops as shrubs in type A increase in height. It is a short-lived stand structure comprising shrubs and sapling trees, low growing shrubs (e.g. bramble) are likely to be less abundant. It occurs during the later stages of the stand initiation phase and may extend into the early phase of stem exclusion. If basal area is low it may persist into the later stages of stand development. At medium and high basal areas it will only occur when stands are managed as all-sized stands (Table 6.6).

C. Open understorey structure

Resource definition: Stands with no or little low shrub or woody vegetation (i.e. <5 m of the ground).
Strong association: Pied flycatcher, Redstart, Tree pipit, Wood warbler.
Weak/moderate association: Spotted flycatcher. **Stand features**:

- Negligible low vegetation 0.5–4 m tall but with moderate or patchy ground flora
- Little bracken or bare ground (often grassy ground cover)
- Taller trees in mature stands.

Silvicultural notes

Stands with this structure are not found during stand initiation, but can occur at all other stages of stand development (Table 6.6). At high stocking densities the shade cast by the overstorey will maintain the open understorey conditions but at lower densities, grazing (or heavy browsing by deer) will be necessary. Generally has good overall canopy cover with more trees and smaller gaps between them than type D, grazed upland oak woods are a typical example of this type.

D. Open canopy structure

Resource definition: Woodland with significant gaps between the crowns of individual trees. Such trees may be open-grown with spreading canopies and often have relatively high amounts of dead/decaying wood.

Strong association: Lesser spotted woodpecker, Pied flycatcher, Redstart, Spotted flycatcher, Tree pipit.

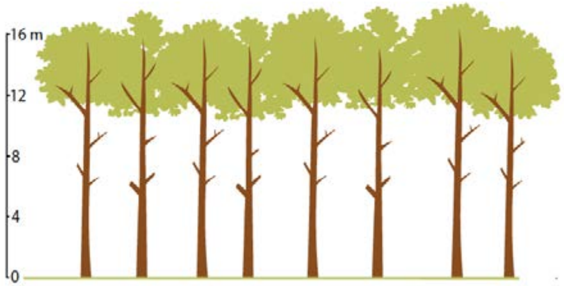
Weak/moderate association: Nightjar, Wood warbler. **Stand features**:

Within our sample we had few or no stands of this type and it was not possible to identify stand features from analyses of the data.

Silvicultural notes

Stands with this structure are only found at low stocking densities within the understorey re-initiation and all-sized stages of stand development (Table 6.6). Typical wood pasture where grazing (or heavy browsing by e.g. deer) will be necessary to maintain open understorey conditions.

E. Closed canopy – few strata



Resource definition: Stands where the canopy layer is relatively simple often associated with single-aged mid-growth phases.

Strong association: Wood warbler.

Weak/moderate association: Hawfinch, Lesser spotted woodpecker, Pied flycatcher, Redstart, Spotted flycatcher.

Stand features:

- Negligible understorey <2 m above ground (horizontal visibility more than 10 m)
- Low basal area
- Little bracken or bare ground (often grassy ground cover).

Silvicultural notes

Found during the stem exclusion and early understorey re-initiation phases of development in medium and highly stocked stands (Table 6.6). Is often the typical structure throughout much of the rotation for stands managed using a thin and clearfell system. Not a desirable structure for the target species of woodland birds but suitable management can transform these stands into others having greater variety in the shrub and understorey strata.

F. Closed canopy – multiple strata

Resource definition: Stands where the canopy layer is relatively complex forming several foliage strata often associated with more mature growth phases. Multiple strata could be derived from mixtures of trees of different ages or from high canopy depth within individual trees.

Strong association: Hawfinch, Lesser spotted woodpecker, Pied flycatcher, Spotted flycatcher, Wood warbler.

Weak/moderate association: Marsh tit, Redstart, Song thrush.

Stand features:

- High canopy cover (>90%)
- Tall mature stands with high diameter at breast height
- Little bracken
- Good herb ground cover.

Silvicultural notes

Only found in stands with medium and high stocking density during the late understorey re-initiation and all-sized management phases of development (Table 6.6). Such structures are likely to arise when using methods of continuous cover forestry which create conditions allowing the development of a patchwork of shrubs and regenerating understorey trees beneath the overstorey.

6.5 Discussion and conclusions

The sites sampled in this study were a representative sample of broadleaved lowland woodlands in England and Wales. We found that the majority of study plots were late thicket (stem exclusion stage) or mature (understorey re-initiation stage) stands. The stands that had received recent silvicultural interventions were more uniform in structure, with a reduced stem number and understorey cover. Deer pressure on woodland habitats was clear from the intensive vegetation survey, and findings were consistent with what is known of deer impacts on vegetation. The greatest impacts were on the reduction of understorey density.

In total 49 bird species were recorded from the study plots. This includes all 17 target species, although Lesser redpoll, Nightjar, Willow tit and Hawfinch were encountered too infrequently for inclusion in the analysis. We found that higher understorey density at 1.5 m, increased stem size (basal area), greater diversity of stem sizes, canopy cover and tree height were related positively to the abundance of the target bird species. However, silvicultural thinning decreased stem size diversity and tree species density and reduced understorey density (at 1.5 m and above 4 m); high deer browsing pressure also reduced understorey density (at 1.5 m and 4 m). We conclude that silvicultural thinning, as normally practised in late thicket and mature stage stands, does not improve the habitat for target bird species, whereas management of deer browsing does. These findings are supported by evidence from the literature which suggests that thinning (as currently practised) decreases the shrub layer and reduces the number of dead or damaged trees, with consequent negative effects on numbers of ground- and shrub-nesting birds and brings no benefits overall to bird populations.

Using the field survey data, we detected differences in the abundance or presence of individual bird species in relation to habitat features hypothesised to be important from the literature. For example, certain bird species were associated with or avoided habitat features of shrub cover up to 4 m tall, tree size and height and canopy cover, in a predictable way. This suggests that within the typical lowland broadleaved woodlands in England and Wales, target bird species are associating with the expected habitat features. Increasing the provision of these features will potentially lead to increases in target bird species abundance. Certain types of stand management are reported in the literature (mostly on conifer systems) to deliver these habitat features and benefits for birds. Harvesting and restocking initially creates conditions of temporary open ground benefitting, for example, Tree pipit, and later on results in increases in dense low shrubby vegetation, which was shown to be of benefit to six of the target species.

The uniform stand structures encountered in our study reinforce the view that a very high proportion of lowland broadleaved woodland in England and Wales lacks structural heterogeneity. Creating a more diverse structure through woodland management could lead to increased resource provision for the target species. Tailoring management for each species may prove challenging, as this research demonstrates that the combination of required habitat features is highly species-specific. Instead we propose that woodland management for birds (and potentially for other biodiversity) is focused on delivering a mixture of different stand structures at the landscape scale. Six characteristic stand structures have been described for lowland broadleaved woodlands. Together they should deliver breeding season resources for all the target species and most other species of woodland birds. Stand structures are possible at only certain stand development stages and their occurrence can be further influenced by basal area of the stand and grazing/browsing pressure. Silvicultural intervention can maintain structures, e.g. type A (low dense shrub layer) in stands developed beyond stem initiation (establishment) stage or encourage their development, e.g. type F (closed canopy, multiple strata) by using methods of continuous cover forestry. The most frequently occurring structures found currently in lowland broadleaved woodlands in England and Wales (stand type E), are of least value to woodland birds. By using silvicultural management to move stand type E towards other stand types, there is scope to increase the area of woodland that would potentially provide resources for a wider range of woodland birds, including several declining species. Maintaining a range of stand structures will also benefit other woodland species, for example structure types D and F will support 60% of the priority (FC, 2011a) non-avian species, such as Invertebrates, Lichens and Bryophytes associated with lowland broadleaved woodland (see Fuller et al., 2014, Appendix 7).

As well as strengthening our knowledge base, this research has provided new insights into woodland management for birds in lowland broadleaved woodlands in Britain and underpins a classification of characteristic stand structures. The classification provides a framework to understand and manage woodland development with the aim of delivering breeding season resources for woodland birds.

Chapter Seven: Niches for Species, a multi-species model to guide woodland management: an example based on Scotland’s native woodlands

An adapted version of this chapter is inpress as:

A. Broome, C. Bellamy, A. Rattey, D. Ray, C.P. Quine, K.J. Park. Niches for Species, a multi-species model to guide woodland management: an example based on Scotland’s native woodlands. *Ecological Indicators*.

Contributions: AB conducted the knowledge review and developed the species-habitat database and habitat classification, DR provided initial ideas on delivery of data in a spatial model, CB researched spatial data and developed rule-set and model functionality, AR and TC refined and tested model. AB wrote the manuscript with inputs from CB, DR and AR. KP and CPQ reviewed research development and commented on earlier drafts.

7.1 Abstract

Designating and managing areas with the aim of protecting biodiversity requires information on species distributions and habitat associations, but a lack of reliable occurrence records for rare and threatened species precludes robust empirical modelling. Managers of Scotland’s native woodlands are obliged to consider 208 protected species, which each have their own, narrow niche requirements. To support decision-making, we developed Niches for Species (N4S), a model that uses expert knowledge to predict the potential occurrence of 179 woodland protected species representing a range of taxa: mammals, birds, invertebrates, fungi, bryophytes, lichens and vascular plants. Few existing knowledge-based models have attempted to include so many species. We collated knowledge to define each species’ suitable habitat according to a hierarchical habitat classification: woodland type, stand structure and microhabitat. Various spatial environmental datasets were used singly or in combination to classify and map Scotland’s native woodlands accordingly, thus allowing predictive mapping of each species’ potential niche. We illustrate how the outputs can inform individual species management or can be summarised across species and regions to provide an indicator of woodland biodiversity potential for landscape scale decisions. We tested the model for ten species using available occurrence records. Although concordance between predicted and observed distributions was indicated for nine of these species, this relationship was statistically significant in only five cases. We discuss the difficulties in reliably testing predictions when the records available for rare species are typically low in number, patchy and biased, and suggest future model improvements. Finally, we demonstrate how using N4S to synthesise complex, multi-species information into an easily digestible format can help policy makers and practitioners consider large numbers of species and their conservation needs.

7.2 Introduction

Globally, biodiversity is under threat, many species are legally protected but resources for conservation are diminishing (Bottrill et al., 2008; MacDicken et al., 2015; Possingham et al., 2015). Maintaining habitat for species has been part of national and international conservation planning for decades and networks of protected areas exist globally (Orlikowska et al., 2016). However, whilst the IUCN has set a target of designating 10% of terrestrial habitats as protected areas (IUCN, 1993), it is recognised that this percentage of landcover, it's location, spatial configuration, and the actions prescribed within it may not be sufficient to support species, particularly in the face of rapid environmental change (Wiersma et al., 2018; Dinerstein et al., 2017; Rodrigues et al., 2004).

In the context of biodiversity protection in the temperate broadleaved and mixed forest biome, where habitat restoration is a priority, the choice of where to apply conservation effort for most benefit is critical (Dinerstein et al., 2017; Morales-Hidalgo et al., 2015). Such decisions are often directed by international conventions and directives on the environment, which are devolved to a regional level of administration for implementation (JNCC, 2018; EC, 2018). For example, in the UK, Scotland has listed 208 protected woodland species (mammals, birds, invertebrates, fungi, bryophytes, lichens, herptiles and vascular plants which are strongly associated with woodlands) (Scottish Action Coordination Group, 2008). Forestry policy and practice have been designed to deliver habitat enhancement and protection measures for these species (Forestry Commission, 2017), in line with wider conservation effort targeting species which are rare and/or at risk of extinction (Favaro et al., 2014; Winter et al., 2013). However, developing and adhering to these types of guidelines is contingent on knowledge of what habitat features a species requires and how these are distributed. This is complicated by the fact that many of these protected species are cryptic and poorly recorded (Minin and Moilanen, 2014). The challenge is further increased when there is a need to deliver conservation management for multiple protected and data-deficient species simultaneously. This challenge is faced by many land managers and owners.

To address gaps in species records and poor knowledge on habitat conservation needs, research has focussed on predicting where species are likely to occur using empirical models. These Species Distribution Models (SDMs) relate known species presence-absence or presence-only data with environmental variables to determine species-environment relationships and to predict habitat suitability over large extents (Elith and Leathwick, 2009; Guisan and Thuiler, 2005; Guisan and Zimmermann, 2000). They have been widely used to characterise and map habitat suitability for single species or taxonomic groups (e.g. Bellamy et al., 2013; Cooper-Bohannon et al., 2016; Johnson and Gillingham, 2008). However, SDMs may fail to accurately predict species habitat suitability when reliable occurrence data are sparse (Stockwell and Peterson, 2002; Wisz et al., 2008; although see Pearson et al., 2007), the full range of environmental variation across a species range is not represented (Austin 2002), the species is not in equilibrium with its environment (Dormann 2007; Soberon and Nakamura, 2009), or the impact of biotic interactions are not considered.

Whilst spatial data are available on broad woodland types across the UK (FC, 2011b) and other fine-scale attributes for some UK woodlands (e.g. dominant tree species, woodland structure, deadwood presence; Patterson et al., 2014), species records available via Local Environmental Record Centres or online data portals (e.g. NBN, 2017) typically suffer from sampling bias, low sample sizes and a lack of confirmed absences. This is particularly the case for rare, inconspicuous or cryptic species because of the difficulties in their detection or identification (Phillips et al., 2009; Newbold 2010). In addition, despite advances in data portal accessibility, the complexity and time investment involved in extracting high-resolution records for several hundred species, filtering them for reliability and accuracy, and interpreting the results alongside habitat data, means that this is unlikely to be undertaken by forestry decision makers. Using well recorded and better-known species as surrogates for wider biodiversity has been tested, but studies show surrogates perform less well when used to represent other taxa e.g. birds representing butterflies (Dorey et al., 2018; Margules and Pressey, 2000; Prendergast et al., 1993).

Expert-based habitat suitability models (EHSMs) provide a solution as useful alternatives to SDMs when inadequate occurrence records preclude accurate empirical modelling (Fourcade, 2016), or when funds for collecting new substantive datasets are limited (Doswald et al., 2007; Fourcade, 2016; Murray et al., 2009). EHSMs use both expert knowledge and evidence-based reviews from published scientific literature describing a species' habitat requirements and ecology, combined with spatial environmental datasets (e.g. land cover type, topography, aspect) describing the availability of these habitats, to predict the occurrence of species (e.g. Eycott et al., 2012; Ziegler et al., 2015). This approach has been extensively used by conservation agencies in the USA, where many EHSMs have been developed by drawing on the national resource of species specialist knowledge (Crance, 1987; Drew and Collazo, 2012; Drew and Perera, 2011). However, EHSMs are usually built for individual species (e.g. Leblond et al., 2014) and validation is nearly always neglected (Iglecia et al., 2012).

Here we present a multi-species EHSM approach, ‘Niches for Species’ (N4S), to enable forest policy makers and managers to consider multi-species management within Scottish forests. We use the term ‘niche’ to describe a set of habitat features that a species is strongly associated with, from which we can estimate species distributions whilst ignoring constraints such as competition. This is analogous to the ‘potential niche’, although we are only considering a narrow set of niche variables (Jackson and Overpeck, 2000). Our aim was to provide a simple-to-interpret spatial modelling framework for predicting the distribution of suitable habitat for multiple protected species. The main objectives were to develop an approach which could: incorporate all protected species associated with woodland for an entire (administrative) area; provide habitat requirement information for all those species; predict the potential distributions of those species consistently across a range of scales, whilst restricting predictions to climatically suitable areas where possible. Our modelling approach was wider and more ambitious in scope (a greater number of species and a wider range of taxa) than other attempts to inform conservation planning with multi-species models (e.g. Franco et al., 2009; Lentini et al., 2015; Minin and Moilanen, 2014) and as such is a novel application of EHSMs. Although developed for protected woodland species, the framework could be adapted for use with other habitats or suite of species. In addition, we aimed to test the model predictions against species occurrence records, despite our concerns that the low sample size, low resolution and high sampling bias associated with such records could limit agreement with EHSM predictions.

7.3 Material and methods

7.3.1 The Niches for Species framework

There are eight stages to the modelling framework (Figure 7.1). Stage 3 is unique to the N4S methodology; the development of a hierarchical habitat classification provided a structured system for categorizing species' niches. The incorporation of microhabitat information is rarely implemented in these types of landscape-scale, spatial approaches, despite their strong association with biodiversity (Michel & Winter, 2009). By nesting the levels, we take account of context dependency in species-microhabitat associations i.e. species microhabitats may only be important in certain types and structures of the habitat. Stage 8 (validation) is rarely performed in EHSM development. Details on how we have implemented these stages for woodland protected species in Scotland are given in Section 2.2., along with the list of attributes used and their sources (Tables 1 to 3). Output maps from Stage 7 can display single species predictions or aggregate information by polygon to show predicted species richness, for example.

7.3.2 This woodland application

We applied the N4S model to map the potential distribution of woodland protected species in Scottish native woodlands.

Expert knowledge on species-habitat requirements

We reviewed the available data documenting the habitat requirements for 208 protected species, considered to occur in Scotland and use woodland as their primary habitat (Scottish Action Coordination Group, 2008). These represented a wide range of taxonomic groups: lichens, bryophytes and liverworts; invertebrates; fungi; birds; vascular plants; mammals; reptiles and amphibians. Evidence sources were classified in to four categories:

Evidence type 1- information from habitat association analyses supplied directly to myself by species experts in the statutory nature agencies (Scottish Natural Heritage, Natural England, Natural Resources Wales), and nature non-government organisations (NGOs) (Butterfly Conservation, Plantlife Scotland, British Trust for Ornithology). These sources were used particularly where peer reviewed information was lacking on habitat associations under British conditions.

Evidence type 2 – books and peer reviewed scientific articles detailing protected species requirements; these were sourced by searching online journals and journal directories.

Evidence type 3 - information obtained from publications produced by nature agencies and nature NGOs and from websites likely to be subject to peer-review e.g. for Lepidoptera we used Butterfly Conservation (Butterfly Conservation, 2017)

Evidence type 4 – web sites where the review process was unconfirmed, and which might include anecdotal evidence.

For most taxa, roughly half of the sources of evidence were peer-reviewed websites and grey literature (evidence type 3), and the remainder were drawn evenly from the other three sources of evidence (Table 7.1). Differences in the use of evidence source by taxon is indicated when the percentage of data fields supported is considered (Table 7.1). Here there is a reliance on specialist and less available knowledge (type 1) for the more cryptic species (e.g. lichens, fungi), compared to more widely accessible reports and information notes provided by nature conservation NGO's and nature agencies (type 3), for the better-known taxa (e.g. birds, vascular plants). Overall, only a low proportion of data fields were supported by type 4 sources of evidence, where data accuracy is uncertain, as it may not have been confirmed or checked by species experts (Table 7.1).

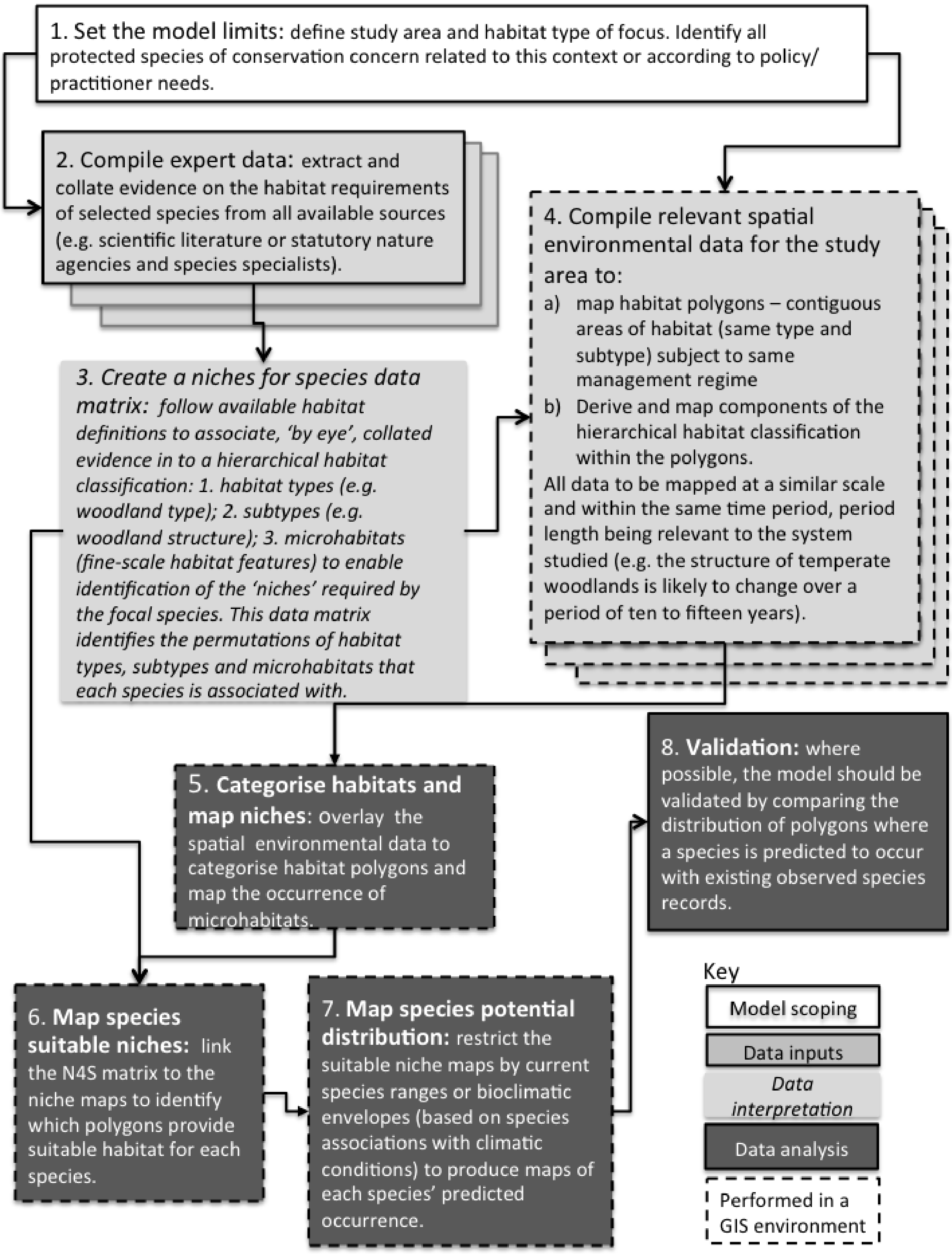


Figure 7.1 A schematic flow chart illustrating the steps involved in Niches for Species (N4S) expert-based habitat suitability modeling framework to map the distribution of niches and species potential occurrence.

We collated the information systematically for each species, recording associations with woodland type or tree species, and microhabitat requirements. Microhabitats represent features of the habitat that may be present at a particular location for a minimum of 5 to 10 years and offer particular microclimates and conditions which may be used by some species only at certain times of the year. Details on species requirements throughout the lifecycle, including differences at early and mature life stages, where appropriate (e.g. for invertebrate species) were also collected. All information included was referenced. A sample of the resulting database is given in Appendix 7.1

Table 7.1 Number of sources of evidence by evidence type (and the percentage of data field entries supported) used in identifying habitat requirements, by taxon.

Taxon (number of species)	Collated expert knowledge covering individual species (type 1)	Peer-reviewed papers and books (type 2)	Websites (known quality review process) and nature agency reports (type 3)	Websites (unknown review process) and anecdotal evidence (type 4)
Lower plants (Lichens , Liverworts and Bryophytes) (69)	3 (82%)	6 (2%)	5 (16%)	0
Invertebrates (52)	8 (2%)	7 (53%)	36 (28%)	13 (17%)
Fungi (21)	1 (6%)	1 (58%)	9 (36%)	0
Birds (16)	1 (33%)	4 (11%)	7 (56%)	0
Vascular plants (10)	1 (20%)	2(21%)	6 (45%)	5 (14%)
Mammals (8)	2 (43%)	3 (9%)	8 (48%)	0
Herptiles (Amphibians and Reptiles) (3)	2 (70%)	0	2 (30%)	0

For 179 of the 208 protected woodland species (69 lower plants (lichens, bryophytes and liverworts); 52 invertebrates; 21 fungi; ten vascular plants; 16 birds; three herptiles (amphibians and reptiles) and eight mammals), there was sufficient information on habitat requirements for their inclusion in the N4S model. These species were allocated to woodland niches.

Habitat classification - Niches for Species (N4S) matrix

We constructed a hierarchical woodland classification which captured the habitat requirements for all species based on the collated expert information. Where possible, the classification used established descriptors of woodland habitat already familiar to forestry decision-makers e.g. woodland type and structure class (Figure 7.2):

i. Habitat type: At the highest level of the habitat classification is woodland type. Seven native woodland types are recognised and described (Maddock 2008) (Figure 7.2).

ii. Habitat subtype: At the second level of the classification hierarchy is structure type. Any woodland type may have stands (representing a portion of the woodland with the same structure, size and age, and considered a single management unit) according to six structure types – these include five stand development stages and a sixth *permanently open* type (Table 7.2).

Sources of expert knowledge often documented which of the woodland types, and which of the stand structure types, a species was associated with. However, where the expert review did not provide this information, we used the canopy or understorey tree species, or the ground flora the species was associated with to guide its allocation to the woodland type following the National Vegetation Classification (Rodwell, 1991). Where stand structure was not specified in the expert knowledge review for a species, we used information on species' detailed resource and microclimate preferences to inform the structure class within which a species was associated, such as: the use of old growth tree features; the requirement for openness or shade; a reliance on tree seeds; a preference for foliage density at different heights in the canopy.

iii. Microhabitat: From the Stage 2 review describing species resource needs we identified ten microhabitats (Figure 7.2) within each woodland type and structure class that covered various fine-scale requirements of every protected species. These microhabitat types nested within each structure type (Figure 7.2).

Having defined each unique woodland type-structure-microhabitat combination as a niche, each species was associated with one or several of these to reflect the range of woodland niches it is associated with according to the review evidence; these associations formed a N4S matrix.

Table 7.2 Summary of structure types used in the classification of niches providing habitat for 179 protected woodland species in Scotland in the Niches for Species model. The structure types are based on the Native Woodland Survey Scotland (NWSS) survey criteria (NWSS, 2013; Patterson et al., 2014).

Structure type	**Description**
Permanently Open	Open habitats: grassland, water or areas where there are constraints to planting trees e.g. rocks, geology, roads.
Temporary open	Area that has been thinned, clear felled, coppiced in last 4 years.
Regeneration and Scrub	Woodland without an overstorey - tree seedlings (< 1m tall), saplings (trees > 1m tall and with girth of up to 7cm diameter at breast height (1.5m)) and shrubs.
Pole stage	Trees and shrubs fill the area and compete, ground flora is shaded out and no other plants colonise. Some canopy trees and understorey shrubs die due to competition. Trees and shrubs not yet bearing seed/fruit (immature). Trees have a diameter at breast height of > 7cm and < 20-30cm and are usually above 5m height.
Mature	Trees producing seed/berries. Crown/canopy usually spreading and at its maximum development. Canopy die-back (up to 10%) from competition for light and/or wind/snow damage.
Veteran ancient	Characterised by the presence of individual trees which have a large girth and show least three signs of old growth and decay. e.g. major trunk cavities/progressive hollowing, fungal fruiting bodies (e.g. from heart rotting species), high aesthetic interest (e.g. pollard or old coppice stool).

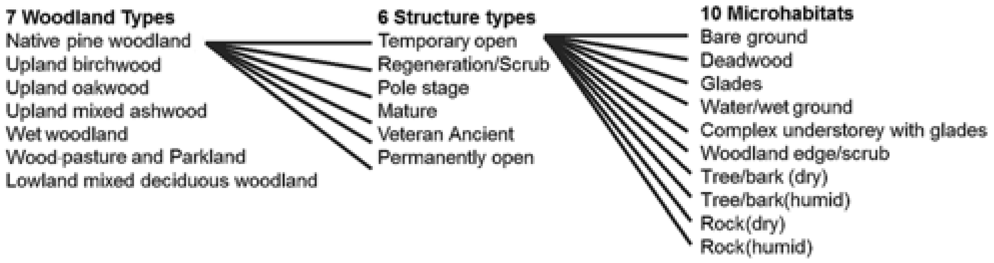


Figure 7.2 Hierarchical representation of the breakdown of a species resource requirement niche to illustrate the Niches for Species system of habitat classification into niche components.

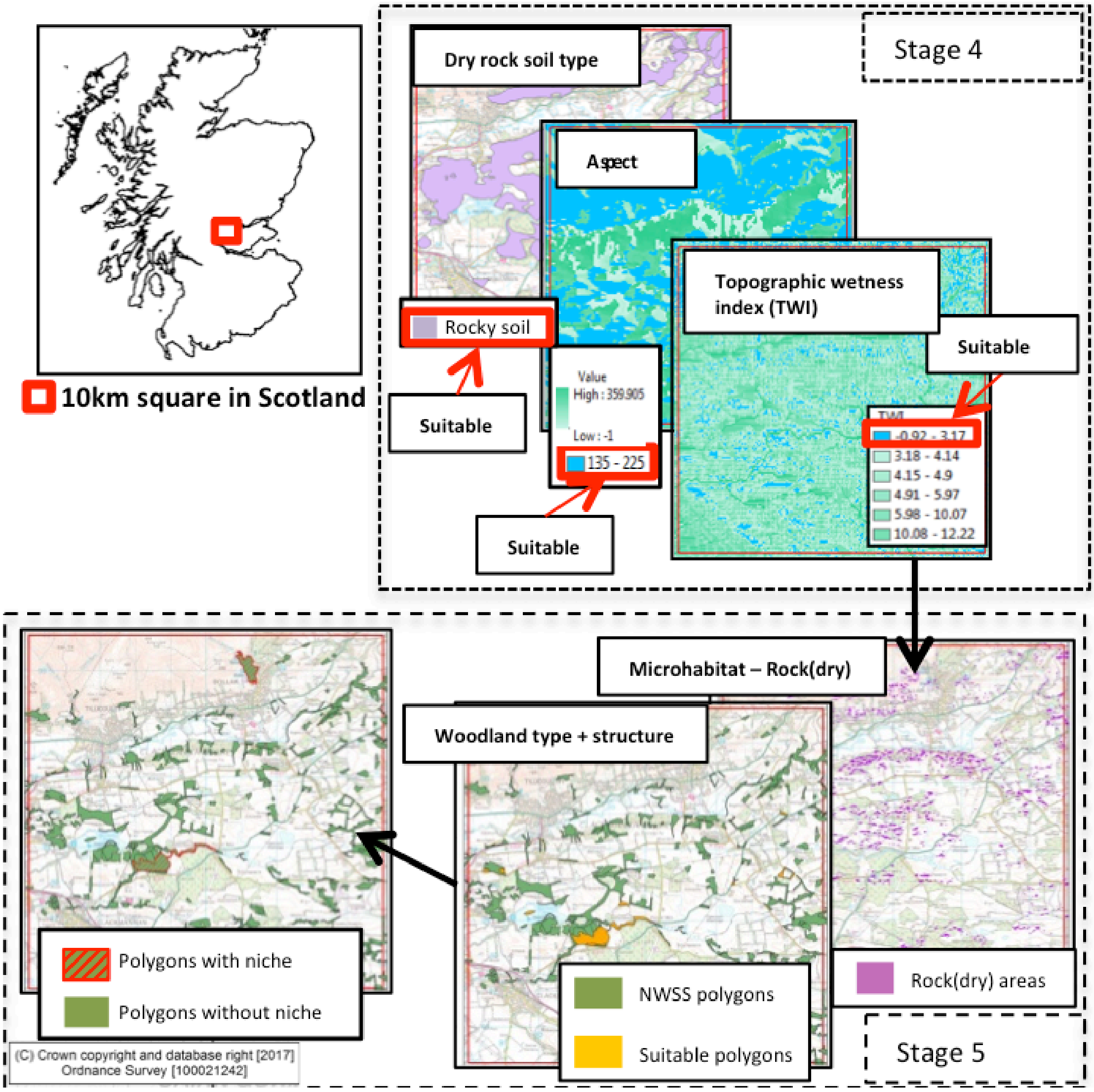


Figure 7.3 Graphical representation of the Niches for Species model development for Stage 4- deriving niche components (this example for microhabitat type rock (dry)) from environmental spatial data, and Stage 5- categorising habitats and mapping niches by combining microhabitat presence with NWSS polygon information (in this example 'suitable' NWSS polygons are of habitat type upland oak woodland and subtype (structure) is mature).

Mapping woodland polygons and niche distributions

To map woodland polygons, we used the Native Woodland Survey of Scotland (NWSS) (Patterson et al., 2014). This spatial dataset provided information on native woodlands across Scotland according to their type (Biodiversity Action Plan Priority Woodland types: Maddock, 2008), structure and other features. The data were gathered from all of Scotland's native woodlands during 2006-2013 by trained surveyors according to a standard protocol (NWSS, 2013). Attributes are provided at the scale of the woodland polygon, which is defined as a discrete area ≥0.5ha and having a minimum width of 20 m, and in which structural elements occupying a minimum of 5% of the woodland area have been mapped. Therefore, a polygon can be considered analogous to a stand, and there are approximately 95,800 NWSS polygons mapped across Scotland, ranging in size from 0.5 ha to 800 ha with a mean size of c.4 ha (Figure 7.3).

The NWSS data provided information that allowed us to classify most woodland polygons into the two higher-level niche component categories, woodland type and woodland structure (Table 7.3). To identify ‘wood-pasture and parkland’ woodland type, which is not a NWSS woodland category, we overlaid Scotland’s Country Parks dataset (Scottish Natural Heritage) and updated the woodland type of any polygons with a centroid overlapping a park. The ‘permanent open’ or ‘temporary open’ woodland structures were identified as NWSS open habitat or clear fell polygons. These open polygons lacked woodland type information, so they were assigned the same woodland type as the adjacent woodland polygon with the shared longest border, calculated using a Geographic Information Software (GIS) (Esri, 2013). We made this assumption in the absence of historical NWSS data that might provide evidence of earlier woodland type. To map the distribution of the 10 microhabitats, we reviewed the relevance of NWSS data attributes alongside various other spatial environmental datasets (singly or in combination) available for Scotland (Table 7.3). Data layers were extracted from non-NWSS data by selecting polygons (vector data) or cells (raster layers) using a GIS, that met specified attributes. For example, areas that were likely to have wet sites were identified as those falling within 25 m of linear water features or wetland habitat features identified from vector landcover maps, or as flat cells (≤0.5° slope) with high topographic wetness index values (Sørensen et al., 2006) using a 25 m digital elevation model (Table 7.3). Sources of all data layers used and whether vector or raster are provided in Table 7.3.

Table 7.3 Rule-set for combining spatial environmental data (type- vector=V, raster=R and sources of data shown in brackets) to describe potential niches present in the native woodlands of Scotland.

Niche Component	**GIS rule**
Woodland type[1]	
Upland mixed ashwood	Dominant NWSS woodland type for polygon (NWSS)
Upland birchwood	
Upland oakwood	
Lowland mixed deciduous	
Native pine	
Wet woodland	
Wood-pasture and parkland	Any NWSS polygon with centroids overlapping the Scotland’s Country Parks dataset (NWSS; Scotland’s Country Parks)
Structure type	
Permanently open	NWSS polygons recorded as ‘open land’ habitat type, which were ≥1 ha and shared an edge with a wooded NWSS polygon[2] (NWSS)
Temporary open	NWSS polygons recorded as ‘clear fell’ dominant habitat type which were ≥1 ha and shared an edge with a wooded NWSS polygon[2] (NWSS)
Regeneration or Scrub	‘Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Visible regeneration', 'Established regeneration' or 'Shrub' or ‘Scrub’(NWSS)
Pole	‘Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Pole Immature' or 'Pole immature' (NWSS)
Mature	‘Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Mature' (NWSS)
Veteran ancient	‘Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Veteran' (NWSS)
Microhabitat	
Deadwood	NWSS polygons where deadwood was recorded by surveyor (NWSS)
Water/wet ground	NWSS polygons where (a) NVC[3] types associated with wet woodland habitats were recorded or, (b) they were intersected by: (i) inland water or wetland habitat polygons (OSMM or LCM inland water features) or, (ii) DEM cells with low slope (<=0.5˚) and within the top seven deciles of topographic wetness index values (NWSS; OSMM**;** LCM; DEM**)**
Woodland edge/scrub	NWSS polygons where (a) scrub was recorded by the surveyor (NWSS**) or,** (b) that have ‘hard edges’ i.e. aren’t completely surrounded by other woodland polygons (NWSS; NFI)
Tree/bark (dry)	NWSS polygons with hard woodland edges (see woodland edge / scrub description) that overlap DEM

Niche Component	GIS rule
	cells with a southerly aspect (**135 - 225**˚) and are within the bottom decile of topographic wetness index values (NWSS; DEM)
Tree/bark (humid)	NWSS polygons that (a) overlap DEM cells with a northerly aspect (>315˚ or ≤45˚) or, (b) overlap DEM cells with low slope (<=0.5˚) and are (c) within the top seven deciles of topographic wetness index values (TWI) or, (d) within 25 m of inland water or wetland habitats (OSOR or LCM inland water features)(NWSS; DEM; TWI; OSOR; LCM)
Complex understorey with glades	NWSS polygons with 10 - 70% canopy cover and (a) regeneration (established or visible; ≥10% cover) and shrub structures (≥10% cover) or, (b) ≥6 canopy structure types recorded by the surveyor (NWSS)
Glade	NWSS polygons with 10 – 70% canopy cover (NWSS)
Rock (dry)	NWSS polygons intersected by soil polygons with 'rocky' properties and DEM cells with a southerly aspect (**135 - 225**˚) and within the bottom decile of topographic wetness index values (NWSS; Scottish soils; DEM; TWI)
Rock (humid)	NWSS polygons intersected by rocky soil polygons and (a) overlap DEM cells with a northerly aspect (>315˚ or ≤45˚) or, (b) overlap DEM cells with low slope (<=0.5˚) and are (c) within the top seven deciles of topographic wetness index values or, (d) within 25 m of inland water or wetland habitats (NWSS; Scottish soils; DEM; TWI; OSOR; LCM).
Bare ground	NWSS polygons. intersected by a footpath or forest track feature (footpaths)

Data sources: NWSS = Native Woodland Survey Scotland (V) (Patterson et al., 2014); Scotland's Country Parks = Scottish Natural Heritage (V); OSMM = Ordnance Survey Master Map (V)(Ordnance Survey, 2016); LCM = Centre for Ecology and Hydrology Land Cover Map 2007 vector map (V)(Morton et al., 2011); DEM= 25 m resolution digital elevation model (R)(EU-DEM, 2016); NFI = Forestry Commission's National Forest Inventory map (V)(FC, 2011b); TWI = topographic wetness index (R)(Sørensen et al., 2006; EU-DEM, 2016); OSOR = Ordnance Survey Open Rivers (V); Scottish soils = a combination of two different scale maps at 1:10,000 and 1:250,000 (V)(Lilly et al., 2010); Footpaths = Forestry Commission Scotland forest paths, tracks, rides, and boundaries (V)(FC Scotland, 2016).

[1] see Maddock (2008) for definitions

[2] Assigned the woodland type of the wooded polygon (those classified as Native woodland' or 'Nearly-native woodland') with which they shared the longest border length with.

[3] National Vegetation Classification (NVC) see Rodwell (1991).

Mapping niche occurrence in polygons using spatial environmental data

Once the NWSS woodland polygons had been classified by type and structure, microhabitat presence-absence was predicted by overlaying the NWSS polygons with the various microhabitat input data layers in a GIS. A rule-set was established for mapping the presence of microhabitats that depended on particular combinations of microhabitat input layers. The simplest microhabitat to map was *deadwood,* as NWSS surveyors estimated deadwood volume on a single site visit per woodland polygon during the seven year-long field survey (Table 7.3) (NWSS, 2013). The remaining nine microhabitats were more complex to map, requiring more than a single data source (for details of data sources used to map the microhabitats see Table 7.3). For example, identifying the microhabitat *rock (dry)* used several spatial layers (Figure 7.3) combined using a logical rule-set to integrate information on land cover, soil and topographic position (e.g. slope and aspect) of the polygon. The rule-sets were automated in ArcGIS Model Builder (v10.2) (Esri, 2013). The 'zonal statistics' tool was used to identify polygons overlapping input raster cells, and 'select by location' used to identify polygons intersected by input vector layers. Any amount of overlap between a NWSS polygon and a microhabitat input layer resulted in recording the microhabitat 'presence/absence' in the polygon (although microhabitat 'absence' unused), and the area or amount of microhabitat cover within a polygon was not considered.

Mapping species habitat suitability

Using Model Builder and Python scripts in ArcGIS, we implemented a rule-set to link the NWSS niche map with the N4S matrix. A NWSS polygon was predicted to be suitable when the combination of woodland type-woodland structure and microhabitat presence matched a species' habitat requirements. Binary fields were added to the spatial database to indicate a polygon's predicted suitability (0 or 1) for each species.

Mapping species potential distribution

As many of the protected species have restricted ranges across Scotland, we limited predicted species occurrence by classifying any NWSS polygons outside of modelled current bioclimatic envelopes as unsuitable. Bioclimatic envelopes were available for 51 species (23 species of invertebrate, 17 lower plants, 1 vascular plant (Ellis et al., 2014; Pearce-Higgins et al., 2015)) (Appendix 7.2). In the absence of these data we mapped population ranges from 10 km resolution NBN Gateway species records (NBN, 2016) for all survey years using the Minimum Convex Polygons (MCPs) (Rurik and Macdonald, 2003) in ArcGIS. MCPs were generated for 90 species representing all taxa. For 38 species there was insufficient data (fewer than three 10 km squares adjacent to one another) (Appendix 7.2).

7.3.3 Validation of model

Validation species occurrence data

We selected ten species to use in a validation exercise. The validation compared the potential distribution predicted by N4S with existing species occurrence records. The validation species were selected to represent a range of woodland types, taxonomic groups, and traits (wide to narrow niche breadth; vagile to sessile; easy to observe to cryptic). We used only data recorded at a 100 m resolution or finer (≥6 figure grid references) to ensure we could accurately attribute records to polygons (Dymytrova et al., 2016). Records were used from a sixteen-year period (2000 to 2016), in line with the NWSS data (surveyed 2006 – 2013). To gain insights into how well the N4S model predicted areas without the potential to support protected species, we incorporated pseudo-absence records into the analysis as adequate absence records were not available. Pseudo-absence records were created following the “surveyed absence” or “target group” strategy which uses location records of species from the same taxonomic group, where it is assumed that the focal species was not recorded as it was absent (Gomez-Rodriguez et al., 2012; Hanberry et al., 2012; Phillips et al., 2009). The choice of only 10 validation species was largely influenced by the availability of species records for which we could obtain some pseudoabsence data.

Ultimately, choice of validation species was constrained by data availability. For two bird species - *Muscicapa striata*, *Turdus philomelos* - data at the required resolution were available only from surveys of one woodland type (native pine woodland) limiting testing of model predictions to between woodland type and structure with and without microhabitat. N4S model predictions were fully tested for the remaining eight validation species: three lower plants- *Collema fasiculare*, *Pseudocyphellaria norvegica*, *Gomphillus calyciodes*; one vascular plant- *Linnaea borealis*; and four invertebrates- *Cupido minimus*, *Carterocephalus palaemon*, *Boloria euphrosyne*, *Osmia uncinata*.

Validation data analysis

Duplicate species records (same date and location) were removed. The proportion of field records falling within polygons predicted to be suitable or unsuitable for each of the validation species were calculated for presence and pseudo-absence records. We applied a cumulative binomial probability test (R Core Team 2012) to estimate whether the number of presence records lying within suitable polygons of the N4S model was greater than could have been predicted by chance alone, according to the area of suitable woodland habitat available within the species' range.

We also tested the degree of agreement between the N4S model predictions and the information from the presence/pseudo-absence datasets by constructing confusion matrices using SAS version 9.3 (SAS, 2011) (and generating Cohen's Kappa statistic (k), where k=1 indicates perfect agreement, k=0 agreement by chance alone and k<0 disagreement (Cunningham, 2009). A system of subdivision of k has been suggested, for which we tested the six categories: "No agreement" (k<0); "Slight agreement" (k≥0 and <0.2); "Fair agreement"(k≥0.2 and <0.4); "Moderate agreement"(k≥0.4 and< 0.6); "Substantial agreement" (k≥0.6 and <0.8); "Almost perfect agreement" (k≥0.8 and <1.0) (Landis and Koch, 1977). The deviation of k values from zero was tested statistically (H0: k = 0; one-sided probability reported as testing agreement i.e. k>0). All tests were performed for each species and at three levels of the habitat classification hierarchy i.e. where occurrence of the target species was predicted from the presence of 1) suitable woodland type only, 2) woodland type + structure type or 3) woodland type + structure type + microhabitat type.

7.3.4 Choice of Niches for Species model outputs

The N4S model output (map of protected woodland species potential occurrence based on the availability of niches) can be viewed at a variety of scales. We selected three scales considered appropriate for different policy or practice queries: 1) a national-scale overview of species richness which may be applicable to supporting strategic forest policy decisions, 2) a landscape-scale assessment of species richness which may support tactical decision making in forest planning, and 3) an individual species map with associated habitat data which we envisaged might be used in practice for operational decisions guiding management interventions.

7.4 Results

7.4.1 Spatial environmental data used to map niche occurrence in polygons

Most of the niche components were derived directly from the NWSS data (Table 7.3). For the remainder, information was derived from other available spatial datasets and their reliability was limited by their relevance, accuracy and precision (Table 7.3). For example, there were no fine resolution spatial data available to describe the microhabitat *bare ground.* Therefore, we assumed this microhabitat would be found along footpaths and tracks, and used spatial data on these features to map the likely occurrence of this microhabitat.

7.4.2 Validation

The strength of the agreement (i.e. higher Kappa value) varied among species (Table 7.4). There was some agreement (Kappa>0) between model predictions and the occurrence for nine of the ten validation species (No agreement found for *T. philomelos*), but this was ‘Slight’ for seven of the remaining nine species’ (Landis and Koch 1977). Higher Kappa values (Kappa = 0.296 - ‘Fair agreement’ to Kappa = 0.807- ‘Almost perfect agreement’) occurred for the species *O. uncinata* and for *L. borealis*. Results from the probability tests (Kappa and binomial) were largely consistent. For five of the ten validation species associations between distribution records and predicted availability of suitable polygons was better than would be expected if species occurrence had been allocated at random to the woodland polygons. For two species the results approached statistical significance, for one level of the habitat classification hierarchy (e.g. woodland type + structure) tested. Judged on the frequency of agreement (between actual and predicted occurrence of species when the N4S model was run at the three levels of niche hierarchy complexity) the N4S model appeared to perform equally well at the intermediate (woodland type + structure) and most detailed (woodland type + structure + microhabitat) hierarchy levels (Table 7.4). However, the agreements with the highest levels of significance ($p<0.05$) for the binomial test and Kappa value occurred when the model included microhabitat (Table 7.4). This suggests that where agreements are found these are stronger when niche identification included microhabitat features.

Table 7.4 Summary of correspondence between the habitat availability for ten validation species predicted using Niches for Species (N4S) model and records of species occurrence and pseudo-absence at three levels of niche hierarchy (1 = woodland type only; 2= woodland type + stand structure; 3= woodland type + stand structure + microhabitat). Kappa (k) subdivisions: "No agreement" (k<0); "Slight agreement" (k≥0 and <0.2); "Fair agreement"(k≥0.2 and <0.4); "Moderate agreement"(k≥0.4 and< 0.6); "Substantial agreement" (k≥0.6 and <0.8); "Almost perfect agreement" (k≥0.8 and <1.0) (Landis and Koch, 1977). One-sided probability reported as testing for where k is positive; H0: k = 0. “Binomial” refers to a binomial probability test; H0: the number of validation species records found within suitable woodland polygons is no better than random within the sampled woodland polygons. Sampled polygons being those containing a pseudo-absence record a validation species record or both. Probability test level of significance (for both Kappa and binomial tests): *p<0.05, **p<0.01, ***p<0.001, na = not applicable for one-sided test.

	Niche hierarchy					
	1		**2**		**3**	
Validation species	**Kappa value (p =)**	**Binomial**	**Kappa value (p =)**	**Binomial**	**Kappa value (p =)**	**Binomial**
Collema fasiculare	Slight agreement 0.105 (p=0.067)	p=0.098	Slight agreement 0.095 (p=0.103)	p=0.147	Slight agreement 0.022 (p=0.386)	p=0.483
Pseudocyphellaria norvegica	No agreement -0.107 (na)	p>0.999	Slight agreement 0.005 (p=0.455)	p=0.444	Slight agreement 0.014 (p=0.358)	p=0.253
Gomphillus calyciodes	Slight agreement 0.008 (p=0.419)	p=0.518	Slight agreement 0.126(p=0.053)	p=0.078	Slight agreement 0.108(p=0.081)	p=0.118
Linnaea borealis	Almost perfect agreement 0.807 (***)	**	Slight agreement 0.128 (***)	**	Slight agreement 0.065 (***)	***
Cupido minimus	No agreement -0.0013 (na)	p=0.863	Slight agreement 0.042 (***)	**	Slight agreement 0.045 (***)	***
Carterocephalus palaemon	No agreement -0.018 (na)	p>0.999	Slight agreement 0.022 (p=0.075)	p =0.056	Slight agreement 0.004 (p=0.381)	p=0.262
Boloria euphrosyne	Slight agreement 0.013 (***)	**	No agreement -0.025 (na)	P=0.999	No agreement -0.016 (na)	P=0.999
Osmia ucinata	Slight agreement 0.006 (p=0.139)	p=0.231	Fair agreement 0.296 (***)	***	Fair agreement 0.223(***)	***
Muscicapa striata	NA	NA	Slight agreement 0.041 (*)	p=0.076	No agreement -0.016 (na)	p=0.641
Turdus philomelos	NA	NA	No agreement -0.024 (na)	P=0.999	Insufficient values	p=0.999

7.4.3 Example Niches for Species model outputs

National species richness map

The national scale map (Figure 7.4) highlights the extent of native woodlands covered by the NWSS dataset (included in the N4S model), and shows the potential occurrence of protected woodland species within these woodlands. Woodlands with high species richness (>20 to 30 protected woodland species per woodland polygon) are reasonably well spread throughout Scotland although the native woodlands of the River Dee valley and the River Spey valley in north-eastern Scotland stand out as being areas of particularly high species richness.

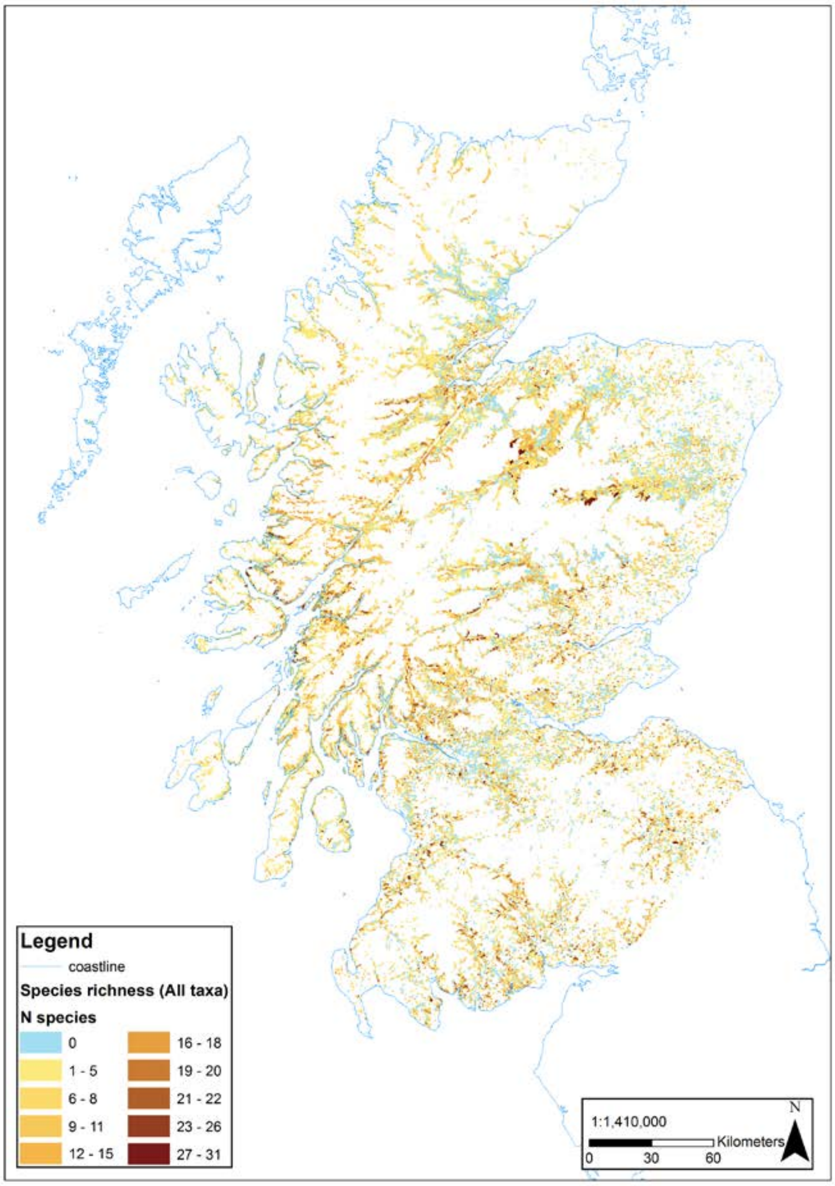


Figure 7.4 Species richness of native woodlands in Scotland based on the predicted potential distribution of all 179 protected woodland species.

Landscape scale species richness output

The 10 km x 10 km area of upland Scotland selected to illustrate the N4S model landscape scale output (Figure 7.5) depicts a highly wooded landscape area, where nearly half of the area (4,377 ha) comprises native woodlands. A few polygons have the niche potential for a high number of protected woodland species (up to 31) and most have the potential to support ten or more species. However, several polygons have low species richness (0 to 10 protected species per polygon).

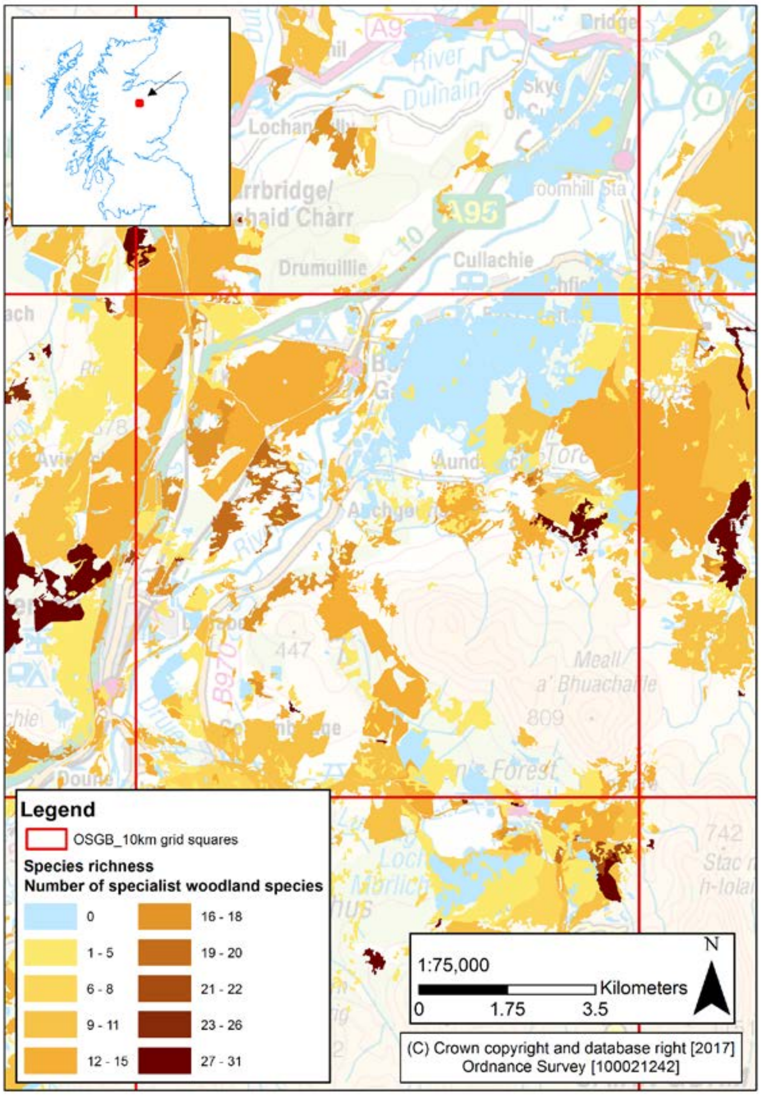
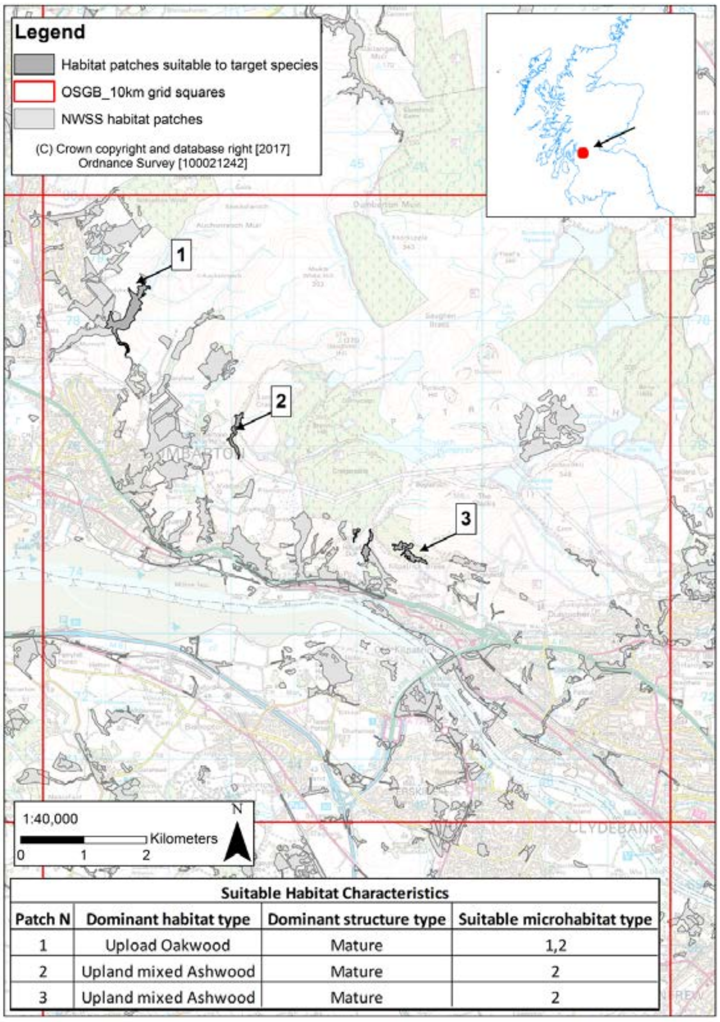


Figure 7.5 Sample output from the Niches for Species model showing predicted distribution of protected woodland species richness by native woodland polygon in a 10 km x 10 km (Ordnance Survey Great Britain) area of a typical upland landscape in Scotland.

Individual species-niche output
More detailed information can be extracted from the N4S model (Figure 7.6). For example, the lower plant *Dumortiera hirsuta* was one of the species predicted to occur in the sample landscape we have used to illustrate the finest scale output from the N4S model. The model output gives the locations of the polygons *D. hirsuta* is predicted to occur within (Figure 7.6). These comprise woodland types upland oakwood and upland mixed ashwood, all with a mature stand structural stage. *Dumortiera hirsuta* is most likely to be associated with the water/wet ground and rock(humid) and bare ground microhabitats where available within these polygons.



Suitable Habitat Characteristics

Patch N	Dominant habitat type	Dominant structure type	Suitable microhabitat type
1	Upload Oakwood	Mature	1,2
2	Upland mixed Ashwood	Mature	2
3	Upland mixed Ashwood	Mature	2

Figure 7.6 Sample output from the Niches for Species model showing predicted location of *Dumortiera hirsuta*, a protected woodland species in native woodland polygons in a 10 km x 10 km area (Ordnance Survey Great Britain). Niche information associated with *D. hirsuta* is included; a niche is defined by the combination of woodland type, structure type and microhabitat (1 = water/wet ground, 2 = rock(humid)). (NWSS- Native Woodland Survey Scotland).

7.5 Discussion

We provide a framework to link expert species knowledge with spatial environmental datasets to predict simultaneously, for multiple taxa, the availability of habitat for protected species. In applying our N4S model to protected woodland species in Scotland, we found that the type and accessibility of expert knowledge on habitat requirements varied between taxa, but that there was sufficient information to include 179 of the 208 species. Relevant spatial environmental data were also available to classify native woodlands into type and structure, and to map the distribution of most microhabitats with confidence. Species records did not consistently accord with the predictions of species occurrence by the model: good agreement was shown for five out of ten of the validation species, based on the niche hierarchy giving best results. By mapping protected species potential occurrence, the quality of habitat for supporting biodiversity can be visualized in a simple form by spatial outputs of protected species richness by woodland polygons; interpreted from the same input data either at the whole administrative region, landscape or forest level.

7.5.1 Adequacy of data and model strengths

The relatively simple species-habitat association evidence in the N4S model has been drawn from information provided by species experts, and, although of good quality, much of the information was not published and therefore needed to be sought directly from the experts. Based on the percentage of data field entries for different taxa supported by each of the four evidence types, it appears information for cryptic species is less accessible (mostly via expert knowledge-evidence type 1 and peer-reviewed journals- evidence type 2) than for the better-known species, as expected. The literature on biodiversity indicators suggests there is a sound basis to making links between habitat features and species occurrence (Regnery et al., 2013; Gao et al., 2015) and the inclusion of fine scale habitat features (e.g. structure type and microhabitats in the N4S model) can be important for certain species (Harvey and Platenberg, 2009; Dymytrova et al., 2016; Horak, 2017).

We have high confidence in the quality of the spatial data as 65% of the 23 different habitat categories and microhabitats used in the N4S model (7 woodland types, 6 structure types and 10 microhabitat types) were derived directly from existing attributes in the input datasets. A third of these attributes relied on information derived from various other spatial data. However, we had low confidence in predicting just one attribute - the bare ground microhabitat. Although beyond the scope of this study, we recommend validating the N4S model using a targeted survey of polygons in which an assessment of the predicted niche occurrence has been verified. This would increase our confidence in how well spatial data combine to describe features on the ground. We have relied on the detailed woodland survey NWSS data to locate many of the niches and such data may not be universally available. Nevertheless, the approach illustrated, of classifying habitat niches and describing these using spatial data would allow the use of alternative or replacement spatial datasets. We recommend sourcing and integrating alternative spatial data to ensure that habitat layers remain current. For example, we could integrate a forest structure layer interpreted from aerial photography or LiDAR data (where this is available) to update the woodland structure information within the polygons (McInerney et al., 2011).

The N4S model does not take account of interactions among species and assumes that if the correct habitat is available there will be no constraints on potential species use. This assumption, like SDMs in general, may lead to over prediction of species occurrence (Phillips et al., 2006). Although N4S does not account for the landscape surrounding a woodland patch, broader scale influences that affect species distribution are factored in to the N4S model by constraining predictions by bio-climatic or distribution envelopes. Inclusion of envelopes has been shown to improve model performance in SDMs based on species records (Lobo et al., 2011; Zarnetske et al., 2007), primarily because it enables some environmental data to be incorporated.

7.5.2 Model validation

Consistent with our expectations, validation showed limited correspondence between predicted potential species locations (woodland polygons) and recent species presence records (agreements were significant for half of the validation species). Including detailed information about species' resource requirement (microhabitat) in our expert-based habitat suitability model did appear to improve the model performance in the validation tests for the subset of species where agreement was found between predicted and recorded species occurrence. It is possible that this is due to weak relationships between some but not all taxa represented by the validation species and microhabitats (Goa et al., 2015; Regnery et al., 2013) and could also result from poor spatial definition of microhabitats from the data sets we have used. However, we anticipated that poor model performance could also result from the lack of availability of high-resolution species presence records available for validation. Although the resource of species records for Britain is large, surveys are not always carried out systematically (instead favoured locations are targeted for survey), it is uncommon for all areas to be surveyed regularly, and only rarely is species absence data collected (NBN, 2017). In studies when data meeting these survey criteria are deployed, good agreement has been found between the empirical data and the expert-based classifications of habitat choice (Leblond et al., 2014; Reif et al., 2010). The lack of availability of good quality species records has been argued (e.g. Phillips et al., 2006) as a reason to develop predictive models of distribution based on knowledge, as in N4S, rather than records.

7.5.3 Application

Niches for Species is now being applied in several ways with model uncertainty described according to the scale of application. For forest policy makers, the model provides an analysis of the whole of the native woodland resource in Scotland (both within and outside protected areas) and indicates where there are species ‘hotspots’ or habitats where particular sets of rare or threatened species are likely to occur. As N4S considers all the protected species of interest for the region, it performs as well, or better than the current alternative national analysis method conducted for the UK using coarser (2km resolution) data, and the better recorded species e.g. birds as surrogates (Franco et al., 2009). Furthermore, the N4S model has the advantage of providing information on the habitats associated with areas that may be prioritised due to potential protected species occurrences: Franco et al. (2009) recognised that the lack of such information was a shortcoming in their SDM. For forestry decision making, visualising the configuration of potential protected species occurrence at the landscape-scale can help planners consider how to minimise forest operations impacts on species rich areas (FC 2017; UKWAS, 2008). When used in a scenario analysis, N4S can provide planners with estimates of how potential species lists and overall species richness may vary with choice of woodland type and location, as a result of decisions to meet woodland expansion targets (Sing et al., 2013). At this scale of application, uncertainties regarding the accuracy of the model should be checked by applying local experience to compare habitat types, and likely diversity of niches with the location of species rich areas indicated by the model. At a finer scale, knowledge of potential occurrence of a protected species within a woodland polygon may alert the need for an expert survey to confirm species presence. This is consistent with the recommended application of many SDMs (Buechling and Tobalske, 2011; Dymytrova et al., 2016; Lentini et al., 2015).

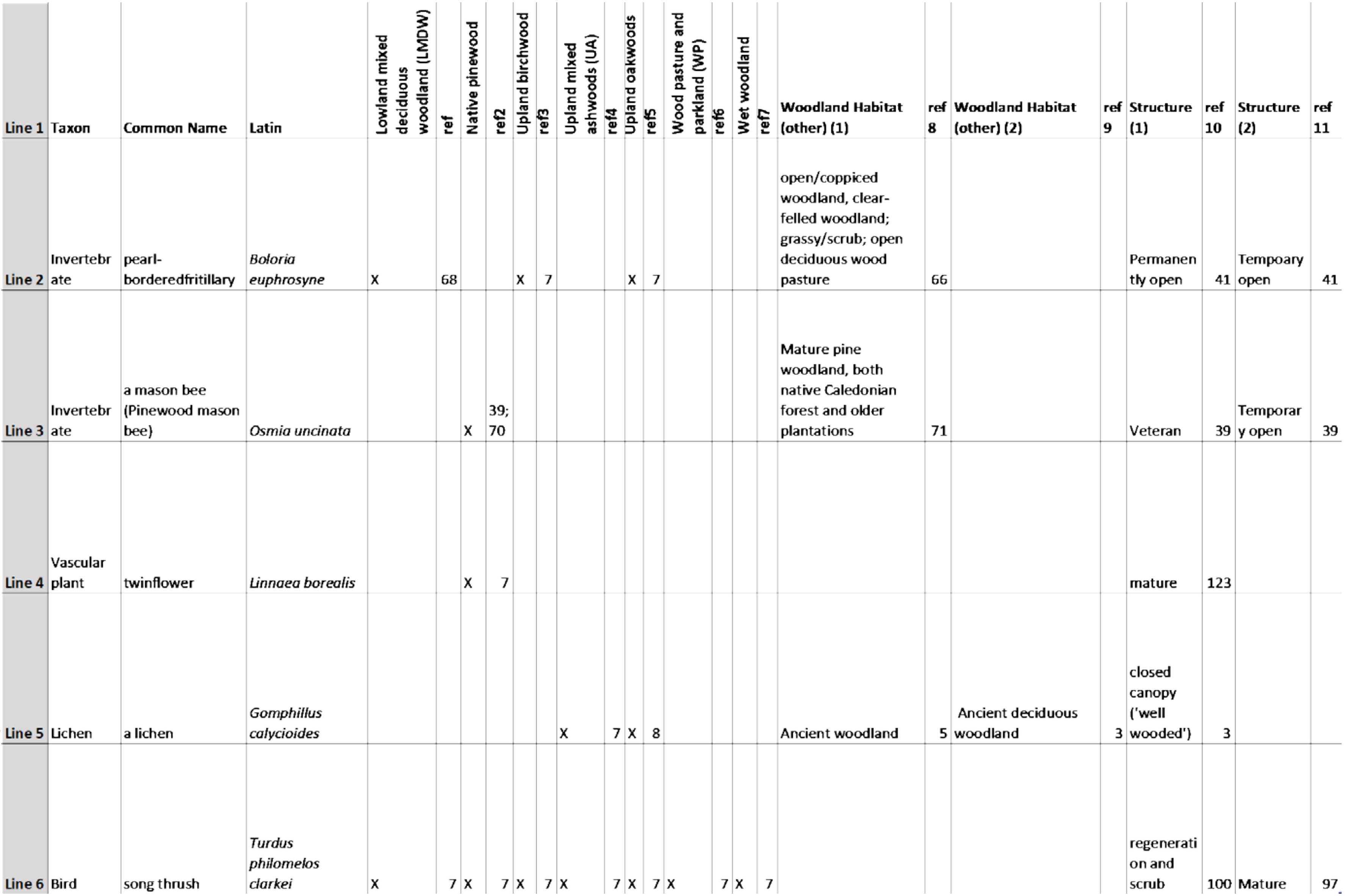
Forestry practitioners and policy makers are tasked with applying management in ways that will meet international and national obligations for conserving biodiversity in the most efficient manner (CBD, 2010; FC, 2017). Obligations are articulated through law and policy devolved to a country/regional level. In all cases information is needed on where the most threatened species occur within the landscape, and how species presence may change in response to habitat management at a variety of scales (Barrows et al., 2005; Egoh et al., 2014;). Our challenge was to produce a model which encompassed all the protected species Scottish forestry decision makers are legally obliged to consider. Our approach incorporates the available wealth of ecological knowledge on species using high resolution spatial data and avoids the need to rely solely on species records or surrogate species. The N4S model provides forest decision makers with information on the occurrence of niches for nearly all the protected species associated with woodlands in Scotland. For many species, actual locations may not be known due to their rarity and/or their cryptic nature; and additionally, there may be uncertainty about habitat features to which their location is related. The output map format with associated attribute table listing the woodland type, structure and predicted presence and absence of each microhabitat and protected species, helps to improve knowledge of species needs and location of potential niches.

Niches for Species can help forest practitioners guide conservation management, but we acknowledge some weaknesses, which may limit its application, and suggest improvements. The model may lack high levels of accuracy that would otherwise be valuable to forest policy makers and practitioners. However, high levels of accuracy are not always needed by decision makers, and more timely action may ultimately be more cost effective than delayed action (Cook et al., 2013). This is particularly so at a time of austerity and a decline in priority afforded to biodiversity policy. We recommend this expert-based EHSM approach as a method to integrate complex information relating to multiple and often data-deficient species in a format which allows land policy makers and managers to consider equally, large numbers of species and their conservation needs.

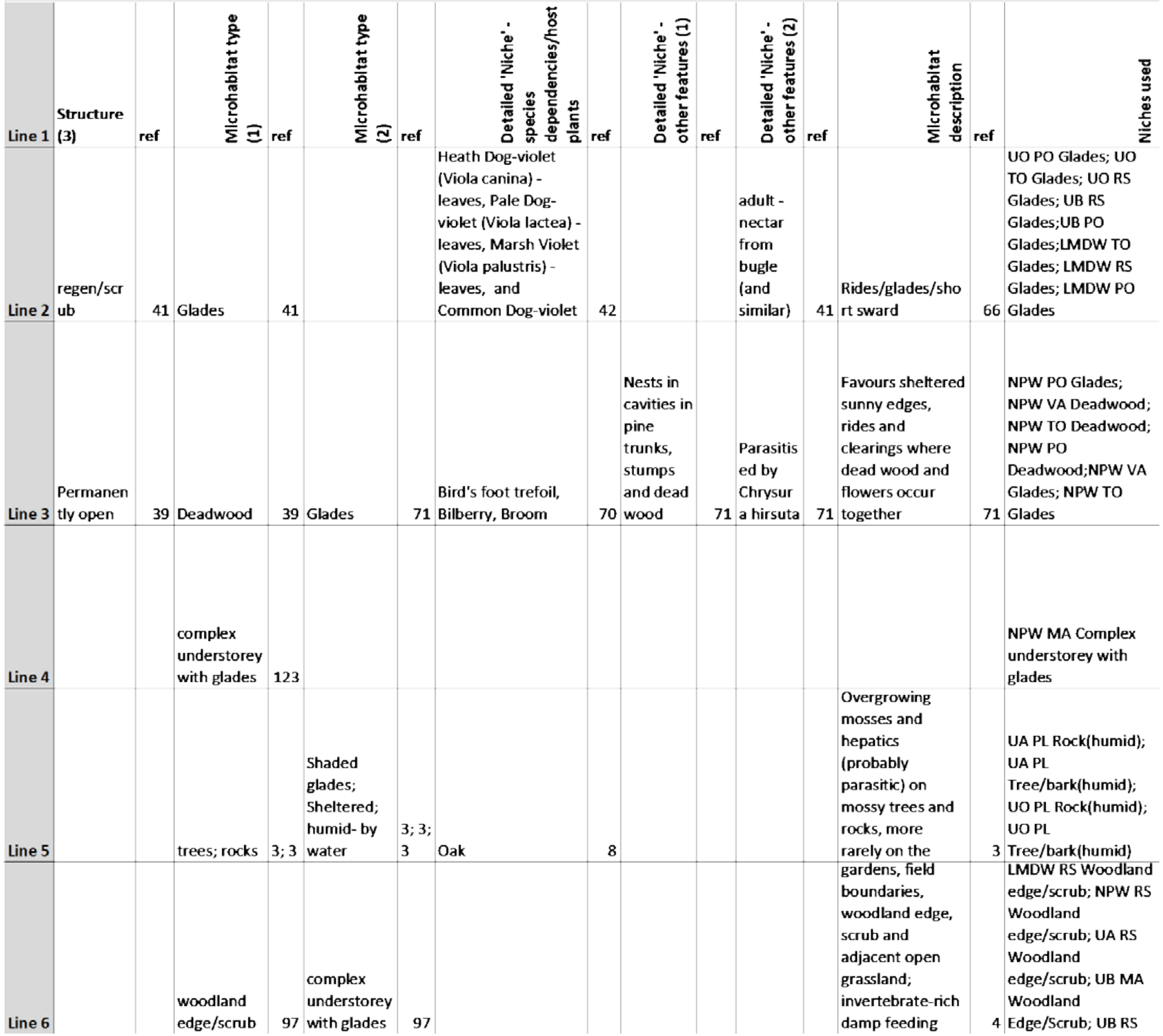
7.6 Acknowledgments

I would like to thank the many NGO and nature agency staff who have provided data for and guidance on model development including Sarah Smyth, Dave Genney, Colin Beale, Deborah Long, Tom Prescott, Chris Ellis, Brian Coppins, Rob Critchlow, Jonathan Webb, Gordon Patterson, John Tullie, Colin Edwards, Richard Thompson, Kenney Kortland, Murdo Macdonald, Andy Scobie and John Calladine. Thanks also to Georgianna Barnard, Thomas Connolly, Katrina Dainton and Vanessa Burton for assistance with the research and to Kevin Watts and the anonymous reviewer whose comments helped reshape this chapter. This work was funded by the Forestry Commission Science and Innovation Strategy Research Programme 3.

Appendix 7.1 A small sample of database of ecological information associated with species included in the Niches for Species model



Line 1	Taxon	Common Name	Latin	Lowland mixed deciduous woodland (LMDW)	ref	Native pinewood	ref2	Upland birchwood	ref3	Upland mixed ashwoods (UA)	ref4	Upland oakwoods	ref5	Wood pasture and parkland (WP)	ref6	Wet woodland	ref7	Woodland Habitat (other) (1)	ref 8	Woodland Habitat (other) (2)	ref 9	Structure (1)	ref 10	Structure (2)	ref 11
Line 2	Invertebrate	pearl-borderedfritillary	*Boloria euphrosyne*	X	68			X	7			X	7					open/coppiced woodland, clear-felled woodland; grassy/scrub; open deciduous wood pasture	66			Permanently open	41	Tempoary open	41
Line 3	Invertebrate	a mason bee (Pinewood mason bee)	*Osmia uncinata*			X	39; 70											Mature pine woodland, both native Caledonian forest and older plantations	71			Veteran	39	Temporary open	39
Line 4	Vascular plant	twinflower	*Linnaea borealis*			X	7															mature	123		
Line 5	Lichen	a lichen	*Gomphillus calycioides*							X	7	X	8					Ancient woodland	5	Ancient deciduous woodland	3	closed canopy ('well wooded')	3		
Line 6	Bird	song thrush	*Turdus philomelos clarkei*	X	7	X	7	X	7	X	7	X	7	X	7	X	7					regeneration and scrub	100	Mature	97



Line 1	Structure (3)	ref	Microhabitat type (1)	ref	Microhabitat type (2)	ref	Detailed 'Niche' - species dependencies/host plants	ref	Detailed 'Niche' - other features (1)	ref	Detailed 'Niche' - other features (2)	ref	Microhabitat description	ref	Niches used
Line 2	regen/scrub	41	Glades	41			Heath Dog-violet (Viola canina) - leaves, Pale Dog-violet (Viola lactea) - leaves, Marsh Violet (Viola palustris) - leaves, and Common Dog-violet	42			adult - nectar from bugle (and similar)	41	Rides/glades/short sward	66	UO PO Glades; UO TO Glades; UO RS Glades; UB RS Glades;UB PO Glades;LMDW TO Glades; LMDW RS Glades; LMDW PO Glades
Line 3	Permanently open	39	Deadwood	39	Glades	71	Bird's foot trefoil, Bilberry, Broom	70	Nests in cavities in pine trunks, stumps and dead wood	71	Parasitised by Chrysura hirsuta	71	Favours sheltered sunny edges, rides and clearings where dead wood and flowers occur together	71	NPW PO Glades; NPW VA Deadwood; NPW TO Deadwood; NPW PO Deadwood;NPW VA Glades; NPW TO Glades
Line 4			complex understorey with glades	123											NPW MA Complex understorey with glades
Line 5			trees; rocks	3; 3	Shaded glades; Sheltered; humid- by water	3; 3; 3	Oak	8					Overgrowing mosses and hepatics (probably parasitic) on mossy trees and rocks, more rarely on the	3	UA PL Rock(humid); UA PL Tree/bark(humid); UO PL Rock(humid); UO PL Tree/bark(humid)
Line 6			woodland edge/scrub	97	complex understorey with glades	97							gardens, field boundaries, woodland edge, scrub and adjacent open grassland; invertebrate-rich damp feeding	4	LMDW RS Woodland edge/scrub; NPW RS Woodland edge/scrub; UA RS Woodland edge/scrub; UB MA Woodland Edge/Scrub; UB RS

Footnote to Appendix 7.1:
ref: 3- Plantlife Scotland Niche (2009) Lower plant niche analysis. Internal report to Plant life, unpublished; 4- Webb, J.R., Drewitt, A.L. & Measures, G.H., 2010. Managing or species: Integrating the needs of England's priority species into habitat management. NERR024 Woodland_spreadsheet. Available at: http://publications.naturalengland.org.uk/publication/30025; 5 - Bromley, M. (2007) Analysis of Forestry Commission Wales S42 priorities (internal report to Forestry Commission, unpublished); 7-SNH (2008) Priority habitat descriptions, internal report to SNH, unpublished; 8 - http://wales-lichens.org.uk/apprentices/content/gomphillus-calycioides ; 39- Anon (1999) *Osmia uncinata* (a mason bee) Action Plan

UKBAP_Tranche2-ActionPlans-Vol4p136-137, JNCC, Peterborough, http://jncc.defra.gov.uk/PDF/UKBAP_Tranche2-ActionPlans-Vol4-1999.pdf ; 41- Brereton, T. (1999) The distribution, ecology and conservation of the pearl-bordered fritiilary butterfly *Boloria euphrosyne* in Scotland. Information and Advisory Note

Number 114 Scottish Natural Heritage, Edinburgh, http://www.snh.org.uk/publications/on-line/advisorynotes/114/114.htm ; 42- http://www.harpps.org.uk/harppsapp/harpps2/web/secure/autecology, Pearl bordered Fritillary autecology page in HaRPPS Accessed December 2015; 66- http://butterfly-conservation.org/679-1384/pearl-bordered-fritillary.html ; 68-http://butterfly-conservation.org/679-3211/small-pearl-bordered-fritillary.html ; 70- http://www.ukbutterflies.co.uk/species.php?species=palaemon ; 71- Falk, S. and Lewington., R.2015 Field Guide to the Bees of Great Britain and Ireland ; 97 - Fuller, R.J., Bellamy, P.E., Broome, A., Calladine, J., Eichhorn, M.P., Gill, R.M. and Siriwardena, G.M. (2014). Effects of woodland structure on woodland bird populations with particular reference to woodland management and deer browsing (WC0793/CR0485). Defra, London.
;100- Broome, A., Fuller, R.J., Bellamy, P.E., Eichhorn, M.P., Gill, R.M.A., Harmer, R., Kerr, G., Siriwardena, G.M., 2017. Implications of lowland broadleaved woodland management for the conservation of target bird species. Forestry. Commission. Research. Note 28, 1–12. Forestry commission, Edinburgh; 123 - Kohn, D. (2003) Dossier for Linnaea borealis. Unpublished report to Plantlife Scotland. Plantlife International, Salisbury.

Niches = Woodland type (7- as listed in table S3) + Structure (*Permanent Open*-PO; *Temporary Open* – TO; *Regeneration/Scrub* –RS; *Pole Stage* – PL; *Mature* – MA; *Veteran and Ancient* –VA) + Microhabitat (*bare ground; complex understorey with glades*; *deadwood; glades; rock(dry); rock(humid); tree/bark(dry); tree/bark(humid); water/wet ground; woodland edge/scrub*).

Appendix 7.2 Protected woodland species occurring in Scotland which are included in Niches for Species model and approach used to constrain predicted distribution (lack of ‘X’ indicates no constraints applied).

Species group	Species	Approach to constrain species predicted distribution[1]		
		Bioclimatic envelope (source)[2]		MCP range[3]
		Ellis	Pearce-Higgins	
Bird	*Anthus trivialis*			X
Bird	*Caprimulgus europaeus europaeus*			X
Bird	*Carduelis cabaret*			X
Bird	*Coccothraustes coccothraustes*			X
Bird	*Cuculus canorus canorus*			X
Bird	*Loxia scotica*			X
Bird	*Muscicapa striata striata*			X
Bird	*Phylloscopus sibilatrix*			X
Bird	*Poecile montanus kleinschimdti*			X
Bird	*Poecile palustris*			X
Bird	*Prunella modularis occidentalis*			X
Bird	*Pyrrhula pyrrhula pileata*			X
Bird	*Tetrao tetrix britannicus*			X
Bird	*Tetrao urogallus*			X
Bird	*Turdus philomelos clarkei*			X
Bird	*Turdus philomelos subsp. hebridensis*			
Herptile	*Anguis fragilis*			X
Herptile	*Triturus cristatus*			X
Herptile	*Vipera berus*			X
Invertebrate	*Acronicta psi*		X	
Invertebrate	*Acronicta rumicis*		X	
Invertebrate	*Agrochola helvola*		X	
Invertebrate	*Agrochola litura*		X	
Invertebrate	*Agrochola lychnidis*		X	
Invertebrate	*Allophyes oxyacanthae*		X	
Invertebrate	*Amphipyra tragopoginis*		X	
Invertebrate	*Apamea remissa*		X	
Invertebrate	*Atethmia centrago*		X	
Invertebrate	*Blera fallax*			
Invertebrate	*Boloria euphrosyne*			X
Invertebrate	*Boloria selene*		X	
Invertebrate	*Brachylomia viminalis*		X	
Invertebrate	*Caradrina morpheus*		X	
Invertebrate	*Carterocephalus palaemon*			X
Invertebrate	*Chiasmia clathrata*		X	
Invertebrate	*Chrysura hirsuta*			
Invertebrate	*Cossus cossus*		X	
Invertebrate	*Cupido minimus*			X
Invertebrate	*Diarsia rubi*		X	
Invertebrate	*Diloba caeruleocephala*			
Invertebrate	*Ennomos erosaria*		X	
Invertebrate	*Ennomos quercinaria*		X	
Invertebrate	*Epione vespertaria*			
Invertebrate	*Erynnis tages*			X
Invertebrate	*Eugnorisma glareosa*		X	
Invertebrate	*Euxoa nigricans*		X	
Invertebrate	*Formica exsecta*			X

Species group	Species	Approach to constrain species predicted distribution[1]		
		Bioclimatic envelope (source)[2]		MCP range[3]
		Ellis	**Pearce-Higgins**	
Invertebrate	*Formicoxenus nitidulus*			X
Invertebrate	*Graphiphora augur*		X	
Invertebrate	*Hammerschmidtia ferruginea*			X
Invertebrate	*Hoplodrina blanda*		X	
Invertebrate	*Lipsothrix ecucullata*			X
Invertebrate	*Lipsothrix errans*			X
Invertebrate	*Lochaea ragnari*			
Invertebrate	*Lycia hirtaria*		X	
Invertebrate	*Melanchra pisi*		X	
Invertebrate	*Monocephalus castaneipes*		X	
Invertebrate	*Mythimna comma*		X	
Invertebrate	*Notioscopus sarcinatus*		X	
Invertebrate	*Orthosia gracilis*		X	
Invertebrate	*Osmia uncinata*			X
Invertebrate	*Philodromus margariatus*			X
Invertebrate	*Rheumaptera hastata*			X
Invertebrate	*Saaristoa firma*		X	
Invertebrate	*Scotopteryx chenopodiata*		X	
Invertebrate	*Spilosoma luteum*		X	
Invertebrate	*Trichopteryx polycommata*		X	
Invertebrate	*Xanthia icteritia*		X	
Invertebrate	*Xanthorhoe ferrugata*			X
Invertebrate	*Xestia castenea*			X
Invertebrate	*Xylena exsoleta*		X	
Lower plant	*Acrobolbus wilsonii*			X
Lower plant	*Anaptychia ciliaris subsp. ciliaris*	X		
Lower plant	*Anomodon longifolius*			X
Lower plant	*Arthonia atlantica*			
Lower plant	*Arthonia cohabitans*			
Lower plant	*Arthonia invadens*			
Lower plant	*Arthonia patellulata*			X
Lower plant	*Arthothelium dictyosporum*			X
Lower plant	*Arthothelium macounii*			X
Lower plant	*Bacidia circumspecta*			X
Lower plant	*Bacidia incompta*	X		
Lower plant	*Bacidia subincompta*			X
Lower plant	*Biatoridium monasteriense*			
Lower plant	*Bryoria furcellata*			X
Lower plant	*Buellia violaceofusca*			X
Lower plant	*Buxbaumia viridis*			X
Lower plant	*Caloplaca ahtii*			X
Lower plant	*Caloplaca flavorubescens*			X
Lower plant	*Caloplaca lucifuga*			
Lower plant	*Caloplaca luteoalba*			X
Lower plant	*Catapyrenium psoromoides*			
Lower plant	*Catillaria alba*			
Lower plant	*Chaenotheca gracilenta*			
Lower plant	*Chaenotheca laevigata*			
Lower plant	*Cladonia botrytes*			X
Lower plant	*Collema fasciculare*	X		
Lower plant	*Collema fragrans*			
Lower plant	*Diplotomma pharcidium*			
Lower plant	*Dumortiera hirsuta*		X	

Species group	Species	Approach to constrain species predicted distribution[1]		
		Bioclimatic envelope (source)[2]		MCP range[3]
		Ellis	**Pearce-Higgins**	
Lower plant	*Fuscopannaria sampaiana*	X		
Lower plant	*Gomphillus calycioides*	X		
Lower plant	*Graphis alboscripta*			X
Lower plant	*Gyalecta ulmi*			X
Lower plant	*Habrodon perpusillus*			
Lower plant	*Homomallium incurvatum*			
Lower plant	*Jungermannia leiantha*			
Lower plant	*Lecania chlorotiza*	X		
Lower plant	*Lecanographa amylacea*	X		
Lower plant	*Lecanora cinereofusca*			X
Lower plant	*Lecanora quercicola*			
Lower plant	*Lecidea erythrophaea*			X
Lower plant	*Lejeunea mandonii*			
Lower plant	*Leptogium cochleatum*			X
Lower plant	*Leptogium hibernicum*			X
Lower plant	*Leptogium saturninum*			X
Lower plant	*Megalospora tuberculosa*	X		
Lower plant	*Melanelia subargentifera*			
Lower plant	*Orthodontium gracile*			
Lower plant	*Orthotrichum gymnostomum*			
Lower plant	*Orthotrichum obtusifolium*			X
Lower plant	*Orthotrichum pumilum*			
Lower plant	*Pallavicinia lyellii*		X	
Lower plant	*Parmeliella testacea*	X		
Lower plant	*Peltigera malacea*			X
Lower plant	*Pertusaria velata*			
Lower plant	*Polychidium dendriscum*			X
Lower plant	*Porina hibernica*	X		
Lower plant	*Pseudocyphellaria intricata*	X		
Lower plant	*Pseudocyphellaria norvegica*	X		
Lower plant	*Pyrenula dermatodes*			
Lower plant	*Radula carringtonii*			X
Lower plant	*Ramonia chrysophaea*	X		
Lower plant	*Ramonia dictyospora*			
Lower plant	*Rinodina isidioides*			X
Lower plant	*Schismatomma graphidioides*			X
Lower plant	*Sclerophora pallida*			X
Lower plant	*Usnea florida*	X		
Lower plant	*Wadeana dendrographa*	X		
Lower plant	*Wadeana minuta*			X
Mammal	*Erinaceus europaeus*			X
Mammal	*Felis silvestris*			X
Mammal	*Lutra lutra*			X
Mammal	*Martes martes*			X
Mammal	*Nyctalus noctula*			X
Mammal	*Pipistrellus pygmaeus*			X
Mammal	*Plecotus auritus*			X
Mammal	*Sciurus vulgaris*			X
Vascular plant	*Cephalanthera longifolia*			X
Vascular plant	*Crepis mollis*			X
Vascular plant	*Juniperus communis*		X	
Vascular plant	*Linnaea borealis*			X
Vascular plant	*Melampyrum sylvaticum*			X

Species group	**Species**	**Approach to constrain species predicted distribution[1]**		
		Bioclimatic envelope (source)[2]		**MCP range[3]**
		Ellis	**Pearce-Higgins**	
Vascular plant	*Moneses uniflora*			X
Vascular plant	*Monotropa hypopitys*			
Vascular plant	*Polygonatum verticillatum*			X
Vascular plant	*Sorbus arranensis*			X
Vascular plant	*Sorbus pseudofennica*			
Fungi	*Bankera fuligineoalba*			X
Fungi	*Hydnellum aurantiacum*			X
Fungi	*Hydnellum caeruleum*			X
Fungi	*Hydnellum concrescens*			X
Fungi	*Hydnellum ferrugineum*			X
Fungi	*Hydnellum peckii*			X
Fungi	*Hydnellum scrobiculatum*			X
Fungi	*Hydnellum spongiosipes*			
Fungi	*Hypocreopsis rhododendri*			X
Fungi	*Phellodon confluens*			X
Fungi	*Phellodon melaleucus*			X
Fungi	*Phellodon niger*			X
Fungi	*Phellodon tomentosus*			X
Fungi	*Phylloporus pelletieri*			
Fungi	*Piptoporus quercinus*			
Fungi	*Sarcodon glaucopus*			X
Fungi	*Sarcodon scabrosus*			X
Fungi	*Sarcodon squamosus*			
Fungi	*Stropharia hornemannii*			
Fungi	*Tricholoma colossus*			
Fungi	*Tricholoma robustum*			

[1] Where data were available, modelled current bioclimatic envelopes or Minimum Convex Polygons (MCPs) around species record locations were used to restrict the patches predicted to be suitable by the N4S tool. We applied the Ellis et al. (2014) envelopes in preference to the Pearce-Higgins et al. (2015) envelopes and either of these in preference to the MCPs. Where data were unavailable no restriction was applied for that species' range.

[2] Bioclimatic Envelopes: when applying the bioclimatic envelopes developed by Ellis et al. (2014) we used the 'maximum training sensitivity plus specificity' threshold a fixed threshold. As this detail was not available for the Pearce-Higgins et al. (2015) data, we chose a fixed threshold of 0.7 to determine predicted suitable bioclimatic zones from the continuous logistic probability data.

[3] Minimum Convex Polygons: species records were extracted at the 10 km square resolution from the UK national archive of biodiversity monitoring data (the National Biodiversity Network Gateway https://nbnatlas.org/). Minimum Convex Polygons (MCPs) were drawn around squares where three or more squares were adjacent to one another (isolated single or paired presence squares were excluded). All records were used with no date restriction applied.

Chapter Eight: An evaluation of thinning to improve habitat for capercaillie (*Tetrao urogallus*)

An adapted version of this chapter has been published as:

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Contributions: CPQ designed the survey. AB and TC carried out data analysis. AB wrote the manuscript, and TC and CPQ commented on an earlier draft.

8.1 Abstract

In Scots pine (*Pinus sylvestris*) forests the composition of the ground flora can be affected by the amount of light reaching the forest floor, influencing the balance between the three common ericaceous shrubs bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*). A pinewood ground flora with more than 20% bilberry cover is considered good habitat for capercaillie (*Tetrao urogallus*), a large forest grouse of considerable conservation interest throughout Europe. Old, semi-natural Scots pine woodland is considered its prime habitat in Scotland, although this is limited in area compared to twentieth century planted forests. Action to manipulate environmental conditions within Scots pine plantations by altering light levels to favour bilberry through thinning and felling could potentially increase greatly the area of available capercaillie habitat in Scotland.we implemented a five year study to look at bilberry response to variable intensity thinning in two Scots pine plantations, where thinning followed management guidance for capercaillie available at the time. Bilberry was present in both forests but a positive response to thinning was not universal; although at both sites, bilberry cover increased significantly over five years with levels >20% cover reached, this could only be attributed to the thinning treatment at one of the sites. A treatment of small patch clearfelling did not lead to losses in bilberry. Management guidance published after the trial had begun, identified the appropriate intensity of thinning for enhancing bilberry cover at our study sites, indicated by the relative increase of bilberry in the plots where the prescription had been followed. Although there was no significant treatment effect by year five, 42% average bilberry cover was reached at one site tested. However the format of this guidance, a range of stem density-tree height combinations, was difficult to apply using typical forest management data and we explore redefining the guidance as a post thinning stand basal area range.We suggest >22 to <31 $m^2 ha^{-1}$ basal area would be appropriate in Scots pine plantations established at normal spacing and subject to the commonest form of selective thinning regime. This range in basal area can be achieved without conflicting with management for timber production. Our results also support small patch clearfelling as a method of diversifying plantation age structure which is compatible with maintaining capercaillie brood habitat.

8.2 Introduction

Capercaillie (*Tetrao urogallus*) is a bird of boreal and temperate forests of north and central Asia and Europe, but its range has greatly reduced in western and central Europe as a result of many local extinctions (Storch, 2001; Watson and Moss, 2008). Conservation concerns prompted by these declines have resulted in capercaillie being included in Annex I, II(B) and III(B) of the EC Birds Directive (Directive 2009/147/EC). In addition, under the EC Birds and EC Habitats Directive (Directive 92/43/EEC), capercaillie is a specific designated feature of many of the Natura 2000 sites, and large parts of the capercaillie range within the EU countries of central and western Europe are covered by Natura 2000 designated sites. The responsibility for protecting the interests of these sites is shared between different authorities, including state forest agencies who have implemented policy changes to integrate forestry practices with capercaillie habitat requirements as a key conservation measure (Eurosite, 2007; Storch, 2007, 2001; The Scottish Government, 2012). In the UK, capercaillie became extinct in the eighteenth century but was re-introduced successfully during the first half of the twentieth century. However, having suffered declines in the last 25 years, the capercaillie population is now limited to certain areas of Scotland (Eaton et al., 2007; Wilkinson et al., 2002), with the most recent population estimate of 1285 (95% CI: 822–1882) individuals (Ewing et al., 2012). Old, semi-natural Scots pine woodland has been considered the prime habitat of capercaillie in Scotland and contain the highest densities of birds (e.g. Picozzi et al., 1992) although this could be confounded by the higher probability of detecting birds in native pinewoods compared to plantation woodlands (Ewing et al., 2012). Recent surveys confirm conifer plantations, especially Scots pine, can support capercaillie populations (Petty, 2000; Eaton et al., 2007). Semi-natural Scots pine woodlands in Scotland cover less than 20 thousand hectares (FC, 1999) but Scots pine plantations potentially offer at least five times more area of habitat (Mason et al., 2004). Extensive new plantings of Scots pine woodland have occurred in the last 20 years in Scotland (FC, 2013, 2002; Anon, 2002) and these provide large opportunities for capercaillie habitats in the future. An important way of halting species decline in Britain is foreseen by enhancement of capercaillie productivity (Caledonian Partnership, 2002) and specific actions have been taken including improvements to the condition and extent of brood habitat to achieve this (Moss et al., 2000; Storch, 2001). Woodlands provide a number of habitat factors required by capercaillie. For habitats used in winter, for example, structural and compositional features such as the presence of pine and spruce trees and solitary, branched trees have been shown to be important (Gjerde, 1991a; Storch, 2001; Bollmann et al., 2005). Whereas a good spring and summer habitat, providing both cover and food for capercaillie adults and broods, is considered to be a wood with a developed ground flora that is rich in bilberry (*Vaccinium myrtillus*) (Picozzi et al., 1999; Storch, 2001, 1993). Chicks in their first 3–4 weeks are almost entirely dependent on invertebrates; in Scotland primarily Lepidoptera larvae but also ants, spiders and beetles (Picozzi et al., 1999). Later, the birds feed on the leaves and berries of bilberry (Summers et al., 2004; Spidø and Steun, 1988). The extent of cover of bilberry has been shown to be positively correlated with the biomass of invertebrates (Lakka and Kouki, 2009; Summers et al., 2004) and positively related to breeding success of capercaille (Baines et al., 2004). Recent work by Hancock et al. (2011) found that management which increased bilberry cover led to more capercaillie usage and more chick food.

Ground vegetation is strongly influenced by the canopy, which in turn affects the levels of usually several different site resources governing composition of the ground flora (Wagner et al., 2011). However, previous studies suggest that within woodlands on the same, poor and acidic soil type e.g. pinewoods, the balance of the ericoid species including bilberry and shade tolerant grasses such as wavy hair-grass (*Deschampsia flexuosa*), is controlled primarily by the availability of light (Humphrey, 1996; Hester et al., 1991). However, herbivores also influence bilberry cover and depending on the context, have been shown to have positive (Hancock et al., 2010) or negative effects (Welch, 1998). Action to manipulate environmental conditions within plantations offers the potential for increasing brood habitat in particular by altering light levels to favour bilberry (Kortland, 2006). The relationship between stand structure and ground flora composition has been described from space-for-time substitution studies (multiple sites of different ages studied in same year) in seminatural Scots pine woods and plantations of other conifer species (Picozzi et al., 1992) and a guide to quantify capercaillie habitat and determine appropriate stand management (target stem density per hectare and tree height) has been produced for Scotland (Moss and Picozzi, 1994). Parlane et al. (2006) reported findings relating bilberry cover to canopy light transmittance in Scots pine stands in guidance published subsequent to the commencement of our trial. However, as both these studies were correlative and focussed on management to benefit capercaillie, application of the resulting conservation guidance to management of Scots pine plantations is restricted in two ways. Firstly, there is the issue of the transferability of the relationships to stands of different origin, structure and stand history and whether the recommended practice is indeed effective. This can be addressed by testing experimentally whether correlations found in these earlier studies reflect a causal link, as our work described in this paper has attempted to do. Secondly, stand management rarely occurs solely to deliver capercaillie habitat, and habitat management may need to be achieved by modifying operations primarily conducted for other reasons such as timber production. Regular thinning is recommended to maximise timber production (Rollinson, 1988) and timber quality of Scots pine plantations (MacDonald et al., 2010a) following prescriptions given in yield models for forest management (Edwards and Christie, 1981; Matthews, 2008). However, as indicated in the National Inventory of Woodlands and Trees 1995–1999 (Quine et al., 2007; J Gilbert pers comm., 2007), between 55% and 80% of the plantation forests in Scotland remain unthinned possibly due to the low value of the produce in early thinnings and the net cost of the operations (Mason, 2007). Forest management is influenced by timber prices, with more money for forestry activities being available when the timber prices are high (Mason (2007). Timber prices showed a 70% decline between 1995 and 2003 with a varying amount of recovery since 2006 (IPD, 2004, 2011). In contrast, management recommendations for capercaillie conservation, including glade creation and thinning within plantation woodlands (Moss and Picozzi, 1994; The Capercaillie LIFE Project, 2004) could result in overcutting and early, intensive thinning, with the associated losses in volume production (Rollinson, 1988) and impacts on the timber quality (Ikonen et al., 2009; MacDonald et al., 2010b; Mäkinen and Isomäki, 2004). Providing appropriate guidance and incentives for forest management in capercaillie areas in Britain which can balance timber production and conservation objectives is therefore a recognised need. In 2002, EU funding was available to encourage forest management interventions to improve capercaillie habitat in pinewoods in the oceanic boreal region (The Capercaillie LIFE Project, 2004). This paper reports on the success of the stand thinning measures (and specifically variable intensity thinning and small glade creation) in improving spring and summer habitat quality for capercaillie broods and adults. These measures were assessed in a designed study. The main aims of this study were:

1. To test whether the cover of bilberry increased in response to variable intensity thinning and small patch clearfelling.

2. To assess the applicability of two different sets of current conservation management guidance (Moss and Picozzi (1994) and Parlane et al. (2006)) to Scots pine plantation management, and thereby strengthen the evidence base for this conservation measure (Sutherland, 2006).

8.3. Methods

8.3.1 Study sites

Study sites were located in two forests (Inshriach and Novar) in northern Scotland, in areas identified during the EU LIFE Nature project as typical Scots pine plantations requiring thinning to improve brood habitat (Kortland, pers. comm.). The sites have a similar climate, experiencing around 900 day-degrees above 5 °C and a summer and winter rainfall of 400 and 550 mm, respectively (Pyatt et al., 2001). Mean (minimum and maximum) temperatures are 0.0 °C and 5.2 °C in January and 9.4 °C and 16.1 °C in July (Met Office, 2013). Both sites have similar podzolic soils. (Table 8.1). Iron and humus-iron podzols are the main soil type associated with pinewoods in the oceanic boreal region (Wilson and Puri, 2001; Godbold and Lukac, 2011).

The plantations at the Inshriach and Novar sites were established in the early 1960s. At the start of the study the stands were stocked to a similar density, with trees of similar average girth (Table 8.1). The management history of these two sites was however different. Inshriach Forest is managed by the government forestry agency, the Forestry Commission, and had already received its first thinning. Novar Estate is a privately owned estate; at the commencement of study the stand had not yet been thinned and no previous crop records were available. Although the composition of ground vegetation was similar and bilberry occurred frequently at both sites (Table 8.1), at the start of the study, Inshriach had a higher cover of bilberry (just under 20% cover) compared to Novar (less than 10% cover). Mostly roe deer (*Capreolus capreolus*) but also red deer (*Cervus elaphus*) are present at both sites.

Table 8.1 Summary of site and stand information for the two study sites (Inshriach and Novar).

Study site	Inshriach	Novar
Location	Strathspey, Highland, Scotland 57°7'N, 3°51'W	Easter Ross, Highland, Scotland 57°46'N, 4°27'W
Study site area	50 ha	30 ha
Aspect	NW	W-SW
Slope	4.5°	12.5°
Planting year of Scots pine stand	1961	1962
Average stem density	1700 stems ha^{-1}	1600 stems ha^{-1}
Average diameter at breast height (1.3m)	16 cm	18 cm
Estimated yield class[a] (Site index[b])	6-8 (18-25)	8 (22-25)
Soil type [c] Typical profile [d] pH (H20) (1:2.5) [e] A Horizon: average (min – max) B Horizon: average (min - max)	Podzol O 0 - 3cm 0 - 3cm Ah 3 - 7cm 3 - 7cm E 7 - 20cm 7 - 20cm Bhs 20 - 60+cm 20 – 60+ Stones and Gravel 50% 4.26 (3.75 - 4.78) 4.89 (4.45 - 5.16)	Podzol O 0 - 6cm Ah 6 - 12cm E 12 - 25cm B(g)hs 25 - 50cm Bx 50cm + Stones 20% 4.27 (4.08 - 4.37) 4.9 (4.77 - 5.01)
Ground flora- vascular plant species of frequent occurrence (average %cover)	Bilberry *Vaccinium myrtillus* (18%) Wavy hair-grass *Deschampsia flexuosa* (40%) Cowberry *V. vitis-idaea* (6%) Heather *Calluna vulgaris* (6%)	Bilberry (6%) Wavy hair-grass (40%)
Ground flora- moss species of frequent occurrence	Glittering wood-moss (*Hylocomium splendens*) Red-stemmed feather-moss (*Pleurozium schreberi*)	Glittering wood-moss, Red-stemmed feather-moss, Waved silk-moss (*Plagiothecium undulatum*)

[a] Estimated yield class follows Edwards and Christie (1981). [b] Site index after Hägglund and Lundmark (1977). [c] Classification according to the standard Forestry Commission scheme (Pyatt and Suarez, 1997). [d] Horizon nomenclature follows Avery (1990).

[e] pH was measured using a glass-electrode meter in a 1:2.5 w/v suspension of soil in de-ionised water.

During the course of the study (2002–2007), both sites experienced a wet growing season in 2007 but below average rainfall in 2003 and 2006; temperatures were above average for both sites with the growing season of 2003 being particularly warm (Met Office, 2010; Stathspey Weather, 2010).

8.3.2 Thinning treatments

Thinning treatments were designed and applied with the aim of enhancing the habitat for capercaillie. In line with the established guidance for enhancing bilberry cover (Moss and Picozzi, 1994), the proposed variable thinning treatment was intended to be conducted at normal to twice the normal thinning intensity suggested in yield models for Scots pine (Edwards and Christie, 1981). A patch clearfell treatment was included at Inschriach, consistent with recommendations for glade creation favourable for broods, and a no thin control was included at both sites.

At Inshriach, the original study layout was seven randomised blocks of four 50 m x 50 m plots. Four treatments (Control, Normal Thin, Double Thin and clearfell) were randomly allocated to plots within a block. However, application of the treatments in the course of normal harvesting operations did not maintain a consistent separation between thinning intensities and so both were amalgamated into one Variable Thin treatment for analysis purposes; in one block a proposed thinning was not carried out on one plot. The final layout comprised 28 plots (six blocks with one Control plot, one clearfell plot and two Variable Thin plots, and one block with two Control plots, one clearfell plot and one Variable Thin plot) (Figure 8.1).

At Novar the study was laid out on a site that had been very recently thinned to benefit capercaillie habitat under the auspices of the LIFE project. The operations aimed to create a variable thinned woodland by alternating strips of variable thinning with non-thinned areas; the strips were arranged systematically along a forest road and not with respect to existing site conditions. The clearfell treatment was not applied at Novar in order to maintain timber production potential for the owner. Eight 50 m x 50 m plots were randomly allocated to the thinned and non-thinned areas, to establish four plots with a Control treatment and four with a Variable Thin treatment (Figure 8.1).

Thinning and felling was carried out mechanically by a wheeled harvesting machine, access routes or racks were cut in the forest and trees were removed from the plots by the harvester stationed on the racks; the harvester therefore did not enter and impact on the ground conditions of the plot. The thinning residues (branches and foliage from the felled trees) were removed from the plots. These were used in the construction of brash mats in the racks for the harvester to move over, thereby protecting the soil from compaction and erosion.

For both sites, pre and post thinning basal area (m^2 ha^{-1}) and stem density (stems ha^{-1}) in each plot was measured shortly following intervention from cut stumps and standing trees; stem taper was assessed in each plot to allow conversion of cut stump diameter to diameter at 1.3 m (conventionally used to calculate basal area) (Matthews and Mackie, 2006). Measures of stand top height (m), consistent with the methods of Matthews and Mackie, 2006, had been taken by the site managers prior to thinning at Inshriach only.

8.3.3 Measuring herbivore effects

Bilberry responses to thinning could be confounded by grazing by herbivores. In an attempt to separate grazing from thinning effects, one of the vegetation assessment quadrats was protected from herbivores (see Section 8.3.4.). As a further measure, presence of dung of a range of herbivores (roe deer, red deer, sheep (*Ovis aries*) and rabbit (*Oryctolagus cuniculus*)) (MacDonald and Barrett, 2005) was assessed annually in each of the circular quadrats (see Section 8.3.4). At the same time, any droppings of capercallie were also recorded. However, too few records of herbivore dung or capercaillie droppings were collected during the trial for analysis.

Figure 8.1 Plan of study sites with locations of 50 m x 50 m treatment plots (above) Inshriach site with each plot labelled by block number (1 to 7) and treatment (1 = Control, 2 = Variable Thin (planned to be at normal thinning intensity), 3 = Variable Thin (planned to be at twice normal thinning intensity), 4 = clearfell); (below) Novar site with plots labelled by treatment (1 = Control, 2 = Variable Thin), no blocking was applied.

8.3.4 Vegetation assessments

At both sites, the vegetation assessments followed the same split plot design; each 50 m x 50 m plot contained five, 2 m x 2 m square (vegetation assessment) quadrats, one of which was caged against herbivores. Each square quadrat was positioned at the centre of a circular quadrat (5.6 m radius) used for assessment of stand basal area (Matthews and Mackie, 2006) (see Figure 8.2). Pre-thinning baseline ground vegetation assessments were made within the same year (growing season) that the thinning was applied (July 2003 (year 1) at Inshriach and September 2003 at Novar) and at the end of the next four growing seasons (September to October) in 2004 (year 2), 2005 (year 3), 2006 (year 4) and 2007 (year 5). Two sets of recorders were used for the duration of the trial, the first assessed both sites in year one and two, and the second both sites for the remainder of the study. All observers were trained to the same standard prior to taking part in the study. Bilberry was in leaf at each assessment time. Although levels of defoliation by caterpillars can vary from year to year (Atlegrim and Sjoberg, 1995; Hancock, 2011), we assumed these were similar in areas under different treatments. Percentage cover of all ground and moss layer vegetation species, with cover of greater than five percent, was recorded and cover was estimated to the nearest 5%. The cover of species occurring in different layers within the vegetation was assessed separately giving a total cover value for the quadrat; this value could therefore exceed 100%.

8.3.5 Data analysis

Bilberry response to treatments

We used SAS version 9.3 for statistical analysis (SAS Inst., 2000). We tested the response of bilberry (absolute% cover values) to treatment, caging, year and their interactions in a repeated measures analysis of variance (ANOVA rm), using a linear mixed effects model, REML (Patterson and Thompson, 1971), to incorporate the random block, plot, and quadrat effects and fixed treatment effects (treatment, caging and year) and to allow for any imbalance in design, as appropriate. Covariance structures were described using an autoregressive function which assumes decay in correlation with increasing separation between measurements (i.e. time). Data were analysed at the quadrat (sub-plot) level to utilise the split plot design i.e. to include analysis of treatment, caging and their interaction. Examination of residuals suggested no data transformation was required.

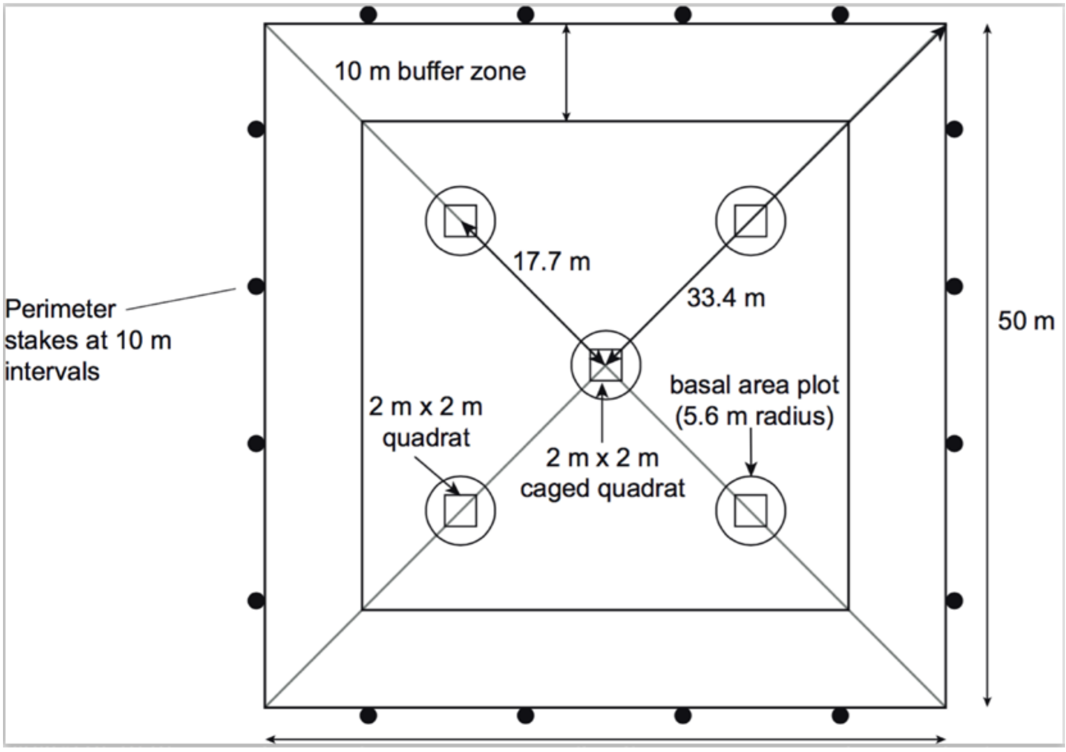

Figure 8.2 Plot layout used at both study sites (Inshriach and Novar) showing area thinned/clearfelled (for treatment plots) or left unthinned (for control plots), and locations of basal area (round) and vegetation (square) assessment quadrats.

Comparison of response with expectations based on existing guidance

In order to test the suitability of existing guidance, we contrasted our measurements with the published management guidance of Moss and Picozzi (1994) and Parlane et al. (2006). We determined the expected response by locating our stands within the guidance frameworks using stand measurements and published yield models. We made two comparisons:

i. To hypothesise whether the basal area and stand conditions of the study sites would be suitably changed by thinning to create the conditions to encourage bilberry cover, [Hypothesised response]. This comparison was carried out in order to assess whether the thinning regime used at the study sites followed that given in the published management guidance and to indicate whether the management guidance was suitable for use in plantation situations.

ii. To determine whether at the end of the trial the change in bilberry cover at our study sites over the trial period was better where prescriptions from the guidance had been followed given the post thinning stand conditions (stem density and tree height), [End comparisons].

For the ‘Hypothesised response’ we plotted the stem densities and stand heights at the intervention times in a model Scots pine plantation of the same Yield Classes (YCs) as our study sites. We compared the guide stem densities and tree heights considered to benefit bilberry given by Moss and Picozzi (1994) and Parlane et al. (2006) and our trial stands according to the stem densities we planned to create following a thinning intervention of between normal and twice normal thinning intensity.

For the ‘End’ comparison we compared stem density and tree height data for each plot to those given in the thinning guidelines proposed by Moss and Picozzi (1994); Fig. 4, page 11) and by Parlane et al., (2006; Fig. 2, page 277). This could be completed reliably for the plots at Inshriach, as only here the assessment of tree height had followed appropriate methods (Matthews and Mackie, 2006). For Inshriach data, we allocated plots to three treatments according to whether they had been thinned to prescription (T), had received ‘other’ thinning treatments (O) by either being under-thinned (post thinning stem density greater than that prescribed) or over thinned, this later category included clearfelling of plots, or were unthinned control plots (C). We analysed the response of bilberry to the three treatments over the five years of the study, following the method described in Section 8.3.5.

As a further comparison with the management recommendations of Parlane et al. (2006), we derived the stand basal area (in m^2 ha^{-1}) associated with the prescribed stem density and tree heights in two ways. Firstly, using the canopy transmittance (the proportion of incident radiation that is transmitted through the canopy) equation (Parlane et al., 2006) and the relationship between canopy transmittance and stand basal area (in m^2 ha^{-1}) derived for Scots pine stands (Hale et al., 2009). Secondly, using the yield models for Scots pine for stands established at normal (2 m) initial spacing and subject to the commonest type of selective thinning (‘intermediate’ thinning) (Matthews, 2008), and of Yield Class

4–14. This range of Yield Class represents the variation in growth rates which can be sustained by Scots pine stands within the distribution range of capercaillie in Scotland (FC, 2011c) on sites where the soil fertility is suitable for bilberry growth (MacDonald et al., unpublished).

8.4 Results

8.4.1 Bilberry response to thinning treatments

At the start of the trial before the thinning, basal area within the different treatment plots were similar between the two sites except for the clearfell (CFELL) treatment at Inshriach where the pre-thinning basal area was lower (mean of 27 m^2 ha^{-1}) (Table 8.2). Thinning reduced the basal area below that of the control in all treatments. The mean post-thinning basal areas in the variably thinned were similar at both sites and the transmittance, as derived from the basal area measurements (Hale et al., 2009), was 0.35 at Novar and 0.33 at Inshriach (Table 8.2).

The change in bilberry cover over time was generally positive. The cover of bilberry increased over the five years at both of the study sites but the influence of thinning treatment was only apparent at one site (Novar). At Inshriach, the only significant effect was that of year (ANOVA rm, $F_{4,474} = 16.45$, $P < 0.0001$) with mean %cover of bilberry increasing from 16% in year one to 32% in year five (Figure 8.3a). At Novar, the increase in bilberry cover was larger in the variably thinned plots than the control plots (treatment*year, ANOVA rm, $F_{4,140} = 4.54$, $P = 0.0018$), resulting in a mean %cover of bilberry of 24% in the variably thinned plots and 5% in the control plots by year five (Figure 8.3b). Year effect was significant (ANOVA rm, $F_{4,140} = 8.65$, $P < 0.0001$) but treatment effect alone was not. There was no effect of caging on bilberry cover at either site.

The clearfell treatment was only applied at Inshriach. A reduction in bilberry cover in response to clearfell treatment was not shown by the results (Figure 8.3a) as no significant treatment effect (or treatment*year effect) was detected. The response of bilberry cover to clearfell treatment was therefore not different from that seen in the Control or the Variable Thin treatment.

8.4.2 Comparison with conservation management thinning guidance

‘Hypothesised response’

It appeared that the thinning regime applied at the study sites would match Moss and Picozzi (1994) management guidance but only partially follow Parlane et al. (2006) guidance. We forecast (i) a response likely to result in the bilberry cover given by Moss and Picozzi (1994) in all plots at Inshriach (Figure 8.4a) and all but the more lightly thinned plots at Novar (on the basis that Novar is represented by a YC8 stand subject to a 10 year delay to first thinning) (Figure 8.4b) and (ii) based on Parlane et al. (2006) guidance, the creation of conditions optimal for bilberry in the plots subject to normal thinning at Inshriach in the more productive compartments (YC8- second intermediate thinning) (Figure 8.4a), and in the plots most intensively thinned at Novar (Figure 8.4b).

Table 8.2 Mean values (S.E.) for measures of stand variables within the plots at the two study sites before and after thinnin treatments (control (CTRL), variable thin (VT), clearfell (CFELL)).

		Inshriach			Novar	
		CTRL	VTHIN	CFELL	CTRL	VTHIN
Pre-thinning	Basal area average (m^2 ha^{-1})	35 (2.0)	37 (1.0)	27 (1.0)	39 (3.6)	35 (1.8)
	Transmittance[a]	0.28 (0.02)	0.26 (0.01)	0.35 (0.01)	0.25 (0.03)	0.28 (0.02)
Post-thinning	Basal area average (m^2 ha^{-1})	35 (2.0)	29 (0.9)	0	39 (3.6)	27 (1.6)
	Transmittance[a]	0.28 (0.02)	0.33 (0.01)	0.78	0.25 (0.03)	0.35 (0.02)
	Post thin stem density average(stems ha^{-1})	1673 (203)	1089 (74)	0	1690 (123)	920 (41)

[a] derived from basal area measurements using transmittance and stand basal area relationship (Hale et al., 2009).

‘End’ comparisons For Inshriach, on the basis of the Moss and Picozzi (1994) management guidelines, all but two of the 13 variably thinned plots were classed as having been thinned to prescription (T), the remaining variably thinned and the seven clearfell plots were classed as other thinning (O). Following Parlane et al. (2006) guidelines, six of the variably thinned plots at Inshriach were classed as thinned to prescription (T), with all remaining thinned and clearfelled plots being classed as ‘other’ thinning.

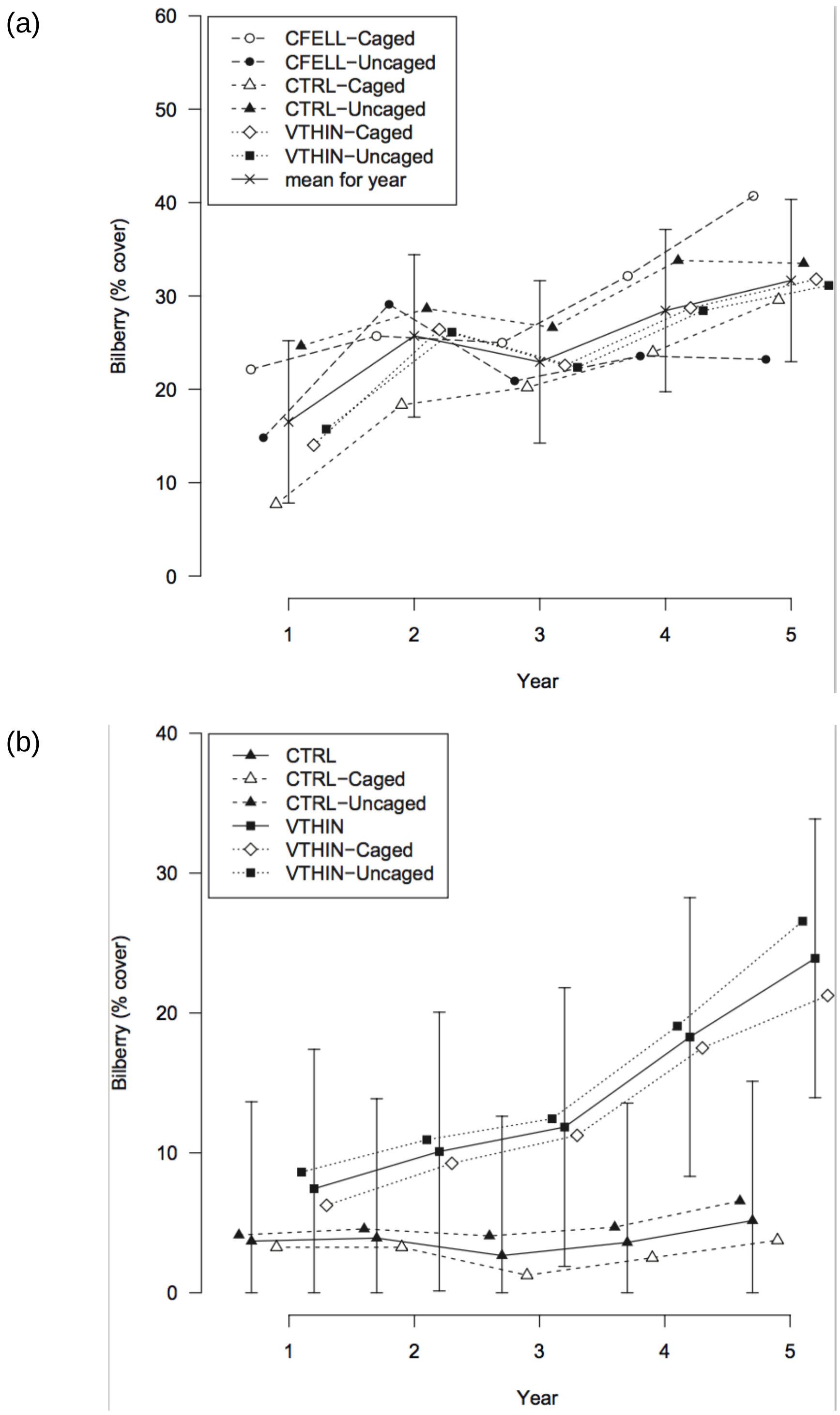

Figure 8.3 Bilberry response to variable intensity thinning (VTHIN), to clearfell treatment (CFELL) (one site) and to control (CTRL), with and without caging, at two sites: (a) Inshriach and (b) Novar. Data points for the same year have been offset for ease of viewing.

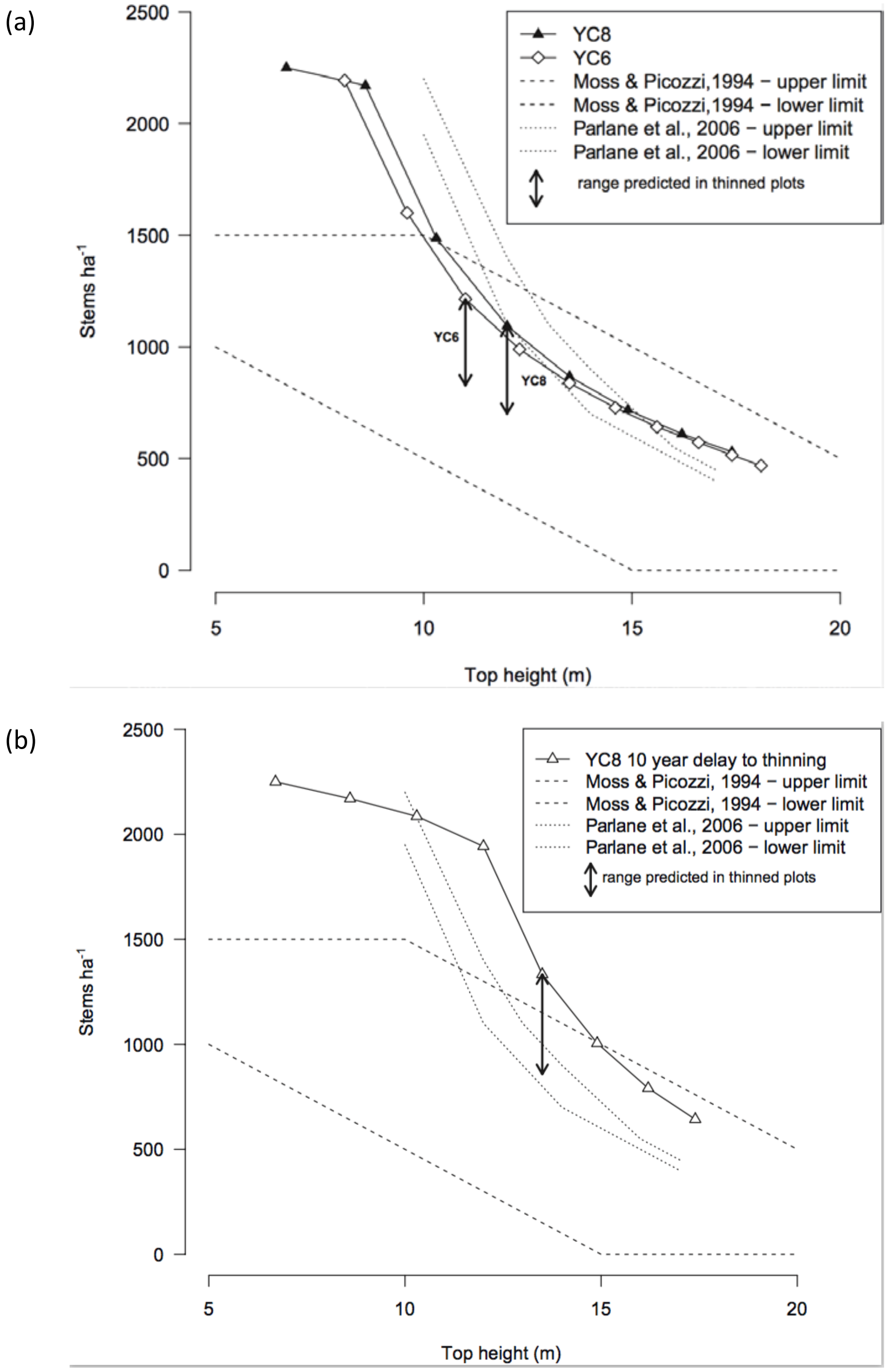

Figure 8.4 Stem density and tree heights in a model Scots pine plantation of Yield Class 8 and Yield Class 6, established at 2 m spacing and subject to intermediate thinning treatments; ranges suitable for bilberry (after Moss and Picozzi (1994) and Parlane et al. (2006)) with predicted effects on stem density of normal and twice normal intensity thinning at (a) second thinning as at Inshriach and (b) delayed (by 10 years) thinning as at Novar.

The ANOVA rm analysis of bilberry cover in the three treatments (T, O, C) over five years showed that whilst treatments diverged significantly over time (treatment*year, ANOVA rm, $F_{8,476} = 3.03$, $P = 0.0025$) with prescription thinning (according to Parlane et al. (2006)) tending to give a rising mean value of bilberry cover compared to other treatments, the final year means did not differ significantly between treatment (treatment ANOVA rm, $F_{2,20.6} = 0.57$, $P = 0.5745$), although treatment T had the highest predicted cover of bilberry (42%) (Figure 8.5). There was also a significant year affect (ANOVA rm, $F_{4,476} = 16.89$, $P < 0.0001$). For plots thinned according to the Moss and Picozzi (1994) prescription, there was no significant treatment effect. There was no effect of caging on bilberry cover in either analysis.

Regarding stand basal areas derived from Parlane et al. (2006), a stand basal area between 23 and 26 m^2 ha^{-1} would appear to create optimal transmittance (0.37–0.33) identified for bilberry. However, according to the yield models for typical Scots pine stands, Parlane et al. (2006) prescribed stem density and tree height combinations are associated with basal areas captured in the range of between >20 and <31 m^2 ha^{-1}. ‘Typical’ model Scots pine stands are considered those established at the normal (2 m) spacing and which have been subject to the commonest type of selective thinning (‘intermediate’ thinning) regime (Matthews, 2008).

Although not formally tested, it would appear that almost all the plots at Novar were thinned in line with the Parlane et al. (2006) guidance. Further, the basal area of these plots ranged from 23 to 29 m^2 ha^{-1} (mean 27 m^2 ha^{-1}; transmittance 0.35 (Table 8.2)) close to optimal range (based on stand conditions and transmittance relationships) and within the broader range (based on stand conditions and yield models) indicated by Parlane et al. (2006). In contrast, of the 13 variably thinned plots at Inshriach (mean basal area 29 m^2 ha^{-1}; transmittance 0.33 (Table 8.2)), eight plots achieved post thinning basal areas within the broader range, with the remainder having basal areas greater than that indicated by the Parlane et al. (2006) prescription.

8.5 Discussion

8.5.1 Bilberry response to thinning and clearfell treatments in study Scots pine plantations

We confirmed that appropriate bilberry cover for capercaillie can be obtained in Scots pine plantations. The final cover values of bilberry exceed 20% in all but the Control treatment at Novar. In the context of the study, this can be regarded as a successful outcome as more than 15–20% bilberry cover is considered suitable for capercaillie breeding success (Baines et al., 2004; Storch, 1994; Summers et al., 2004). Our study provides evidence that applying variable intensity thinning to Scots pine plantations can improve capercaillie brood habitat, however, bilberry cover only responded to treatment in one but not both of the Scots pine plantations studied. Further, the results of the trial only partially support the use of the variable thinning technique as described in management guidance (Moss and Picozzi, 1994; Parlane et al., 2006), to encourage bilberry.

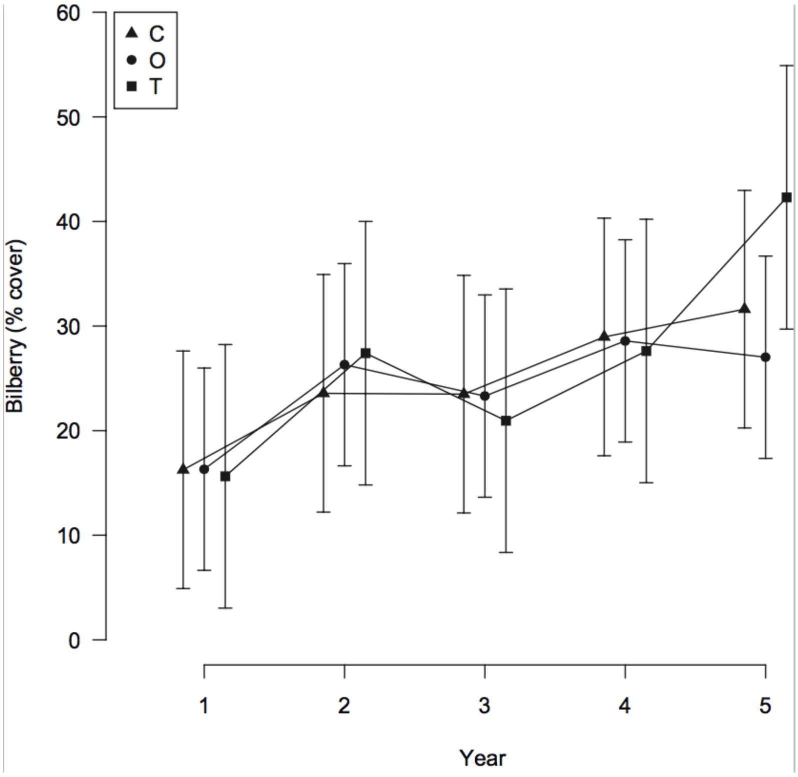

Figure 8.5 Bilberry response at Inshriach to thinning applied according to Parlane et al. (2006) prescription (T), not to prescription (O) and to control (C); predicted mean bilberry cover for treatments, with 95% confidence intervals shown. Data points for the same year have been offset for ease of viewing.

Lack of, or failure to detect treatment effects on bilberry at both sites may be due to differences between the sites and in particular their management history. Although the sites were similar in most respects, Inshriach had been thinned previously and had a higher starting cover of bilberry than Novar. Due to the similarity of the sites with respect to the soil type and in being first rotation plantations established with a monoculture of the same species, we consider that ground flora composition is following the same trajectory of change in response to canopy change at both sites (Hester et al., 1991; Hedwall et al., 2013). However, sites may be at different points along the trajectory, with Novar displaying the response to an initial thinning resulting in clearer differences in bilberry cover in the treatment compared to the control. Whereas the increase in bilberry cover we saw in the control plots at Inshriach is likely be a legacy of the previous thinning and occurring in response to these earlier modifications to the canopy structure that were no longer apparent in our measurements (Thomas et al., 1999). Reduction in bilberry in favour of other competing species may not always be expected to follow canopy regrowth (Strengbom et al., 2004). Nevertheless, we expected that further thinning would provide better conditions for bilberry than in stands where the canopy cover was already recovering and closing (Moola and Mallik, 1998). Bilberry is more abundant in boreal forests where the canopy is neither very dense nor very sparse (Kardell, 1980) and reported occurrence of bilberry under different levels of canopy transmittance in Scots pine woodlands in Scotland, indicates that a relatively narrow range of transmittance provides most favourable conditions (Parlane et al., 2006). It is possible that variable thinning resulted in a broader range of basal areas at Inshriach compared to Novar, and conditions that were too shady for bilberry were created in some of the plots masking a clear treatment response. Given the difference in the starting cover of bilberry at the two sites (average %cover of 18% at Inshriach and 6% at Novar), it may also be important to thin closer to the optimal level where bilberry cover is already high, to gain any benefit from the thinning treatment.

Small patch clearfelling did not appear to be a suitable alternative method to variable thinning, as response of bilberry cover to clearfell treatment was no better than in the Control. Clearfelling is not an intervention previously recommended for enhancing bilberry cover in Scots pine woodlands and a general decrease in bilberry cover with thinning intensity has been reported from a number of studies (Atlegrim and Sjöberg, 1996a; Bergstedt and Milberg, 2001; Crouch, 1986). Five years is a short period of study for bilberry which has been shown to be relatively slow to respond to treatments in other studies (Humphrey, 1996; Bergstedt and Milberg, 2001). This may be why we did not see the large losses in bilberry cover reported by other researchers (Kardell, 1980; Lakka and Kouki, 2009) suggesting that our small patch clearance may have had less of an impact on capercaillie brood habitat than large scale patch clearfell. Questions remain over the overall quality of the brood habitat produced in these open areas as reduced abundance of larvae, linked to the higher phenolic concentration in bilberry leaves, has been reported following clearfelling (Atlegrim and Sjöberg, 1996a,b; Lakka and Kouki, 2009; Nybakken et al., 2013).

8.5.2 Management guidance for thinning

We have concerns over the application of the current conservation management guidance to plantation management. The management recommendations based on target stem density-tree height combinations available prior to our study (i.e. Moss and Picozzi, 1994) were met in the variably thinned plots at both sites in our study and yet did not appear to define the range of stand conditions which had low enough stand density and were light enough for enhancing bilberry growth.

8.5.3 Compatibility between capercaillie brood habitat enhancement measures and other plantation management objectives

The Parlane et al. (2006) prescription would appear to be compatible with timber production objectives. In the model Scots pine stands these target basal areas were achieved from mid rotation to commercial felling age under a intermediate thinning option. Stands thinned like this therefore would conform to the thinning regime designed to maximise the cumulative volume of timber produced (Rollinson, 1988) and thus offers the possibility of combining timber production with capercaillie conservation (MacMillan and Marshall, 2004). Small patch clearfelling treatment (also considered in our study) offers an alternative method of sourcing timber when increasing intensity of stand thinning is undesirable. It might also be appropriate in managing Scots pine woodlands under shelterwood systems and in the transformation of woodlands from an even-aged to an irregular age structure. Both approaches maintain a continuity of forest cover by avoiding large scale clearfelling at the end of the rotation (Mason et al., 2004).

Clearfell gaps (less than 3 ha in size) in some situations provide the small internal habitat patches and diverse woodland structure which can be an important feature of capercaillie habitat (Gossow and Pseiner, 1981; Kortland, 2006; Watson and Moss, 2008). Further, there is evidence that capercaillie select woodland habitat adjacent to more open forest and that providing a mixture of stands of varying density could meet the range of needs of capercaillie (Gjerde, 1991a). However, more work is needed to ascertain that there are not overriding negative effects of introducing clearfell patches on capercaillie populations, for example through increased habitat fragmentation or predation pressures (King et al., 1998; Chalfoun et al., 2002).

Our work has focussed on plot level effects of thinning even aged and uniform monocultures of Scots pine and has related the resulting canopy structure (basal area) to response of bilberry. We have not attempted to consider the direct effects on capercaillie of canopy structure at the scale of the site. The dropping count data collected from the plots were too sparse to be informative. This is not surprising as capercaillie territories, particularly in plantations, are big in comparison to the plot sizes used in the trial (Kortland, pers. comm.). Other information, not recorded as part of this study, on capercaille numbers (male birds at leks close to the study sites and brood counts within the study area of Inshriach) (Bibby et al., 2000) do not provide evidence of a response to habitat improvement. Further studies designed to collect such information would be useful in understanding the merits of altering an even plantation canopy through applying a mixture of the treatments recommended here.

Adapting forest management to improve habitat potential for capercillie has been identified as an economical way of optimising conservation efforts at the landscape scale (Braunisch and Suchant, 2007). Recent research shows capercaillie are more flexible in habitat selection than previously assumed (González et al., 2012; Wegge and Rolstad, 2011), and confirms use of middle-aged plantations (>30 years) by both adults and young broods, as this habitat becomes available (Eaton et al., 2007; Miettinen et al., 2010; Wegge and

Rolstad, 2011). Encouraging tree species diversity (to include e.g. larch and spruce) within pine forests may also be important (Gjerde, 1991a; Kortland, 2006). Implementing a silvicultural system where Scots pine plantations are thinned to the improved prescription (which are largely consistent with maximising timber production) and where even age stands, where large, are transformed through thinning and by using small patch clearfells to create multicohort forest structure, is likely to produce desirable outcomes for capercaillie conservation (Gjerde, 1991a; Miettinen et al., 2010). Such a silvicultural system should be considered by managers, particularly in areas where capercaille are present.

8.6 Acknowledgements

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Chapter Nine: Promoting natural regeneration for the restoration of *Juniperus communis*: a synthesis of knowledge and evidence for conservation practitioners

An adapted version of this chapter has been published as:

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Contributions: AB co-designed the survey with DL and AB conducted the literature review and the field survey. AB carried out data analysis. AB wrote the manuscript, and LW and KP commented on an earlier drafts.

9.1 Abstract

Natural regeneration is central to plant conservation strategies. Worldwide, many *Juniperus* species are threatened due to their failure to regenerate. We focus on *Juniperus communis* in areas of NW Europe where it is declining and ask: what advice is available to land managers on natural regeneration methods, and when applied, how effective has this been? In this Chapter, we synthesize knowledge on the efficacy of management interventions and conditions associated with *J. communis* regeneration. In field trials, we test interventions where knowledge is lacking. We assess regeneration of *J. communis*, creation of regeneration microsites and germination of sown seed in response to the interventions. Our results show that although *J. communis* occurs in different habitats, there is consistency in site conditions important for regeneration (unshaded/open, short ground vegetation, disturbed/bare ground, low herbivore pressure). In calcareous grasslands, areas with regeneration are stony/bare or vegetation is short or sparse; in upland acid grasslands and dry heathlands regeneration locations are disturbed areas sometimes with a moss cover. Several interventions (grazing, scarification, turf stripping) can create regeneration conditions. From the knowledge synthesis we identified cattle grazing and ground scarification for further testing on upland acid grasslands. In the resulting field trials, regeneration was rare and recorded on only one cattle grazed site. An exposed moss layer characterized regeneration microsites but there was insufficient evidence that either intervention increased regeneration microsite frequency. Few sown seeds germinated. We conclude that different interventions or intensities of these appear to be required depending on habitat type. Broadly, on calcareous grassland intense scarification or soil stripping is needed, while on dry heathlands light scarification is suitable. On upland acid grassland, cattle grazing and ground scarification do not reliably result in regeneration. Creation of favourable mossy regeneration microsites is unlikely following intervention, unless soil fertility is low. Land-use change, increased climate warming and pollution are pressures acting on *J. communis* and may cause habitat loss and altered site conditions (e.g. soil fertility), making it difficult to create regeneration microsites at all *J. communis* sites. Other constraints on regeneration may operate (e.g. seed predation and

low seed viability) and managers should assess population and site potential before undertaking management.

9.2 Introduction

Self-sustainability in plant populations is a measure of ecological restoration success, with the occurrence of natural regeneration used as an indicator of a functioning ecosystem (Ruiz-Jaen and Aide 2005; Shackelford et al., 2013). Natural regeneration is central to plant conservation strategies and is considered the key process enabling species to adapt to climate change whilst maintaining local, site adapted, genetic resources and avoiding the risks associated with introducing plant material, such as novel pests and pathogens (Koskela et al., 2013; Lefevre et al., 2013). For conifer species, natural regeneration has been widely and successfully achieved (Matthews, 1989).

World-wide, conifer species in the genus *Juniperus* show varying success of natural regeneration. For example, the North American species *Juniperus occidentalis* (western juniper) and *J. virginiana* (eastern redcedar) are currently undergoing population expansion, whereas challenges to regeneration threaten *J. procera* (African pencilcedar) throughout its geographic range from the Arabian Peninsula to Zimbabwe (Miller et al., 2005; Negash and Kagnew, 2013; Meneguzzo and Liknes, 2015). More typically, juniper species are a conservation concern in only part of their range, generally due to their failure to regenerate. This is the case for the montane species *J. thurifera* (Spanish juniper, incense juniper) of western Mediterranean regions and North Africa, and *J. communis* (common juniper), which occurs in western and eastern hemispheres, north of the equator (Farjon, 2013a, www.iucnredlist.org/details/ 42255/0, accessed 28 Nov 2015; Farjon, 2013b, www. iucnredlist.org/details/42229/0, accessed 28 Nov 2015). Although *J. communis* is not threatened with extinction globally in any of its forms (subspecies or varieties; Farjon and Filer, 2013), the species is struggling to survive in some areas, with changes in land-use practices and site management identified as a factor driving reduction in plant survival and recruitment (Farjon, 2013b).

Within Europe, *J. communis* (represented by the varieties *J. communis* L. var. *communis* and *J. communis* L. var. *saxatilis*) is an important component of designated habitats (calcareous heaths/grasslands and coastal dunes) as given in Annex 1 of the EU Habitats Directive (92/43/EEC 1992). In boreal, alpine and eastern countries of Europe, these habitats are considered to be in ‘favourable’ condition (European Commission, 2009) and unwelcome invasions of *J. communis* into agricultural and other designated grassland habitats have even been reported in Scandinavia and Poland (Falinski, 1998; Rosen, 2006). However, within the Atlantic North and the Atlantic Central zones of Europe (EBONE, 2009, www.ebone.wur.nl/UK, accessed 1 Feb 2012), both in the designated habitats and more widely, *J. communis* populations are declining and *J. communis* is of conservation concern. Factors impacting on natural regeneration of *J. communis* are noted as the main threats to the species (European Commission, 2009; Joint Nature Conservation Committee, 2010).

Success of natural regeneration is influenced by the availability of a seed source and microsites offering the correct conditions for germination and seedling survival (Eriksson and Ehrlén, 1992). For a dioecious, sexually reproducing plant such as *J. communis*, all stages of the plant’s life cycle have to be supported: pollination, viable seed production, seed dispersal and plant establishment, growth and development to reproductive maturity. As shown by studies of other long-lived (c. 200 yr) conifer species, adult survival is likely to have a large influence on *J. communis* population dynamics, with lesser importance placed on recruitment of individuals (indicated by successful germination or young seedling presence) for population survival (Thomas et al., 2007; Münzbergová et al., 2013; Kroiss and HilleRisLambers, 2015). Nevertheless, recruitment appears to be a challenge for *J. communis* populations in the Atlantic North and the Atlantic Central zones of Europe.

Several studies have investigated reasons behind low seed production and viability. Many *J. communis* populations are aging and this is considered to reduce reproductive vigour (Ward, 1982). Diffuse pollution has been shown to interrupt pollination, fertilization and embryo development (Mugnaini et al., 2007), and N deposition, S deposition and increased temperatures can have a similar effect (García, 2001; Verheyen et al., 2009; Ward, 2010; Gruwez et al., 2014). A wide array of arthropods can act as pre-dispersal predators in *J. communis*, including mites (*Trisetacus quadrisetus*) and the chalcid wasp (*Megastigmus* *bipunctatus*) (Ward, 1982; García, 2001). Further, there may be decreased seed dispersal in areas where bird (*Turdus* spp.) numbers are lower (Eaton et al., 2009). Although it is thought that *J. communis* had historically high levels of pollen and seed-mediated gene flow, recent population fragmentation could be reducing effective gene flow, with potential implications for the long-term fitness and survival of small populations even where viable seed production occurs (Van der Merwe et al., 2000; Provan et al., 2008; Vanden-Broeck et al., 2011).

Timing the provision of suitable microsites is critical for successful regeneration of conifers, as most have occasional mast years and the seed germinates when shed or following a short chilling period (e.g. Nixon and Worrell, 1999). *J. communis* has occasional years when seed production is abundant (Raatikainen and Tanska,1993; García et al.,1999; Bonner, 2008; Ward, 2010), but seed also displays a relatively deep dormancy which requires a longer period of exposure to natural winter conditions to break (Baskin and Baskin, 2001; Bonner, 2008). Seed is unlikely to germinate until the second spring following an autumn sowing and even then, germination can be sporadic (Broome, 2003). Conditions suggested for successful germination and establishment of *J. communis* are associated with high light levels and unrestricted water availability (Livingston, 1972; Grubb et al., 1996; García et al., 1999). *J. communis* is a community dominant in a range of open habitat types including upland acid grasslands, dry heathlands and lowland calcareous grasslands, and also occurs as a understorey species in pine woods and upland acid oak woodlands (Barkman, 1985; Rodwell, 1991, 1998a,b; Thomas et al.,2007). It therefore might be expected that the appearance of regeneration microsites and the processes by which they are created to vary with habitat type. Further, failure of *J. communis* to germinate and establish is thought to be due to a reduction in habitat suitability. Changes in site management leading to increased herbivore pressure are given as the primary causes for reduced suitability (Thomas et al. 2007). Therefore, there may be an opportunity to enhance natural regeneration of *J. communis* if management appropriate for the habitat conditions can be identified. *J. communis* is declining within the Atlantic North and the Atlantic Central zones of Europe, and here efforts to conserve the species and address the declines are required by European and country-level legislation. In order to develop better guidance for conservation practitioners we conducted a literature review and field trials to:

1. Synthesize information on conditions associated with *J. communis* regeneration and the efficacy of potential management interventions

2. Test the most suitable candidate interventions identified from the synthesis in field trials, particularly those that appear most practical to implement on the type of sites where managers are keen to restore *J. communis* populations. The specific objectives of the trials were (1) to evaluate natural regeneration of *J. communis* in response to two interventions (scarification and summer grazing by cattle), (2) to identify plant cover and composition of microsites where regeneration occurred, and (3) assess whether the interventions created three measures of microsite condition identified in (2) and in the literature review. Given the uncertainties of seed viability and dispersal for this species, a further objective (4) was to assess the germination of seed directly sown at the sites.

9.3 Methods

9.3.1 Literature search and general review methods

To assess site conditions associated with *J. communis* regeneration and management interventions likely to promote regeneration, we searched for information in two categories: i) surveys of *J. communis* sites and ii) studies where management interventions had been applied. To allow comparisons of *J. communis* response on a comparable range of habitat types and relatively similar range of climatic conditions encountered, within the natural range of *J. communis*, information was sought from countries within Atlantic North and the Atlantic Central environmental zones of Europe (EBONE 2009, http://www.ebone.wur.nl/UK/> project information and products /european environmental stratification page, accessed 1 February 2012).

The scientific literature was searched (up to November 2015) primarily using the Web of Knowledge within the subject areas of environmental sciences, ecology, forestry and biodiversity conservation using Juniperus communis as the key word. Further information was sourced from book chapters and from published and unpublished reports produced by conservation agencies and organisations. Information extracted from the literature we summarised under a common set of headings in two tables (surveys, management studies). The surveys are described (location/habitat type, observations made) and any site characteristics positively or negatively associated with natural regeneration are listed. Similarly for the management studies, data on location/habitat type as well as interventions and outcomes have been listed. Records of soil pH and levels of nitrogen (N), phosphorus (P), potassium (K), aluminium (Al) and calcium (Ca) given in the surveys or studies have been replicated in the tables. Otherwise, we have used any ground vegetation data in conjunction with their indicator values (Hill et al. 1999) to derive scores of soil pH (R), soil nitrogen availability ('N') and soil moisture (F) using a mean abundance/frequency weighted approach (Pyatt et al. 2001). Where possible we have also reported the soil nutrient regime (R + 'N') and soil moisture regime (F) classes associated with the scores (Pyatt et al. 2001). In addition, original data sets have been made available tousfrom two Scottish *J. communis* surveys (Sullivan 2003 and Borders Forest Trust 1997) allowing a more detailed analysis to be conducted. Given the limited number of surveys and studies available, and the wide variation in methodologies followed and types of data collected by these, we followed a literature synthesis approach (e.g. Humprey et al. 2015) rather than a full systematic review or meta-analysis to assess the data (Koricheva & Gurevitch 2013).

9.3.2 Study areas

The study was conducted from January 2005 to March 2011. Four study sites, located in three administrative regions of Scotland were used (Table 9.1): Highland (with one site 'Dorback'); Midlothian (with one site 'Pentland Hills'); and Perthshire (with two sites 'Fungarth' and 'Ballyoukan'). Prior to the experimental management, sites were subject to various levels of grazing throughout the year by sheep (Dorback; Pentlands - a subsection only) and deer and rabbits (all), resulting in a tight sward and/or dense thatch of litter. Very little natural regeneration of *J. communis* had been observed recently at any of the sites, which was felt to be due to inappropriate seed bed conditions resulting from site management prior to the start of the trial (R. Thompson 2003, conservation advisor, Scottish Natural Heritage, Battleby, Perthshire, personal communication; D. Granger 2004, local land manager, Dunkeld, Perthshire, personal communication).

9.3.3 Management treatments

Two sites were subject to scarification treatment (Dorback and Pentland Hills). At Dorback, scarification was performed by a tractor mounted rotary cultivator which produced a patchwork of bare areas of approximately $0.25m^2$ with 1 metre spacing. At Pentland Hills, the vegetation was cut and the ground surface was scarified in $1m^2$ patches using a hand spade, again at 1m spacing. At Dorback and Pentland Hills, the trial had a block design and was blocked with respect to extensive stock grazing at Pentland Hills (see Figure 9.1 for schematic). At both sites deer had access and, with the exception of the extensively grazed area at Pentland Hills, rabbits were excluded.

At the other two sites, Fungarth and Ballyoukan, the treatment was grazing by cattle in the summer (Table 9.1) Stocking densities of cattle were within the range for upland birchwoods in Scotland, where woodland regeneration was occurring in the presence of grazing (Pollock et al. 2005; Table 9.1). The cattle-grazed sites each contained two different vegetation types (Table 9.1) which were represented in both the treatment and control areas. A set of permanent 25 cm x 25 cm quadrats were located in all treatment and control areas (Figure 9.1, Table 9.1). Grazing treatment commenced in 2006 at Fungarth and 2007 at Ballyoukan. Deer and rabbits were excluded from Fungarth but were present in low numbers at Ballyoukan.

9.3.4 Direct sowing

At all four sites at the start of the trial, berries were collected from local *J. communis* bushes (Fungarth, using a local, 4 km distant, population). Seeds were extracted (McCartan & Gosling 2013) and sown in both treatment and control areas. Sowing took place at each site in 20 of the 25 cm x 25 cm quadrats, evenly distributed between treatment and control areas (Table 9.1; Figure 9.1). As 100 seed were sown per quadrat, each site received two thousand seeds. Viability of seeds sown was estimated based on a sample of seed which was tested using the tetrazolium test (Gosling 2003).

Table 9.1 Summary descriptions of sites used, management interventions applied and monitoring in the *Juniperus communis* regeneration trial

Site	Lat & Long (NGR)	Elevation & Aspect	Solid geology	Size[3] (ha)	Intervention - type	- year applied	Habitat/Vegetation type (NVC community code[4]),Site Fertility (SNR) & Wetness (SMR)[5]	Monitoring - number of quadrats	- year (months)[6]
Dorback	57°7'N, 3°5'W (NJ056192)	380m SW	Granite, syenite, granophyre and allied types[1]	5.60	Scarification; Release from sheep grazing	2005	Improved upland acid grassland (U4). SNR M; SMR F-M	20 (Treatment) 20 (Control)	2005-2010 (July - October)
				0.75			Upland acid grassland (U4). SNR P- M; SMR F -M	20 (Treatment) 20 (Control)	
Pentland Hills	55°9'N, 3°2'W (NT229649)	335m SE	Lower Old Red Sandstone - rhyolite and felsite[2]	0.25	Scarification	2005	Wavy hair-grass grassland (U2) SNR VP-P; SMR F-M.	40 (Treatment) 40 (Control)	2005-2010 (September)
				0.13			Bracken community (U20) SNR P; SMR M	40 (Treatment) 40 (Control)	
Fungarth	56°6'N, 3°6'W (NO045425)	130-320m NW	Devonian and Old Red Sandstone-andesitic and basaltic lavas and tuffs[1]	25	Summer cattle grazing (0.44 LSU /ha /year[7]. Breed= Limousin)	2006	Mosaic of upland acid grassland (U4) & bracken community (U20).		2005-2010 (September - November)
							U4: SNR P – M; SMR F – M	40 (Treatment) 40 (Control)	
							U20: SNR P; SMR F – M.	50 (Treatment) 50 (Control)	
Ballyoukan	56°7'N, 3°7'W (NN968570)	180-285m SW	Upper Dalradian-quartz-mica-schist, grit, slate and phyllite[1]	12	Summer cattle grazing (0.41 LSU /ha /year[7]. Breed=Highland	2007	Mosaic of upland acid grassland (U4) and purple moor-grass mire (M25).		2005-2010 (August-October)
							U4: SNR P- M; SMR F-M	50 (Treatment) 50 (Control)	
							M25: SNR VP-P; SMR VM -W.	30 (Treatment) 30 (Control)	

[1] British Geological Survey (1979).;[2] British Geological Survey (1928); [3] includes both control and treated areas; [4] National Vegetation Classification (Rodwell 1991; Rodwell 1998a; Rodwell 1998b):U4- *Festuca ovina-Agrostis capillaris- Galium saxatile* grassland, U20- *Pteridium aquilinum-Galium saxatile* community, M25- *Molinia caerulea-Potentilla erecta* mire, U2- *Deschampsia flexuosa* grassland; [5] Soil Nutrient Regime (SNR) and Soil Moisture Regime (SMR) derived from vascular plant composition (Pyatt et al. 2001) prior to intervention, indicates site fertility and site wetness at start of the trial; increasing soil fertility with SNR classes Very Poor (VP) < Poor (P) <Medium (M); increasing soil wetness with SMR classes Fresh (F) < Moist (M) < Very Moist (VM) < Wet (W); [6] Assessment carried out once in this period of the year; [7] Live Stock Units (LSU) – livestock unit value for suckler cow (including calf at foot) Highland breed = 0.7, Limousin breed = 1.1 (Chesterton 2006); LSU/ha/year = (monthly livestock number in the treatment area averaged over whole year x the livestock unit value for the breed)/ size of treatment area (ha).

9.3.5 Germination and regeneration assessments

J. communis seed germination was monitored annually in all the sown plots. Natural regeneration of *J. communis* was also monitored annually but due to time limitations, this was conducted by searching a 10 m wide buffer around a sample of female bushes (20 bushes per site - 5 bushes per block at Dorback and Pentland Hills, 10 bushes in the treatment area, 10 in the control area at Fungarth and Ballyoukan). A systematic search of the sites for *J. communis* seedlings and young plants was conducted in the final year of monitoring, at the two sites with cattle grazing only. Plant height and root collar diameter were recorded, together with a description of the ground vegetation in a 1 m x 1 m square area around each plant. Species cover was assessed in different vegetation layers to give a total cover value for a quadrat; this value could therefore exceed 100%.

9.3.6 Vegetation monitoring

An even number of permanent 25 cm x 25 cm quadrats were randomly located in the treatment and control areas at each site. At Fungarth and Ballyoukan, sampling was further stratified by vegetation type (Table 9.1). In the annual assessments, species cover (as well as cover of bare ground and litter) was assessed in different vegetation layers to give a total cover value for a quadrat; this value could therefore exceed 100%.

9.3.7 Data analysis

In order to relate regeneration to management treatment the year when *J. communis* seedlings germinated needs to be known. This could be recorded for those seedlings appearing during the trial period in the plots and the monitored buffer around the bushes. However, for the seedlings found outside these areas (during the systematic search), year of germination had to be estimated by dividing seedling root collar diameter by annual diameter stem increment figures. These figures were taken from a *J. communis* dendrochronology study of the early growth of bushes at a comparable site to our study sites (Glen Artney, Perthshire, Scotland; A. Tene 2006, Forest Scientist, Forest Research, Rosin, Midlothian, personal communication).

In order to identify vegetation characterisitics of microsites suitable or regeneration, comparisons between vegetation composition and cover for quadrats containing *J. communis* seedlings and quadrats (a random sample of the 2010 permanent quadrats) where no seedlings were found were made using Principal Component Analysis (PCA). As vegetation cover and composition is expected to change rapidly following disturbance, quadrats with the youngest (1 to 2 year old) *J. communis* seedlings only were included. These seedlings germinated in 2010 or 2011. We examined the effect of the variables with the strongest loadings on PCA axis 1 and 2 in General Linear Models (GLM) with root collar diameter (a proxy for seedling age) as the response variable, for all the quadrats containing regeneration (seedlings ≤1–10 yr). For the GLMs and after inspection of data, root collar diameter was log transformed to stabilise data dispersion, and percentages of plant cover (moss, herbs, grass, *Pteridium aquilinum*), were checked for co-linearity. Plant cover terms that were correlated were tested in separate models as potential explanatory variables. A gaussian error structure was followed. Automated model simplification using Akaike's information criterion (AIC) was applied to find the minimal adequate model with the greatest fit, and residuals were examined for normality (Crawley, 2005).

For the investigation of intervention and site condition measures associated with regeneration microsites, we used ground vegetation data from annual monitoring to describe three site condition measures: vegetation height, occurrence of exposed bare ground (this we defined as >80% bare ground and < 20% for the sum of grass, herbs and moss) and the occurrence of exposed moss cover (>80% moss cover and < 20% for the sum of grass, herbs and bare ground), i.e. 'exposed' describes conditions where bare ground or moss cover is not shaded or over stood by other ground vegetation. For the linear mixed effects model incorporating random block and quadrat effects, and fixed treatment effect, vegetation height data from Dorback and Pentland Hills was square root transformed to stabilise data dispersion; examination of residuals suggested no further data transformation was required. Due to the failure of model convergence for the response of bare ground to treatment, data have been presented descriptively. There were too few data for occurrence of exposed moss in response to treatment to be tested. Due to lack of within-site replication of grazing treatments applied at Ballyoukan and Fungarth, results can only be descriptive, and means and 95% confidence intervals of the three site condition measures have been presented per treatment. All errors reported are standard errors.

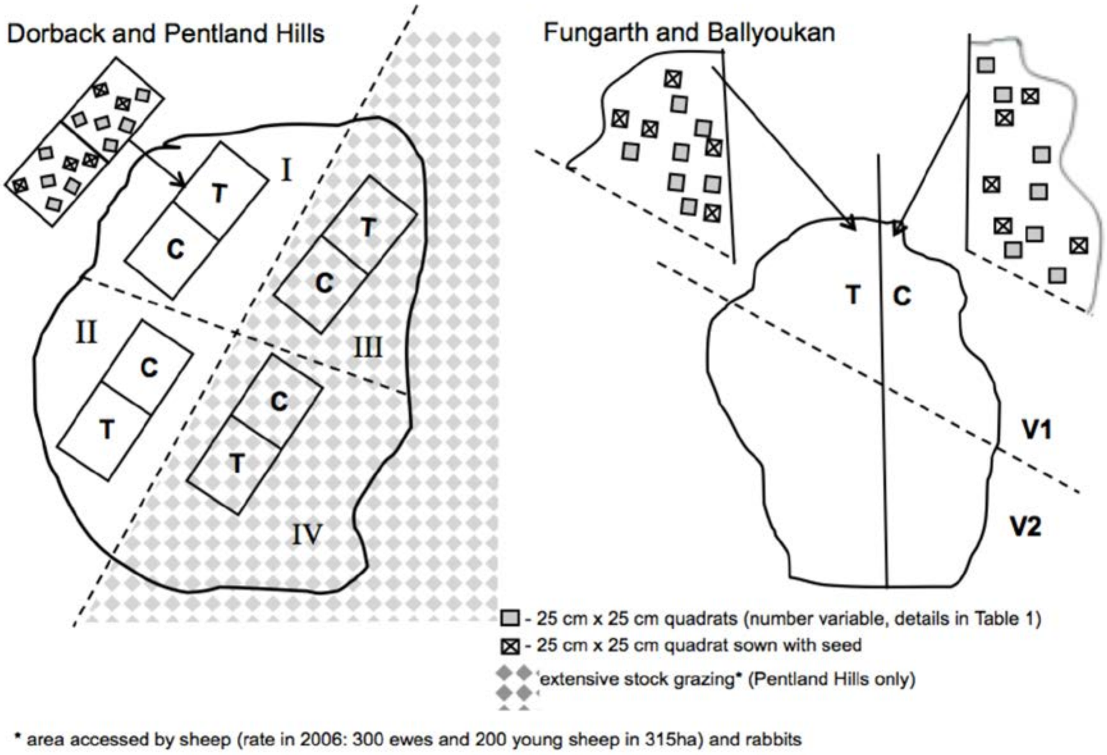

Figure 9.1 Generic design for trial layout at the two Scottish trial sites receiving scarification treatment (Dorback and Pentland Hills) and two Scottish trial sites receiving cattle grazing treatment (Fungarth and Ballyoukan), indicating blocking (I- IV) or site stratification by vegetation type (V1; V2), and replication of treatments (scarification or cattle grazing (T); control (C)).

9.4 Results

9.4.1 Site conditions associated with J. communis *regeneration from the review of regeneration surveys and studies*

Results from 17 regeneration surveys (Appendix 9.1) and seven management studies (Appendix 9.2) have been considered in this review and summarized (Table 9.2). These surveys and studies represent *J. communis* populations occurring on the full range of habitat types that the species occupies in Britain and other countries in the Atlantic North and the Atlantic Central European environmental zones (lowland dry heathlands, calcareous grasslands, upland pine–birch woodlands, upland acid grasslands and montane/coastal heath).

9.4.2 Results from the review of regeneration surveys

The survey methods followed in 16 of the regeneration surveys were consistent: there was an element of identifying sample units of *J. communis* (usually populations), recording evidence of recent regeneration and providing information about site conditions and the land use/site management. Regeneration was defined by the presence of *J. communis* individuals estimated to be around 5 yr old or younger, although detection of very young (1–2 yr old) seedlings is noted as difficult (A. Appleyard 2014, Botanical Surveyor, Salisbury,Wiltshire, pers. comm.). Two regeneration surveys were repeat surveys separated by several decades, a further five were designed to resample historical records and the remainder were generally searches of particular areas of interest, e.g. nature reserves (Appendix 9.1).

Frequency of regeneration was generally low. Reports on eight of the regeneration surveys provide figures for the number of *J. communis* samples containing regeneration out of the total surveyed. These show an occurrence of regeneration in between 5% and 33% (median = 23%) of the sample units, per regeneration survey, respectively (Appendix 9.1). One further survey provided a cumulative count of 160 seedlings ha^{-1} appearing at one site over the course of 3 yr (Appendix 9.1). For the remainder of the regeneration surveys, results are descriptive, with only the terms ‘very little’, ‘several’ and ‘a few’ used to describe the occurrence of regeneration or counts of seedlings reported but no area of survey given (Appendix 9.1). Regeneration appears to relate to parent population size for most habitat types (Table 9.2) with, for example, minimum population

Table 9.2 Support for the effects of site variables on promoting (Δ) or restricting (↓) regeneration of *Juniperus communis* by habitat type. Number of regeneration surveys (S) or management studies (T) reporting effect are indicated beside symbol. Excepting Lowland Heathland, soil pH values are from Pyatt et al. 2001 and soil moisture regime (SMR) and soil nutrient regime (SNR) from Pyatt unpubl. 2000 (SNR classes: Very Poor (VP), Poor (P), Medium (M), Very Rich (VR); SMR classes: Moist (M), Fresh (F), slightly Dry (SD)).

Habitat Upland/Lowland		Bare ground/ disturbance	Reduced sward height	Herbivore pressure		Soil nutrient levels		Soil moisture		Parent population size	
Lowland calcareous grassland/ scrub (NVC types CG3, CG4 & W21); soil pH = 4.5 -7.5, SMR = F, SNR = VR.	S	Δ^{2}	Δ^{2}	$\downarrow^{2}$	-if no break in stock grazing	$\downarrow^{1}$	- better if soil fertility is low	Δ^{1}	-negative effect of summer drought	Δ^{2}	- particularly young bushes and bushes bearing berries
				$\downarrow^{3}$	-if browsing by rabbits	Δ^{1}	- better if soil pH is higher				
				Δ^{3}	-if grazing intermittent						
	T	Δ^{1}	Δ^{1}	Δ^{1}	-if summer sheep grazing used						
				Δ^{1}	-if grazing intermittent						
Lowland heathland (NL/Belgium/ Denmark); soil pH = 3.8-4.8[7,10].	S	Δ^{2}	Δ^{3}	Δ^{2}	-if grazing is managed	Δ^{2}	-with base enrichment of soil				
				$\downarrow^{1}$	-if browsing by rabbits						
	T	$\downarrow^{1}$				Δ^{1}	-with base enrichment of soil.				
		Δ^{1}									
Upland acid & mesotrophic grassland/scrub and heathland (UK-NVC type W19 & H15); soil pH = 3-5, SMR = M-F, SNR = VP-M.	S	Δ^{2}	Δ^{1}	Δ^{2}	-if fluctuating or in pulses	$\downarrow^{2}$	-better on more acidic and nitrogen limited sites	Δ^{2}	-layering promoted (bushes propagate by stems touching ground)	Δ^{5}	
				$\downarrow^{4}$	-if exposed to grazing/more extensive landuse						
	T	Δ^{1}		$\downarrow^{2}$	-if stock and rabbits are not excluded						
Pine/birch woodland (UK –NVC type W17/18); soil pH = 3-4, SMR = SD-F, SNR = VP-P.	S					$\downarrow^{1}$	-better on more nitrogen limited sites	Δ^{1}		Δ^{1}	
	T	Δ^{1}	Δ^{1}	$\downarrow^{1}$	-small rodents and slugs						

size of c. 50 bushes required for regeneration to occur in upland grassland habitats (Appendix 9.1). However, where repeat surveys were conducted, a size of c. 50 bushes required for regeneration to occur in upland grassland habitats (Appendix 9.1). However, where repeat surveys were conducted, a decline in the frequency of regeneration or poor inter-annual seedling survival (P. Woodruffe, A. Appleyard & S. Fitzpatrick 2016, Botanical Surveyors, Salisbury, Wiltshire, pers. comm.) have been reported for *J. communis* in lowland calcareous grassland but not other habitat types (Appendix 9.1). A short sward, and disturbed and bare ground/exposed mineral surface, are associated with regeneration in the surveys of *J. communis* on upland grassland, lowland calcareous grassland and dry heathland sites (Table 9.2, Appendix 9.1). For *J. communis* populations on upland grassland in Scotland and heathland and grassland sites in Ireland, regeneration appeared to be associated with more N-limited sites (Appendix 9.1). On the very poor, dry heathland sites in the Netherlands, there are indications that regeneration is more prevalent on sites with higher base saturation of soil (e.g. 42% compared to 23%) or where there are pockets of higher pH (e.g.mean Hill-Ellenberg R value = 2.4) relative to the acidic surroundings (e.g.mean Hill-Ellenberg R value = 1.4) and also relatively more grass, fewer dwarf shrubs and more early successional mosses (Table 9.2, Appendix 9.1). Further, sites with little competition but shaded due to topographic position have been suggested as sites suitable for regeneration, indicated by the presence of certain moss (*Hylocomium splendens*) and liverwort (e.g. *Lophozia ventricosa*) species characteristic of young *J. communis* stands (Appendix 9.2). Reduced intensity of management (land use and site management) appeared to relate to presence of *J. communis* regeneration in several of the surveys. For example, reduced intensity of grazing by stock [usually sheep (*Ovis aries*), cattle (*Bos taurus*) and other herbivores, e.g. rabbits (*Oryctolagus cuniculus*)] is associated with regeneration in surveys of *J. communis* on upland grassland, lowland calcareous grassland and dry heathland sites (Table 9.2, Appendices 9.1 and 9.2). Less intensive land management appeared to favour regeneration in open ground *J. communis* populations in Scotland, with regeneration being more frequent on land used for a combination of grazing and game interests rather than where management was for stock grazing only (Table 9.2, Appendix 9.1).

9.4.3 Management interventions used to encourage natural regeneration of J. communis from the review of management studies

Reports on seven management studies were sourced; these investigated one or more of the following interventions: ground disturbance; reducing vegetation competition; reducing herbivore pressure and changing soil pH (Table 9.2, Appendix 9.2). Three management studies were designed and monitored sufficiently to allow statistical analysis, while the remaining management studies provided observational data only. Details on the type, extent and duration of interventions aimed at encouraging the regeneration of *J. communis* are given in Appendix 9.2. Low impact ground disturbance, e.g. by turf stripping or scarifying ground by dragging cut *J. communis* bushes, increased regeneration for all habitat types in nearly all the management studies (Appendix 9.2), with failure in one study attributed to the limited area over which interventions were applied and/or poor seed viability (Appendix 9.2). It has been suggested that larger ground disturbance caused by cultivation is detrimental to survival of regenerating and young *J. communis* bushes (Appendix 9.2). Reducing vegetation competition through grazing was successful in two management studies on a calcareous grassland site, as *J. communis* seedlings regenerated either in the presence of sheep grazing (Appendix 9.2) during the summer months or during breaks in the grazing regime (Appendix 9.2), although seedling height was reduced by grazing. In one study, however, vegetation control by mowing or by herbicide treatment did not enhance recruitment of *J. communis* (Appendix 9.2). Successful germination, in a trial where seeds were sown on a dry heathland site, was attributed to increasing soil pH by liming, yet this intervention did not encourage natural regeneration when applied within the adjacent *J. communis* stand (Appendix 9.2). In two separate management studies on upland acid grassland sites, reducing herbivore pressure (e.g. by excluding rabbits) was reported to benefit *J. communis* regeneration, although the significance of the treatment effects could not be tested (Appendix 9.2).

The interventions that appeared to promote regeneration most often (in 11 out of 12 surveys/studies) were those involving ground disturbance and reducing vegetation competition from the surrounding sward, particularly where they were applied in a less intensive way, e.g. turf stripping rather than cultivation, sheep grazing rather than mowing. Lack of seed supply (or insufficient area over which treatment applied to successfully intercept available seed) was suspected as a cause of treatment failure in several of the management studies.

9.4.4 Germination of directly sown J. communis *seed in the field trials*

Only two *J. communis* seedlings were recorded out of the 8000 seeds (2500 of which were estimated as being viable) sown across all four sites, on both occasions in a scarified patch protected from stock grazing at the Pentland Hills site.

9.4.5 Response of J. communis *natural regeneration to intervention observed in the field trials*

We wanted to evaluate the effect of two interventions (scarification and grazing) on *J. communis* regeneration. No regeneration was recorded from within the areas monitored around the *J. communis* bushes at any of the sites. However, more widely within the site at Fungarth, four seedlings (maximum height of 33 cm) were found in 2008 and seven more seedlings were found in 2009. This indicated regeneration was occurring, so a more widespread, systematic search of the cattle grazing sites was instigated. By 2011, a total of 33 seedlings (approximately 10 seedlings ha^{-1}) had been recorded, all at Fungarth; 23 in the grazed and ten in ungrazed area. The grazing intervention had been applied in 2006. The ten ‘seedlings’ germinating prior to 2006 are equally distributed between the treatment and control areas. However, a comparison of the number of seedling germinating in each of the 6 yr when cattle grazing was applied shows that more *J. communis* seedlings germinated in the treated area compared to the control ($t = 2.60$, $df = 7$, $P = 0.032$, $n = 12$).

9.4.6 Vegetation cover and composition characterizing regeneration microsites at one cattle-grazed field trial site (Fungarth)

Axis 1 of the PCA bi-plot (Fig. 1) describes a continuum from quadrats with a high percentage cover of mosses and herbs and low percentage cover of grass or *P. aquilinum* to quadrats with a low percentage cover of mosses and herbs and high percentage cover of grass or *P. aquilinum*. Axis 2 describes quadrats with a vegetation community dominated by *P. aquilinum* to those of the grass-dominated community. Quadrats containing *J. communis* seedlings (1–2 yr old) are associated with higher percentage cover of moss and form a cluster relatively separate from the samples containing no regeneration. Together axis 1 and 2 explain 46% of the variation. Loading values for the species groups used in the PCA are given in Appendix 9.3. Regeneration microsites therefore appear to be characterized by an exposed moss cover, i.e. a cover of moss that is not overlaid by other ground vegetation.

When percentages of plant cover (mosses, herbs, grass, *P. aquilinum* – the variables with the strongest loadings on PCA axis 1 and 2) occurring with *J. communis* ‘seedlings’ up to 10 yrs old are analysed using GLM, percentage moss cover appears as the best explanatory variable of root collar diameter (model with moss having lowest AIC value); ‘moss’ cover was higher (F1,27 = 10.80, P = 0.003; R2 = 0.29, n = 29) where the seedlings were younger, as indicated by smaller root collar diameters (Figure 9.3). Moss cover was negatively correlated with grass cover (correlation coefficient = −0.64). These relationships suggest that there was >80%moss cover and very little grass cover present at the regeneration microsites at time of germination. The main moss species were typical of upland acid grassland sites in Britain (e.g. *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Pleurozium schreberi* and *Hylocomium splendens*; Rodwell 1998b)

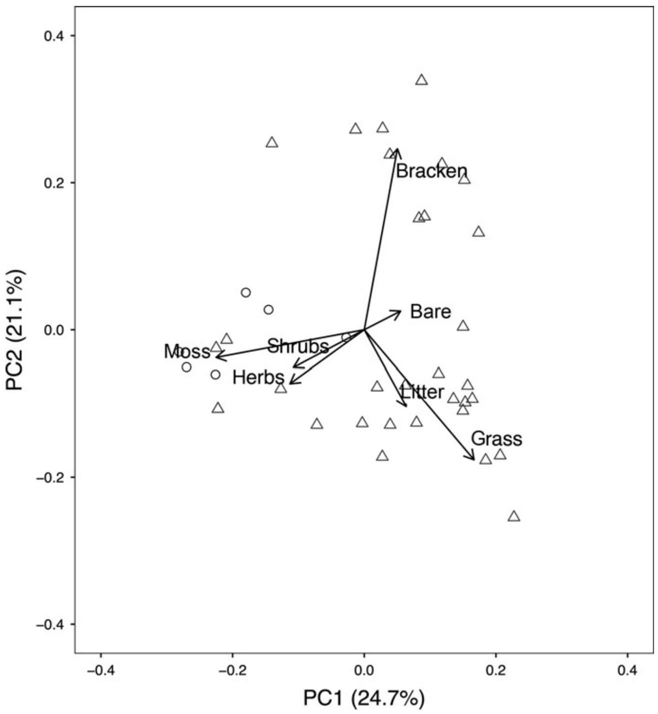

Figure 9.2 PCA bi-plot showing the distribution of ground vegetation cover variables at the field trial site, Fungarth (both grazed and ungrazed area), in samples (n = 45) with (○) and without (Δ) *J. communis* natural regeneration; regeneration indicated by the presence of 1- to 2-yr-old seedlings.

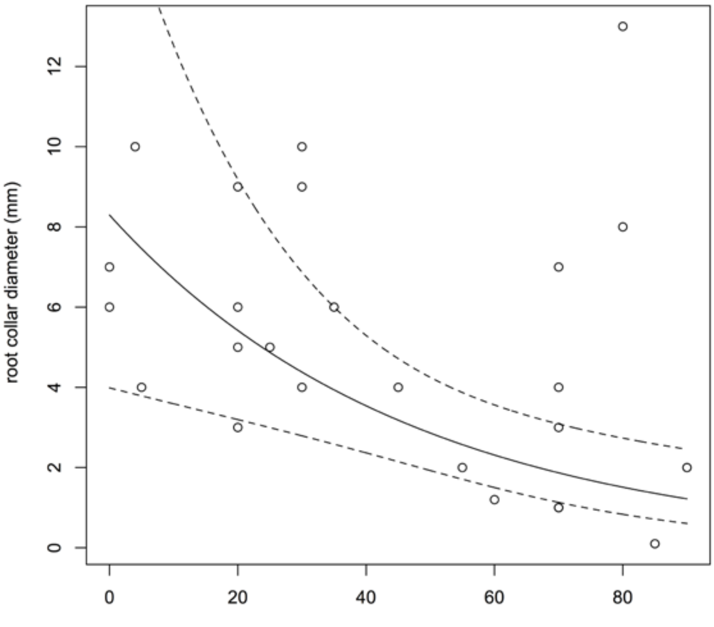

Figure 9.3 Vegetation composition of the *J. communis* regeneration microsites and root collar diameter of seedlings at the field trial site, Fungarth (both grazed and ungrazed area) in 2011. Vegetation composition described as percentage cover of all moss species; relationships were analysed using GLM (solid line indicates the lines of best fit with 95% CI shown as dashed lines).

9.4.7 Creation of regeneration microsites by scarification and grazing treatments used in the field trial

Scarification produced exposed bare ground microsites, which reverted to a grass sward after two and three growing seasons at Pentland Hills and Dorback, respectively (Figure 9.4). An exposed moss cover was observed in very few of the quadrats (c. 10%) during the re-vegetation process, indicating that scarification does not reliably result in a layer of moss covering the ground prior establishment of other ground flora species.

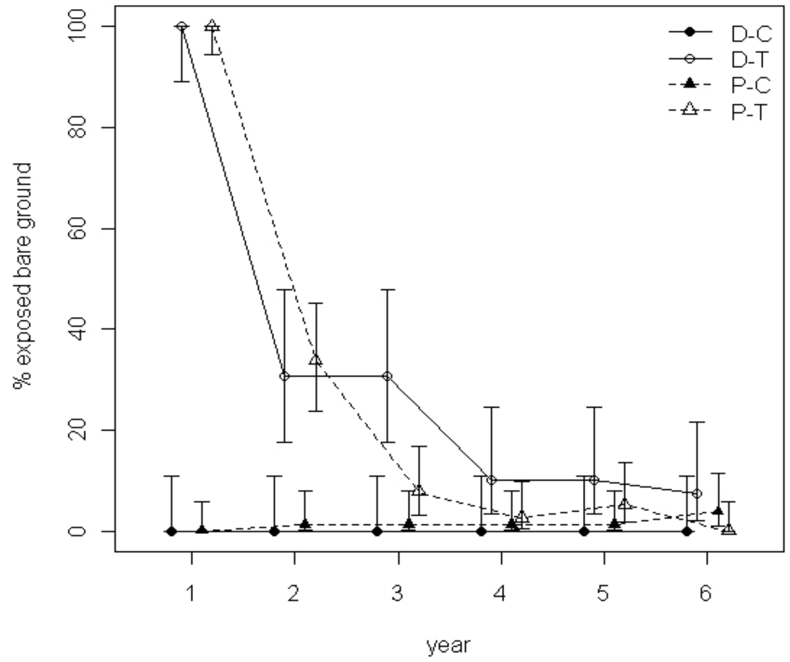

Figure 9.4 Change in exposed bare ground over six years at the two trial sites (Dorback (D) and Pentland Hills (P)) subject to initial scarification treatment, in control (C) and scarified (T) areas; 95% confidence intervals shown. Data points for the same year have been offset for ease of viewing.

Differences in vegetation height between control and treatment plots were still detectable at Dorback and Pentland Hills after five growing seasons following scarification (ANOVA: F1,3 = 12.13, P = 0.040, n = 80 for Dorback; F1,3 = 10.67, P = 0.047, n = 157 for Pentland Hills). Scarified areas had a mean vegetation height of 6.10 −1.14 cm compared to 13.00 − 1.65 cm in the control at Dorback, and 9.80 −2.49 cm in the scarified areas compared to 13.30−2.90 cm in the control at Pentland Hills.

At the grazed sites, exposed bare ground and moss microsites were infrequent (Figure 9.5) and although there is some evidence that frequency of exposed bare ground increased in the final year of the trial at Ballyoukan in the grazed area, there appears to be no effect of grazing treatment on frequency of bare ground at Fungarth or exposed moss at either site. Grazing appears to reduce sward height at Ballyoukan, and at Fungarth there is some evidence of grazing causing a reduction in sward height, especially in comparison with pre-grazed conditions (Figure 9.6).

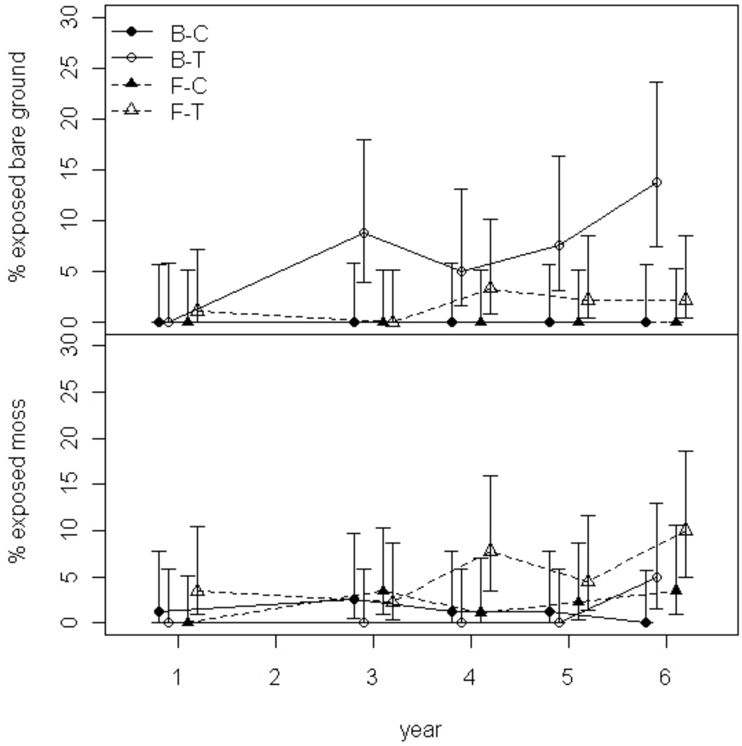

Figure 9.5 Change in occurrence of exposed bare ground and exposed moss cover over six years at the cattle grazed trial sites (Ballyoukan (B) and Fungarth (F)) in control (C) and grazed (T) areas; 95% confidence intervals shown. Data points for the same year have been offset for ease of viewing.

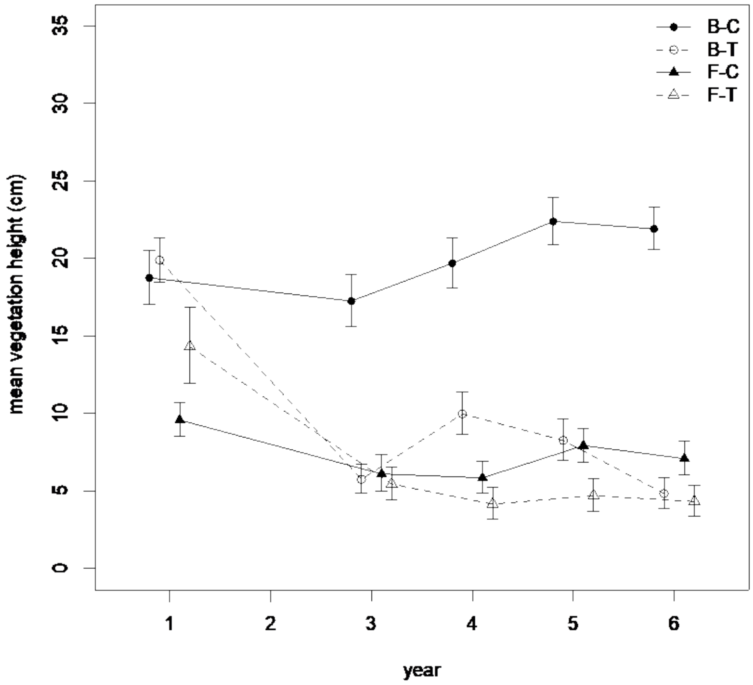

Figure 9.6 Change in vegetation height at the two annually cattle grazed sites (Ballyoukan (B) and Fungarth (F)) over six years in control (C) and grazed (T) areas (no grazing in year one); 95% confidence intervals shown. Data points for the same year have been offset for ease of viewing.

9.5 Discussion

Unlike other parts of Europe (e.g. Alps and Scandinavia) where *J. communis* is in favourable condition (European Commission, 2009), *J. communis* sites within Atlantic North and the Atlantic Central European environmental zones require action to perpetuate *J. communis* populations in the face of multiple threats. It is not clear why these regional differences exist, but in an attempt to control for variations in wide-scale possible influences (e.g. climatic) on *J. communis* regeneration, we examined the options for promoting *J. communis* natural regeneration in the Atlantic North and Atlantic Central zones only. The literature available for synthesis comprised 17 regeneration surveys and seven management studies. Within these, data are often reported qualitatively or the quality of design and monitoring of the surveys and studies are insufficient to allow statistical analysis of data. As with any seedling survey where abundance is low, detection of infrequent and very young seedlings may be difficult and early stages of regeneration may be underestimated (McCarthy et al., 2013). However, an attempt to synthesize this range of information has not been undertaken before, and this study provides insights in to the site conditions and management practices related to successful natural regeneration of *J. communis*. With an aim to strengthen the findings, we tested the most suitable candidate interventions identified from the synthesis using field trials.

9.5.1 Site and microsite conditions associated with J. communis *regeneration.*

The microsite conditions of the seed bed appear to be an important factor influencing regeneration of *J. communis* across the range of habitat types it occupies in the Atlantic North and the Atlantic Central zones of Europe. The regeneration surveys and management studies reviewed here indicate that reducing ground vegetation competition, either by ground disturbance or lowering vegetation height, resulting in open/unshaded site conditions are required for regeneration. However, regeneration microsites vary in the different habitat types. In calcareous grassland habitats, a bare surface appears to be the primary requirement for the regeneration of *J. communis* (Appendix 9.1; Wilkins and Duckworth, 2011). Disturbed ground is also required within pine/birch woodland, acid grassland and dry heathland sites (Appendix 9.1). Microsites where we observed *J. communis* regeneration in the field trials conducted on acid grasslands were characterized by a cover of moss but an absence of taller vegetation. *J. communis* regeneration has been observed associated with a cover of unshaded moss on acid heathland sites and abandoned agricultural land (Falinski, 1998; Appendix 9.1). Presence of moss cover indicates that microsites must have high humidity at ground level – a requirement shown for *J. communis* regeneration in areas of Europe affected by summer drought (García et al., 1999). Mosses, along with lichens are often the first colonizers of nutrient-poor sites, where *J. communis* seedlings frequently occur (Wells et al., 1976). Moss cover has several positive effects on seed bed conditions, such as ameliorating temperature fluctuations, reducing frost heave as well as maintaining moist conditions (Parker et al.,1997; Groeneveld et al., 2007). The importance of preventing desiccation of seed of *Juniperus* species with extended stratification requirements, such as *J. communis,* has long been recognized within the nursery trade (e.g. Heit, 1967). The surface of stone and rock fragments produced when calcareous soils are exposed may also maintain high humidity at the ground surface. Stones can act as mulch, reducing evapotranspiration of soil moisture (e.g. Pérez, 1998; Ma and Li, 2011) or provide a microwatershed effect, creating suitable conditions for seedling establishment (Livingston, 1972). In one survey, regeneration was associated with rock crevices, which are assumed to have higher humidity (Appendix 9.1), and eroding chalk cliffs and limestone outcrops (often created by quarrying) have long been noted as suitable substrates for regeneration (Appendix 9.1; Grubb, 1977; Ward, 1981).

Soil fertility (usually reported in the reviewed literature as N availability and pH) also appears to be an important factor in determining appropriate site and microsite conditions. On acid habitat types, variations in soil fertility, even within a site, affected the occurrence of natural regeneration (Appendix 9.1). Vegetation studies on acid grassland sites reported that soil fertility affected vegetation succession on cleared ground, with a herbaceous sward as opposed to moss developing on sites with higher nutrient status (Miles, 1973). On calcareous sites, the lack of soil in the regeneration microsite results in a relatively lower fertility of the surface material (Wells et al., 1976), and conservation practitioners have observed that on such sites, remaining topsoil acts as a growing medium and seed source for competitive native species, e.g. *Rubus fruticosus* (bramble), which rapidly colonize and shade areas prepared for *J. communis* regeneration (Wilkins and Duckworth, 2011; F. Scully, 2014, Community and Learning Ranger, National Trust, Guildford, Surrey, pers. comm.).

9.5.2 Management methods that create site and microsite conditions for J. communis *regeneration*

The findings of this review suggest that management to create regeneration conditions for *J. communis* on all habitat types should aim to reduce competition from surrounding ground vegetation and provide protection from herbivores, primarily rabbits (Appendix 9.1). Reduced competition was most successfully achieved through manipulating herbivore management or mechanically removing ground vegetation. However, the outcome of applying similar management prescriptions is not always consistent between sites with differing soil fertility, and highlights the difficulty of achieving both reduced vegetation competition and herbivore control (Appendix 9.2). Some evidence suggests that on acid dry heathland intensive disturbance (e.g. by cultivation) creates conditions less suitable for regeneration than the removal of surface litter and vegetation, but there is limited evidence from the literature for the appropriate level of intervention on acid, upland grassland sites (Appendix 9.2). In our trials we tested scarification and cattle grazing in the summer but found they did not reliably enhance the natural regeneration of *J. communis*. Of the two interventions, summer cattle grazing appeared to have more potential for stimulating natural regeneration, but confidence in predicting the results of this treatment at other sites is low. Scarification is clearly an inappropriate treatment on upland acid grassland sites. Evidence for creating regeneration microsite conditions with the two management treatments used in the field trials is also lacking. Unlike other studies (Ozols and Ozols, 2007; Takala et al., 2012), we did not show that a prolonged period of cattle grazing in the summer months increased the area of the site dominated by a moss cover. This was despite the partial removal of the bracken canopy by the cattle at our trial site (Fungarth), the effect of which has been linked with moss colonization in other studies (Novak, 2007). We found scarification was ineffective in creating an exposed moss cover that persisted for several years, instead, a grass sward rapidly developed. Perhaps failure to develop a moss cover at our trial site was due to soil fertility being too high as a result of increasing N mineralization from the soil disturbance (Russell, 1961). On calcareous sites the success of management in promoting *J. communis* regeneration appears to be influenced by the depth of soil overlying the calcareous rock (and therefore the fertility of the site) and structure of the surface. Regeneration was reported to occur in a short sward resulting from stock grazing on thin soils in two of the management studies (Appendix 9.2). These types of sites also appear from the regeneration surveys to be the most suited to producing bare ground microsites through appropriate levels of stock grazing (Appendix 9.1). However, the experience of conservation practitioners suggests that scarification is a more reliable method of producing microsites which support *J. communis* regeneration, particularly when the surface is composed of large chalk fragments (Wilkins and Duckworth, 2011; F. Scully, 2014, Community and Learning Ranger, National Trust, Guildford, Surrey, pers. comm.; J. Carey, 2014, Countryside Officer, Bucks County Council, Aylesbury, Buckinghamshire, pers. comm.). These subtleties of interactions between disturbance type/intensity, habitat type and site fertility, and development of the correct microsite may help explain the apparent contradictions over management regimes (type, duration and periodicity) that give rise to *J. communis* regeneration.

9.5.3 Wider constraints on J. communis *regeneration*

Land use and site management changes, particularly changes in herbivore management and pressure, are viewed as strong drivers for changes in site suitability (Thomas et al., 2007; Farjon, 2013b). Over the last few centuries changing economic pressure has led to marginal land (often steeper slopes or nutrient-poor grassland and heathland, which is often associated with *J. communis* regeneration) being over- or under-grazed by sheep/cattle, abandoned or ploughed (e.g. Wells et al., 1976; Ward, 1981; Appendix 9.2). There is potential to reinstate grazing or increase protection of sites from herbivores, and these types of manipulation have been identified as useful in our synthesis and further tested in the field trials. There have also been wide-scale changes in soil fertility over the last few decades. These changes have been associated with increased soil N levels and acidification as a result of atmospheric deposition of ammonia and nitrogen oxides and by sulphur dioxide, respectively, and, although atmospheric deposition levels across Europe are lower than they were 20 yr ago, there are still some excessive critical loads for N (RoTAP 2012). Where site conditions have changed it might be possible to apply habitat manipulation to develop a seed bed, but the causal factors for site change might have wider impacts. Failure to produce viable seed has been linked to high temperatures and N and S deposition interrupting embryo development (Gruwez et al., 2014). It is possible that at many sites the unsuitability of microsites due to site fertility may indicate more fundamental failures in *J. communis* regeneration.

The importance of an adequate seed supply for successful natural regeneration is supported by the review; all the regeneration surveys that considered population size indicated a positive relationship between population size and regeneration (Appendix 9.1). All the *J. communis* populations studied in our trial produced berries, and viability of sown seed (per population) ranged from 6% to 49%. This would seem adequate for natural regeneration, as Gruwez et al. (2013) reports recruitment at sites with 13% seed viability but no recruitment with 3% seed viability. However, the germination rate was low, with only two of the estimated 2500 viable seeds sown germinating. The absence of germination in our trial may be due to post-dispersal seed predation for example by mice (*Apodemus sylvaticus*; García et al., 2001). Seedlings may have also been removed by small herbivores (rodents and slugs) before we recorded them; losses reported from other studies can be large, e.g. six seedlings out of 10 000 seeds survived the first year (García, 2001). In hindsight, it might have been prudent to have provided protection to the patches of sown seed in our trial.

9.6 Conclusions

Natural regeneration is a fundamental process in the conservation of plant populations, and for *J. communis*, might be the only conservation option where risk of spread of pathogens e.g. *Phytopthera austracedrae* (Green et al., 2014) from planting stock is high. The focus of this work is on relationships between site conditions and habitat management aimed at the restoration, through natural regeneration, of *J. communis* populations in the parts of NW Europe where the species is declining. By drawing together and adding to the existing body of information, we have further highlighted the difficulty in promoting the natural regeneration of *J. communis*. These findings, however, should be considered in the context of the wider constraints to natural regeneration recognized for *J. communis*: population fragmentation influencing gene flow, senescing/aging parent population and pre-dispersal seed predation causing poor and infrequent seed production, reduced dispersal success and low seed viability.

Site conditions tolerated by the parent bushes of *J. communis* can differ from the microsites required for germination, therefore habitat manipulation is required to develop a seed bed. Regeneration microsites need to be open (unshaded by ground vegetation) and provide moist conditions, but may vary in appearance in different habitats. In calcareous grasslands, regeneration microsites are stony/ bare or vegetation is short or sparse; in upland acid grasslands and dry heathlands, microsites are disturbed areas sometimes with a moss cover. Grazing and ground disturbance are two commonly used techniques to create regeneration conditions. However, we found neither treatment to be a reliable intervention for enhancing natural regeneration of *J. communis* in upland acid grassland habitats. Similarly, many regeneration trials reviewed produced inconclusive findings and this synthesis showed mixed results for similar management interventions. No single type and intensity of management intervention appears best in all situations, although grazing a site continuously appears inappropriate. Greater knowledge could be gained if more consistent and quantifiable methods are used in future management studies and regeneration surveys.

From our work we suggest that where interventions are attempted, the soil fertility as well as the moisture availability and vegetation competition should be considered. For example, on acid grasslands focusing on sites where soil nutrient regime is poor, so that the intervention produces an extended successional stage of moss cover prior to development of a grass sward. Further, protection measures should be included as browsing by herbivores, particularly rabbits, is associated with failure of *J. communis* to regenerate, and post-dispersal seed predation may also reduce regeneration success. Managers should assess the potential of the site to support regeneration microsites, apply management measures for a minimum of 5 yr, and be prepared to wait longer for results, as regeneration times are long.

9.7 Acknowledgements

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Appendix 9.1 Juniperus communis regeneration surveys conducted within the Atlantic North and the Atlantic Central environmental zones of Europe.

Citation/ Source	Location and context	Habitat type	Duration	Density (D)/ Frequency (F) of regeneration	Quality of description for:		Conditions associated with regeneration	Conditions not associated with regeneration
					juniper populations[1]	site conditions [2]		
Ward 1973	UK- southern England Survey sites selected on historical records of *J. communis* presence.	Lowland calcareous grassland/ scrub (NVC[3] type CG3, CG4, W21).	Four years (1968 to 1971).	F= 28% (in 86 of 309 1km squares)	Medium	High (+)	- bare ground (reduced competition from other vegetation; no intensive shading) - release from rabbit pressure - shallow soils (on steep chalk slopes, quarries and old track-ways).	
Ward & King 2006.	UK- southern England (county of Sussex). Re-survey (after 30 years) of *J. communis* sites.	Lowland calcareous grassland/ scrub *(*NVC[3] type CG3, CG4 and W21*).*	Three years (2001-2003).	F =14% (in 3 of 22 populations)	Medium	Low (+)	- sparse open grassland - release from sheep and cattle grazing.	- summer drought - rabbit browsing.
Woodruffe, et al. 2016	UK-southern England (counties of Hampshire & Wiltshire)	Lowland calcareous grassland/ scrub *(*NVC[3] type CG3, CG4 and W21*).*	Three years (2014-2016).	D =160 ha^{-1} (cumulative seedling count)	Medium	Low (-)	- fruiting mature junipers, - short grass, moss and bare areas - rabbit grazing	- severe rabbit grazing, - long grass. - survival less near parent plant
Clifton et al. 1995.	UK- northern England (county of Northumbria) Surveys in two different years- in 1973, 130 sites; 1994 a subset of 83 sites (those extant in 1973	Upland acid grassland/scrub (NVC[3]type W19*)*	Two, 1-year surveys (1973 and 1994).	‘Very little’	High	High (+)	- fluctuations in grazing - freedom from grazing - wetter conditions (leading to layering of bushes)	

	plus new records).							
Gilbert 1980.	UK- northern England (Upper Teesdale) 10km^2 where a concentration of *J. communis* sites	Upland acid grassland/scrub (NVC[3] type– W19)	Observations made over 15 years (1960's & 70's).	D =1 m^2 - 5 m^2	Low	High (+)	- bare ground and thin turf adjacent to mature bushes - disturbance of ground vegetation following clearing birch scrub - pulses of heavy stock grazing.	- closed vegetation of common bent and heath bedstraw protection from sheep but not rabbits.
Douglas 2015	UK- northern England (county of Cumbria) Census of upland J. communis scrub	Upland acid grassland/scrub /heathland (NVC[3] – W19, H15)	Four years (2011-2014)	F =33% (in 82 of the 252 sites)	Low	Low (+)		
Long & Williams 2007	UK- upland areas of Britain. Survey questionaires completed by members of the public	Grassland, moorland, broadleaved woodland/scrub, montane, conifer woodland.	On year (2004-2005)	F = 13% (in 43 of 342 sites)	High	Low (+)	- large population sizes (seedlings recorded on 11 of the 203 sites with <50 bushes and 17 of the 42 sites with 50+ bushes)	- no significant associations noted for seedling presence/absence and: habitat type; grazing animals; rabbits)
Sullivan 2003	UK- Scotland (all). Sample survey stratified geographically.	Upland acid grassland/ scrub, montane heathland, Scots pine woodland and upland oak/birch woodland (NVC[3] types– W19, H15, W18 &W11)	Two years (2001 to 2002).	F =28% (in 21 of 76 sites)	High	High (+)	- large population sizes (usually 50+ bushes) - extensive land use - low nitrogen availability and soil pH[4] - soil moisture availability[5]	- stock grazing when on productive/ lowland sites, - higher levels of base and nitrogen enrichment[6]. - extremes of soil moisture availability[7].
Mearns 2001.	UK-southern Scotland (region of Dumfries and Galloway)	Upland acid grassland/scrub and montane heathland (NVC[3]	Two years (1998 to 2000).	F = 5% (in 9 of the 189 populations)	Medium	Medium(-)	larger population sizes.	

	Survey covered c. 3700 km^2.	types– W19 &H15).						
Borders Forest Trust 1997.	Survey of *J. communis* sites in Scotland with historical records or where local knowledge indicated *J. communis* presence.	Upland acid grassland/scrub (NVC[3] type– W19).	One year (1997)	F = 29% (in 19 of the 65 populations)	Medium	High (+)	- larger colony size - management regime of grazing and shooting - old, abandoned sheep tracks - fenced areas with disturbed sheep hefts - tall, ungrazed and unburnt heather - light summer grazing with stock - exclusion of rabbits	- population age structure
Cooper et al. 2012.	Ireland - 11 counties on Atlantic coast	Five habitat types[8]containing *J. communis* identified: 1- Wet grass/heath/ bog 2- Exposed calcareous rock 3- Dry calcareous heath & grassland 4- Dry siliceous heath 5-Dry calcareous /neutral grassland.	Three years (2008 – 2010).	F = 18% (in 22 0f 125 sites) Average % seedlings by habitat type: - 0.5% (habitat type 1); 0.5% (2); 1.2% (3); 3.5% (4); 5.9% (5) (calculated from sites where ≥ 50 bushes, n=45) Significantly higher % seedlings for habitat types 4 and 5.	High	Medium(+)	- large parent populations, - high bush density, and presence of berries - relatively lower nitrogen levels[9]or more calcareous sites (pH = 7.4 versus pH = 6.8) - rocky crevices	- intensive grazing pressure - relatively nitrogen rich sites[10]
Stolz 2010.	Netherlands- province of Drenthe	wet and dry heathlands	One year (2010).	D = 106 seedlings	Low	Low (+)	- shorter ground vegetation - vegetation dominated with grasses[11]	- vegetation dominated with ericaceous shrubs[12]

	(Dwingelderveld National Park) (3700 ha)			within 'focussed survey area'.			- periods of reduced rabbit densities.	
Ginkel & Bulten 2007.	Netherlands- province of Drenthe Survey of 25%.of *J. communis* stands on state, nature conservation organisation and private land.	Heathlands	One year (2005).	D =100 seedlings - at 3 locations of unspecified size	Low	Low (-)	- recently grazing recent removal of shrubs.	
Vedel 1961	Field survey of *J. communis* throughout Denmark; information on Swedish populations (from literature).	Calcareous and heathland sites	Not stated (assume several years).	'several'	Low	Medium(+) Additional attribute: proximity to Juniper seed source	- sparse vegetation cover - bare ground (on heaths, sites with poor sandy soil or bare rock) - deer and sheep grazing creating short vegetation and bare ground - fluctuation in grazing.	
Hommel et al. 2009.	Netherlands- seven provinces (20 nature reserves).	Heathlands	One year (2007).	'A few'	Low	Medium(-)	- shallow litter layer (average depth 1cm) - short, open vegetation (average % cover: dwarf shrubs-7.3, early successional mosses-46.5) - base enrichment of soil (pH in A and E horizons at 4.8).	- relatively deep litter layer (average depth 1.9cm) - relatively tall, dense vegetation (average % cover: dwarf shrubs-24.4, early successional mosses-18.5) - relatively acidic soil conditions (pH of 4.3 and 4.4 in A and E horizons, respectively).
Lucassen et al. 2011.	Netherlands- Maasduinen area (11 sites), Guelderland, Overijssel and Drenthe	Heathlands	Four Months (winter 2010/11)	Regeneration occurrence (no, some and strong).	Low, Additional attributes: seed viability[13]	Low (-)	- base saturation of soil mean = 42% - low infestation mites/scale insects (Carulaspis J. communisi) (classed as 0.5)	- low base saturation of soil mean 23%) - high extractable Al and Al/Ca ratio in soil and plants(at least 2 times

	provinces (5 sites) plus 3 reference sites in Germany and Norway.				- berry infestation with mites - foliar (and ripe berry) chemistry		- viability of seeds 35%	higher than at sites where regeneration = 'many') - low P and K concentration and high N/P ratios - high infestation with mites (classed as >2) - low viability of seeds (15%)
Miles & Kinnaird 1979.	Observation of field seed sowing experiment and establishment and regeneration in Scottish Highlands.	pine/birch communities (NVC[3] type– W17/18)	At least five years (1970's).	Not stated.	Low Additional attributes: - survival of germinating seed -establishment of bushes.	Low (+)	- bare ground and short turf adjacent to *J. communis* stands - protection from rodents (mice eat seed; seedling mortality from small rodents and slugs).	

[1] Quality of description for *J. communis* populations: of the 5 attributes recorded to describe *J. communis* populations (number of bushes, bush condition/size, age structure, regeneration presence, berry presence- 'High' where 4 or 5 attributes recorded, 'Medium' where 3 attributes recorded , 'Low' where 1 or 2 attributes recorded.

[2] Quality of description of site conditions: of 10 attributes describing site conditions, 'High'- where 5 or 6 recorded, 'Medium' - 3 or 4 recorded, 'Low' - less than 3 recorded; 10 attributes describing site conditions recorded are geology, altitude, slope, aspect, associated habitat/NVC type, associated vascular plant species, vegetation height, soil type, soil pH/soil chemistry, site features e.g. rock outcrops. +/- = including/excluding information on land use/management.

[3] National Vegetation Classification (Rodwell 1991, 1998a, 1998b); [4]mean site Hill-Ellenberg R values of 2-3, 'N' values of 1.5-2.5 (Hill et al. 1999); soil nutrient regime = 'Very Poor' (Pyatt et al.. 2001)).

[5]mean site Hill-Ellenberg F values of 3-5 (Hill et al. 1999); soil moisture regime = 'Dry' to 'Fresh' (Pyatt et al. 2001)); [6]mean site Hill-Ellenberg R values of 2-6, 'N' values of 2-5; soil nutrient regime = 'Very Poor' to 'Rich'; [7]mean site Hill-Ellenberg F values of 1-7; soil nutrient regime = 'Very Dry' to 'Very Moist'; [8] Fossitt, J.A., 2000; [9]mean site Hill-Ellenberg 'N' value of ≤2.8 (Hill et al. 1999).

[10] Mean site Hill-Ellenberg 'N' value ≥3.2; [11] mean site Hill-Ellenberg R value of 2.4; [12]mean site Hill-Ellenberg R value of 1.4.; [13]Gosling 2003.

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Appendix 9.2 *Juniperus communis* management studies conducted within the Atlantic North and the Atlantic Central environmental zones of Europe.

Citation/ source	Location/context	Interventions	Duration	Observations made	Response/outcomes/findings	Limitations
Fitter & Jennings 1975.	UK-southern England (Aston Rowant). Chalk grassland with J. communis (NVC1 type W21) Previously burnt & grazed.	Sheep grazing: - rate of 1.2 sheep per ha - timing: autumn, winter, summer - control with no grazing. Sites rabbit fenced prior to treatment.	Seven years	Seedling: - survival - height - crown diameter - stem diameter.	Seedlings regenerate in presence of summer grazed sheep. Growth not hindered by grazing in summer as it is by grazing at other times of the year.	Summer grazing regime assessed for only 2 years as rabbit fencing around treatment failed. Unreplicated within site, only conducted at one site.
Morris et al. 1993.	UK – southern England (Old Winchester Hill). Chalk grassland with J. communis (NVC1 type W21)	Sheep grazing: -rate to remove 75–100% of the herbage per grazing period - timing: spring, summer, autumn -rotated to provide periods of grazing (5years) and no grazing (4 years) different paddocks treated in different years	Twelve years	Seedling: - year of germination - height - survival Established bush height, survival Vegetation height	Regeneration occurs under rotational grazing management (e.g. maximum 60 seedlings/ha/year). More seedlings where: - close to female bushes - short sward height - in period when grazing ceases. Growth and survival of seedlings and young bushes (<10years old) reduced by period of grazing (e.g. 85% lost after grazing period).	Errors likely in seedling number by year estimates, as difficult to: -detect one year old seedlings -determine seedling age. Results difficult to analyse: too few seedlings recording for some treatments individual protection not consistently provided for all seedlings in all years.
Wilkins 2011.	UK- southern England. *J. communis* scrub sites (10) on chalk soils (NVC[1] type W21)	Turf stripping to produce bare ground (1m x 1m) scrapes next to *J. communis* bushes: - protection (vole, rabbit and larger herbivores) with wire mesh cages (T) - unprotected control (C) Scrapes next to male *J. communis* bushes sown with cleaned seed, female-bush scrapes unsown.	Three years	Seedling: - number recruited - location	Regeneration at four sites: - two control sites (1 plus 2 seedlings in scrapes) and two Treatment sites (1 plus 3 in caged scrapes). - occurred in third year (trial started in Autumn 2008, seedlings recorded summer 2011).	- Not a balanced design: local control only installed at some sites; some sites with treatment or control plots, only.

Citation/ source	Location/context	Interventions	Duration	Observations made	Response/outcomes/findings	Limitations
Kerr 1968. Sykes 1976 (seedling data analysis).	UK-southern Scotland (Tynron Juniper wood) J. communis scrub (5 ha) in upland acid grassland/scrub vegetation community. (NVC1 type W19). Re-analysis of seedling data in 1976.	Interventions for regeneration: -stock fencing -rabbit control -bracken cutting -providing bird perches - burning (1 ha, unplanned) Establishment treatments: - weeding, plastic mulching, caging, planting and sowing.	Twelve years (1955 to 1967). Fourteen years (1960 to 1974) for seedling survey.	Seedling (from surveys of reserve): - number - height - survival Seedling (when caged /uncaged): - survival - growth Plant (under different establishment treatments): -survival	Fire can successfully prepare ground for J. communis establishment. More recruitment of seedlings when rabbit numbers are lowered.	Not a replicated design for treatments Short duration of monitoring for most treatments Some interventions were small scale e.g. 2, 1m^2 areas sown with seed, once. For seedling data analysis (1976): Seedling locations not mapped so can't relate to treatments, seedbed conditions or conditions favouring survival/growth-
Clifton et al. 1995. Sutherland 1993.	UK- northern England (Upper Teesdale) Upland acid grassland/scrub habitat (NVC1 type W19).	Three J. communis bush treatments: - coppiced to ground level - coppiced to 1m - removed by dragging/winching. Sites stock and rabbit fenced prior to treatment.	Ongoing –report end third year (1990)	Seedling: - number - location Local site conditions.	Regeneration occurred: when herbivores excluded + dragging bushes (caused ground disturbance and shedding of berries). in 3 years following treatment most in areas shaded by bracken. Survival only where protection in winter from sheep and rabbits.	Presence/absence of control not confirmed. Details of monitoring not given. Monitoring of short duration compared to the known germination profile of sown berries.

Citation/ source	Location/context	Interventions	Duration	Observations made	Response/outcomes/findings	Limitations
Verheyen et al. 2005.	Belgium- province of Limburg (Heiderbos nature reserve). J. communis scrub (10 ha) on dry, heathland site. Regeneration of extant population thought due to abandonment of traditional heathland management 50 years ago. Site ungrazed for last 50 years.	Four treatments - sod cutting + selective herbicide treatment of grasses - cultivating + Calluna vulgaris sown following year - sod cutting All plots mown in at least one year; woody plants cut regularly.	Fourteen years	Demographic change in J. communis population since treatment (23 years later) based on bush: - location - height - stem girth Growth response models used to determine if emergence of new J. communis bushes correlated with management treatments.	Management did not produce younger cohort of J. communis: recruitment (estimated at 5 individuals per ha per year):not enhanced: established bush mortality promoted. conditions created by cultivation less suitable for survival of regenerating/ young bushes than other treatment e.g. sod cutting. Limited availability of bare ground for germination and low viability of seeds, may explain lack of success.	Regeneration interpreted from long term (20years) survival of plants (not annual monitoring). Different treatments applied in different time periods; could be an undetermined treatment *year interaction. Seeds thought to have very low viability. Factors (other than management), negative for regeneration acting during trial period but not during period when extant population established (e.g. lowering water table and nitrogen deposition).
Hommel et al. 2012 (in Dutch).	Netherlands (2 sites)- province of Drenthe (Balingerzand) & Overijssel (De Borkeld) J. communis scrub on dry heathland. Germination trial (seed sown in enclosed plots) and natural regeneration trial (within the J. communis stand) repeated at both sites.	Treatments(Trts): - control /no management (Trt 1) - shallow sod cutting (litter and vegetation removed) (Trt 2) -deep sod cutting (8cm depth , organic topsoil removed) (Trt 3) - deep sod cutting + liming (rate of $200g/m^2$) (Trt 4) spading (to mix soil) (Trt 5) adding of J. communis litter (Trt 6) Germination trial: 1 block of 25, 1m x 1m plots with 0.5m buffers. Four reps of each Trt. Each plot split for sowings in	Four years	Germination trial: Seedling emergence (monitored 2-3 times annually) Natural regeneration trial: - seedling emergence - vegetation development & inventory of species and plant communities associated with J. communis. Soil composition and chemistry for	Germination trial: germination capacity low (0.03% average; 0.28% maximum). treatment effect for all but Trt 6;Trt 3, 4 and 5 had most germination (but did not differ significantly); no germination with Trt 1 (control). seed origin effect not significant location effect (germination capacity higher at Markelo). Soil influence: more germination where higher: clay content, organic matter content, phosphorus and base ion availability, but lower where higher calcium utilization. Regeneration trial: none recorded. Vegetation survey suggests indicator species (mosses and liverworts) of past regeneration	Very low seedling numbers makes detection of positive influences on germination hard to detect.

Citation/ source	Location/context	Interventions	Duration	Observations made	Response/outcomes/findings	Limitations
		March 2008 (1000 berries, 3 origins, per plot) and 2009 (800, 1). Over 300,000 seeds sown; four origins used. Natural regeneration trial: Trts 2, 3 and 4 (5 reps of each), applied along a transect of 15, 1m x1m Trt plots; 5 Trt 1 plots located adjacent to Trt 2 plots.		each trial site(0 - 10cm, 10-20 cm): -clay content - organic matter content - pH - nitrogen, - phosphorous - base ion saturation.	microsites. Indicator species infrequent; not increased by Trts; plots colonised by other but frequent mosses.	

[1]National Vegetation Classification (Rodwell, 1991).

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Appendix 9.3 Loading values (superior to 0.1) for species groups used in the Principal Component Analysis (Figure 9.2) . The Principal Component Analysis investigated the distribution of ground vegetation cover variables at the field trial site, Fungarth (both grazed and ungrazed area), in samples with and without *Juniperus communis* natural regeneration; regeneration indicated by the presence of 1 to 2 year old seedlings.

Species groups	PCA1	PCA2
bracken (*Pteridium aquilinum*)	0.150	0.734
herbs	-0.337	-0.218
grass	0.497	-0.526
shrubs	-0.321	-0.152
moss	-0.671	-0.112
bare ground	0.165	
litter	0.190	-0.309

Chapter Ten: Discussion and Conclusions

10.1 Introduction

Research has attempted to underpin biodiversity conservation policy and implementation plans at the strategic and international level for decades. Now, more than ever, research needs to provide evidence (e.g. on distribution, rarity and trends of species, for management prescriptions and for single species recovery actions) to guide conservation policy decisions and effective conservation practice, aimed at addressing the crisis facing biodiversity. To increase its utility in evidence-based conservation, the evidence provided needs to be appropriate, sound and accessible to end-users. Whilst agreements and policies are set at a global level, action has to be effected at a sector by country scale. In my thesis I present a body of work which demonstrates how this evidence need has been downscaled to meet decision-makers requirements for forestry in Britain. I have accumulated, reviewed and disseminated evidence for protected woodland species. Building on available evidence, my approach has aimed to conduct appropriate and sound research to fill knowledge gaps, whilst delivering information meeting the needs of end-users.

10.2 Building on current knowledge of species to direct appropriate research

There is a variety of taxa considered for protection in British woodlands and a lack of uniformity in what is known about the different taxa (BRIG 2007). This has resulted in a diversity of research needs. I have employed a range of different research methods with the aim of appropriately meeting the different knowledge needs. These have been selected using the framework of five stages used in protected species research (occurrence, autecology, tolerance to environmental change, knowledge dissemination, testing recommended action;Broome et al, 2005).

10.2.1 Knowledge Acquisition stages 1 and 2

Knowledge of protected species occurrence and habitat requirements is critical in conservation decision-making (Rodrigues et al, 2004). *Knowledge Acquisition stage 1* aims to understand species occurrence and *Knowledge Acquisition stage 2* species resource needs. Occurrence data is generally used to track species trends, and species habitat needs are usually assessed separately through autecological studies (Bussard 1991). However, both types of information can be provided by survey and monitoring programs, particularly those where an element of question-driven design is incorporated (Lindenmayer and Likens 2010).

Even for relatively well studied taxa, fundamental knowledge can be lacking, e.g. for critical points of their lifecycle, or indeed there can be misconceptions about their resource needs (Di Minin and Moilanean 2014; Margules and Pressey 2000). This is the case for the Scottish crossbill (*Loxia scotica*). Considered to be an endemic species to Scotland, the Scottish crossbill was assumed to feed exclusively on seed of Scots pine (*Pinus sylvestris*). However, data on the trees and coning levels where Scottish crossbill records were collected indicate that lodgepole pine (*P. contorta*) seed is preferred food over other conifer seeds during the winter months (Chapter 2).

In Chapter 3, I analysed data collected on juniper (*Juniperus communis*) occurrence and regeneration from a national species survey (Sullivan, 2003). Associations with site conditions investigated using species distribution modelling (SDM) (e.g. Phillips et al, 2006) shows that regeneration occurs only within a limited range of climatic and edaphic conditions available at sites still occupied by juniper.

In deploying surveys and monitoring programmes to provide data at *stage 1 and 2,* a tension exists between extent of a range covered and the level of detail of the information collected (Lindenmayer and Likens, 2010). Consequently, there can be limitations to extrapolating monitoring data to explain causal mechanisms (e.g. juniper recruitment limitations), particularly as the monitoring data has not been collected in a way, which can capture responses to novel changes in in environmental conditions (Sutherland, 2006). However, both studies (Chapter 2 & 3) fill fundamental knowledge gaps on woodland protected species (UK biodiversity plan) and by using data from national monitoring schemes ensures that not only is the species occurrence better understood but also the associations which I have found between habitat and species is consistent across major parts of the species’ range (Lindenmayer and Likens, 2010).

10.2.2 Knowledge Acquisition stages 3 and 4

A key requirement for protected species research is to predict the consequences of environmental change brought about through the management actions, and such responses are best assessed experimentally (Sutherland, 2006). For many woodland protected species, knowledge on how they may react to habitat change and/or management is lacking. I have used two studies to illustrate *Knowledge Acquisition stage 3*: Chapter 4 presents moth assemblage responses to coppicing in an English woodland and Chapter 5 epiphytic lichen response immediately post and nine years following conifer removal to restore an Atlantic oakwood site.

Although coppicing is advocated as a vital intervention in rotationally cut coppice woodlands to maintain woodland butterfly species, the effect on species of macro–moths (several of which are woodland protected species) was unknown. This study showed that a wide diversity of moth species could be maintained in a coppice woodland when coppicing was applied, as each coppice stage supported a distinct moth assemblage which established in a new part of the site when and where that coppice stage was provided. As such, coppice moths were tolerant to woodland intervention.

The epiphytic lichen flora in Atlantic oakwoods planted ancient woodland sites (PAWS) were anticipated to be at risk from the rapid and extreme change in environmental conditions created during site restoration. This study provides evidence of the apparent tolerance and physiological recovery of the epiphytic lichen species to the intervention over time.

Studies presented in Chapters 4 and 5, reveal unexpected responses and interactions which may not have been reported using other research methods such as gathering expert opinion, and therefore highlighting the importance of empirical research (Sutherland, 2006). Studies provide the evidence needed by decision-makers in formulating policy or making management decisions particularly in the context of on-going operations as are employed in forestry (e.g. Sutherland 2006; Anon 2015). However, due to financial constraints empirical studies such as these are usually small scale (few sites; short time series) which can limits confidence on how widely applicable and durable the findings will be (Sutherland 2006). Therefore, to prepare the evidence for dissemination to end-users (*Knowledge Acquisition stage 4*) usually requires synthesizing a body of other information to substantiate and provide context to the findings.

I illustrate this type of research in Chapter 6 and 7. Chapter 6 reports the findings from a survey of lowland broadleaved woodlands where specialist woodland bird species' response to management and to deer pressure was assessed. The importance of stand structure and vegetation structure emerges as a key message when empirical findings are integrated with knowledge on bird species' ecological requirements. Interpreting the findings in light of silvicultural experience provides the context for how woodland management can be tailored to deliver more quality habitat for the target bird species. Chapter 7 describes my attempt to deliver detailed habitat requirement information for all the protected woodland species (c.200 species) within an administrative area governed by the same wildlife laws and conservation policies (Scotland). To capture the complexity and diversity of needs of 179 species occurring in seven different native woodland types in to a simple output, I developed the Niches for Species model (N4S).

10.2.3 Knowledge Acquisition stage 5

Targeted conservation measures for species can be incentivised. Historically these have been largely paid for by government funded grant schemes but increasingly, charities, corporate social responsibility programmes and offsetting measures provide a source of funding (Scottish Forestry Alliance; Kleijn and Sutherland 2003). Evidence that measures are effective is high priority to any grant administrator (e.g. Defra 2014). Ideally, evidence based conservation guidance should be 'tried and tested', i.e. following the guidance should result in a habitat change or management action which elicits the same response as previously observed (Chapter and 6) or predicted to occur (Chapter 3) in the target species. This type of research is used in *Knowledge Acquisition stage 5*. It is contingent on the previous four stages and allows for wider testing of recommendations.

In Chapter 8 and 9, I describe an experimental approach to conducting this type of research. Chapter 8 describes how thinning targets for pine woodlands aimed at developing the correct habitat conditions (an abundant cover of bilberry) for capercaillie (*Tetrao urogallis*), have been available for a number of years (Moss and Picozzi 1994; Parlane et al, 2006). However, the evidence these targets are based upon has been gathered from space-for-time substitution studies, where bilberry occurrence within a chronosequence of different aged and therefore stocked and structured pine stands, was assessed (Hutto and Belote 2013). In Chapter 8, I describe how I applied the recommended thinning targets at two pine woodland sites, measured the response of the bilberry over time to the treatment following a before-after, control-intervention design. Research presented in Chapter 8, confirms that applying the thinning targets does promote bilberry (*Vaccinium myrtillus*) cover and provides a translation of the targets stated by previous authors in the units of ‘stems per ha’, to more familiar units of ‘basal area’ used by production forestry managers.

Juniper is the subject of Chapter 9. Juniper is a protected species in many countries due to its decline in abundance and rarity. Failure to regenerate is identified as a major factor contributing to the species’ decline. Different approaches to site management to improve natural regeneration have been recommended in the published and grey literature available from Europe. In Chapter 9, I assess the various recommendations and review the small body of evidence where these recommendations have been tested. I add to the evidence by conducting before-after, control-intervention designed trials where two interventions, appropriate for British upland conditions are tested. I refine the guidance available on the use of scarification and summer cattle grazing as interventions for successful regeneration of juniper. Monitoring, evaluation and refinement, particularly of agri-environment schemes for biodiversity, has been an important area of research in the last decade (Kleijn et al, 2006; Finn et al, 2009; Vickery and Tayleur 2018). However, data are typically provided by a comparison of the target species densities in areas in and outside schemes and can be hard to interpret. Experimental approaches, as I have adopted in Chapter 8 and 9, are recommended (Grice et al, 2004; Kleijn and Sutherland 2003).

10.3 Using ecological theory to provide a sound basis for research

The themes that unite the studies presented in this thesis include identification of resource needs for woodland protected species and understanding how woodland management influences the provision of these resources. The focus of the research I present is primarily at the woodland stand level. I have therefore not considered landscape scale issues (as underpinned by the island biogeography ecological concept; MacArthur and Wilson 1967) such as: distribution of habitat patches supporting the protected species, patch connectivity, and species dispersal abilities (Hanski 1998; Tews et al, 2015). Further, the measure of success for species conservation I have inferred is for maintenance of the population rather than the individual but I have not incorporated research on ecotype /genetic diversity or on population dynamics, and I acknowledge both ecological concepts would be highly relevant to protected species research (Vanhala et al, 2014; Watts et al, 2016; De Vries et al, 2015; Wilberg et al, 2016; Traill et al, 2010). However, the work within my thesis use and link several important ecological concepts (the niche concept, plant succession and disturbance, recruitment limitation, herbivory/predation) thereby providing a sound basis to the research and conservation recommendations made for forestry policy and practice (Perring et al, 2015).

10.3.1 Niche concept

The niche concept enables an articulation of the complex relationships governing species and their habitats (Hutchinson 1957; Phillips et al, 2006). In my thesis, I have utilised this concept by attempting to describe the resources or niche components which appear vital to the species survival, and the way the niche components are affected by management. The search for this information is a theme of the research chapters presented. Most obviously the niche concept is used in Chapter 7 where I construct a classification of habitat (woodland type, stand structure and microhabitat) which reflects the resource needs of 179 woodland protected species in Scotland. The classification underpins an exercise of mapping potential occurrence of these species across their distributional ranges using an expert-based habitat suitability approach (Leblond et al, 2014; Drew and Collazo 2012; Drew and Perera 2011).

In my thesis, I have used both broad and fine-scale descriptors of the niche. At the broad scale, I have used habitat type e.g. ‘upland birchwoods’, ‘lowland mixed deciduous woodland’ (Chapter 7); ‘acid grassland’, ‘lowland heathland’ (Chapter 9) or the descriptor of woodland stand structure e.g. ‘pole stage’, ‘veteran and ancient’ (Chapter 7). In Chapter 6, six woodland stand structures are used to collectively describe the resource requirements of 17 declining woodland bird species (Fuller et al, 2014). I have also shown the importance of microhabitat features in describing the needs of woodland protected species.

Rare and declining species tend to be ‘specialist’ or ‘fussy’ species unable to utilise a broad range of habitat resources but with specific sets of requirements. In my thesis, I investigate and make use of this feature of specialist species. In Chapter 7 niches are described with the aim of linking a specific set of species requirements with spatial environmental data. For example, the niche I define by the combined presence of *wood pasture* woodland type, *veteran and ancient* stand stage, *bark-dry* microhabitat, will offer the precise conditions of the bark features of very old trees which is dry and in well-lit situations. My analysis suggests that in Scotland, this niche provides resources for twenty-five lichen species listed on the Scottish Biodiversity List. Such specific niches characterised by old trees and microhabitat features of deadwood, dry-heavily fissured bark, water filled hollows, shady and wet bark surfaces or sap runs and complex stand structures are often provided in woodlands of long continuity and are associated with specialist species requirements (Alexander 1998; Coppins and Coppins 2005; Whytock et al, 2018). In Chapter 2, I explore crossbill preferences for available and ripe conifer seed versus seed of a particular conifer species. In Chapter 4, the niche concept (woodland structure and microhabitat) is used to substantiate the relationship between moth assemblage change in response to coppice management, by linking the resources available at each coppice stage (structural, plant group and plant species) with the moth species’ resource requirements i.e. food plant for moth larvae and adults). This supports the application of my findings in Chapter 4 beyond the single site of the study.

Work outlined in Chapter 3, showed that niches supporting natural regeneration of juniper (regeneration microsites) are not always present at the sites where juniper populations occur meaning that management interventions would be needed to promote natural regeneration (Sullivan 2003). I attempted to define this specific regeneration microsite or niche across a broader range of habitat types (e.g. calcareous grassland, acid heathland) supporting juniper in Chapter 9, and also investigated how niches could be provided through management interventions. In Chapter 8, I show how the availability of the niche used by bilberry, can be increased by manipulating the light environment through Scots pine stand management (Parlane et al, 2006).

10.3.2 Succession and disturbance

I have shown that the process of vegetation succession and its manipulation is fundamental in delivering conservation management for rare and protected species in woodland habitats, both as habitat type changes from open to wooded, and as woodlands change in age and structural stage (e.g. Bowen et al 2007; Martin et al, 2018). This is illustrated in many chapters of my thesis (Chapters 3, 4, 6, 7, 8 and 9).

Commonly, management considered in this thesis is helping to accelerate the successional stages in woodland development. This is the case, for example, in the study of moth assemblage response to re-coppicing of a sweet chestnut woodland (Chapter 4), and in ground flora response to Scots pine plantation thinning (Chapter 8). Woodland succession captured in the six different (‘characteristic’) woodland stand structures described for lowland broadleaved woodlands, are shown as a product of the interaction between woodland succession and silvicultural intervention (Chapter 6). Understanding this relationship is important as five of the stand structures are important in providing habitat conditions suitable for a range of declining bird species (Chapter 6). Further in Chapter 7, I have used stand development stage as a key descriptor of protected woodland species’ niches. Woodland succession and its manipulation for species conservation is widely reported and in the recent literature has been related for example to the conservation of biodiversity including rare and threatened species (Rocha-Ortega et al, 2018; Neuenschwander and Adomou 2017; Humphrey 2005), rare plants (Douda et al, 2017; Matsushita et al, 2016), fungi (Komonen et al, 2016), and saproxylic beetles (Komonen et al, 2014).

Disturbance is an important process benefitting biodiversity in temperate and boreal forests (Thom and Seidl 2016; Bernes et al, 2015) and many taxa have been identified as ‘disturbance-phase species’ in forest ecosystems (Rosenvald and Lohmus 2008). In my thesis the importance of disturbance affecting succession of open ground habitats is highlighted for the natural regeneration of juniper (Chapter 9). Changes of habitat through succession, perhaps in response to drivers such as nitrogen deposition, is identified as a possible explanation for why juniper is not regenerating at all juniper sites surveyed in the national survey of juniper (Chapter 3). Within a woodland context, disturbance may not always be beneficial to specialist species, and it has been questioned whether the dynamics of a forest plantation systems used in Britain does reflect natural disturbance systems considered to be beneficial to species (Quine et al, 1999).

10.4 Information accessibility and end-user needs

To assess the extent to which the research presented in my thesis is accessible and meets end-users' needs, it is important to consider its impact. The impact of my research is best explained within the context of the different tiers of response options for sustainable management of ecosystems (Vira et al, 2011). The three tiers of options are: 'enabling' options (e.g. legislation, policies); 'instrumental' options (e.g. incentives, practices); 'foundational' options (generation and distribution of knowledge) (Box 10.1; Figure 10.1).

10.4.1 Research impact

My research outlined in this thesis engages with different UKFS response option structure (Box 10.1) as shown by location of the chapters in Figure 10.1. In Figure 10.1, I have also indicated the demonstrated or envisaged impact of my research. Many knowledge exchange processes are subtle, requiring a diversity of impact measures to be employed (Meagher and Lyall, 2013). Following the impact evaluation system advocated by Meagher and Lyall (2013), I can report four different impact types which have either been demonstrated or envisaged as a result of my research.

Box 10.1: Response options for species conservation in British Forestry

Enabling options and the UKFS (Figure 10.1): there is an intention that all forestry activities in the UK should be conducted according to Sustainable Forestry Management (SFM) principles (FC 2017). For species conservation these principles align with requirements of multilateral agreements on biodiversity, with wildlife legislation and with the policy strategies responding to these instruments at the European, UK and country level (JNCC and Defra 2012). The SFM approach is described in the UK Forestry Standard (UKFS; FC 2017). Forestry is devolved and the forestry regulatory body in each country develops a Forestry Strategy which articulates the UKFS in a way which is relevant to the country. The UKFS also applies to the management of the public forest estate and is reflected in the Forestry Strategies and Delivery Plans produced by each country by the public estate management bodies.

Instrumental options and the UKFS: public monies are central to delivery of plans by the public estate management bodies in line with requirements of the UKFS. The UKFS is also reflected in incentivised actions which support Strategy implementation (e.g. Defra, 2007).

Foundational options and the UKFS (Figure 10.1): a raft of guidance supports and refines UKFS delivery (https://www.forestry.gov.uk/ukfs). This relates to broad principles of the UKFS such as biodiversity conservation or to guidance on forestry practice, either that which can be applied broadly across sector (e.g. Ecological Site Classification decision support tools) or to specific operations (e.g. Trout and Kortland, 2012). The guidance supporting the UKFS also encompasses reports on research findings and how these apply in the context of SFM (e.g. Broome et al, 2016). Other information and guidance is produced by or directly for the forestry regulatory bodies or public forest management bodies in each country to aid delivery of the UKFS. For example, the regulator can publish good practice guidance to help woodland managers stay within the law (https://www.gov.uk/guidance/manage-and-protect-woodland-wildlife) or provide guidance on how forestry activities should be undertaken when taking place under a forestry grant (e.g. https://www.forestry.gov.uk/forestry/infd-7q3f5k). The body managing the public forest estate underpins its Forestry Strategies with a specific set of guidance documents such as Operational Guides and Instructions.

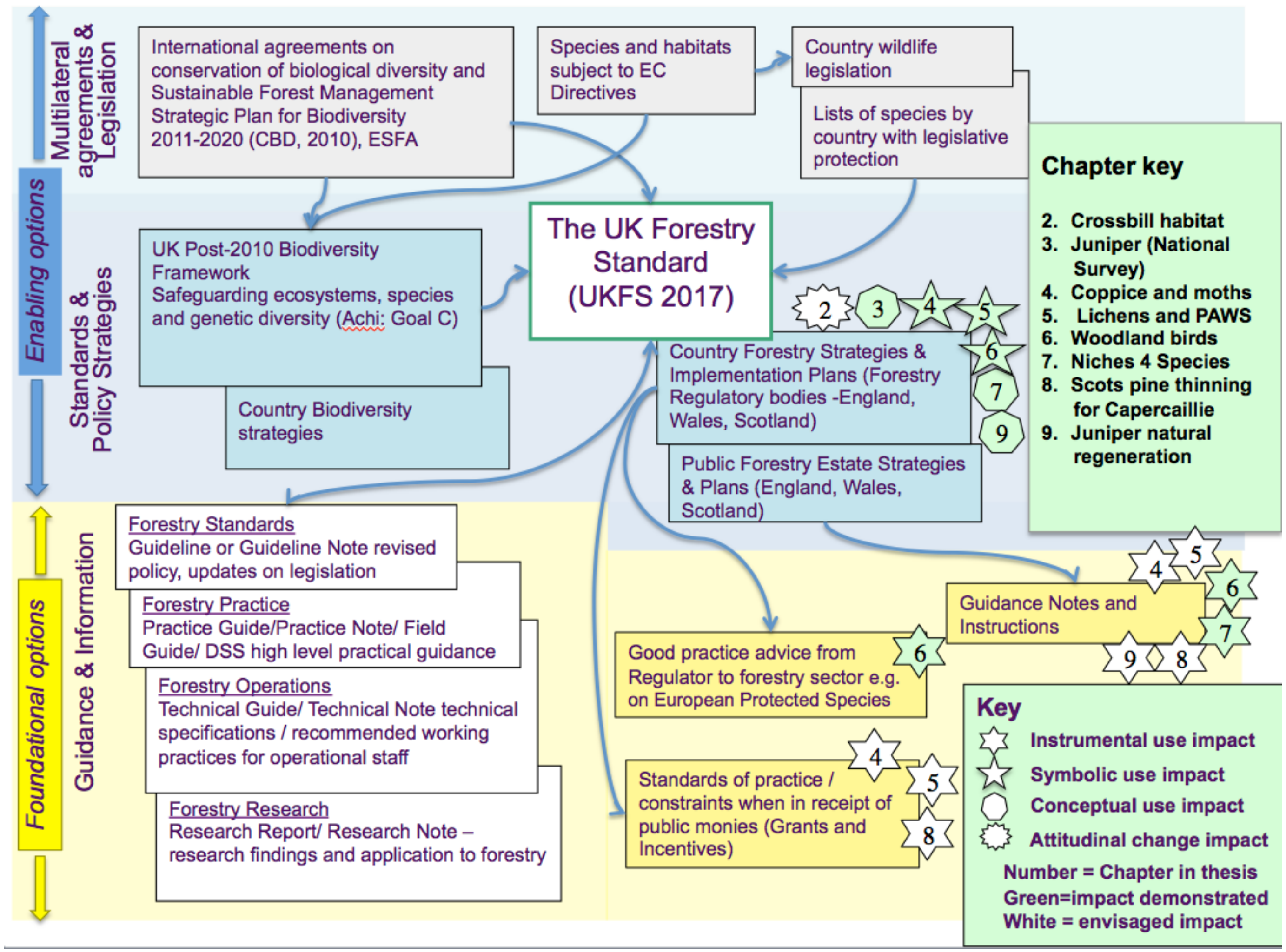

Figure 10.1 Impact of my research within the context of response options for sustainable management of British forests. The ‘enabling’ options are divided in to those relating to international agreements and legislations, and national and country policies. The ‘foundational’ options are described by a range of knowledge sources ranging from the guidance series produced to support the UK Forestry Standard (e.g. Guides and Notes on Standards and Practice) to bespoke advice and guidance relating to specific Forestry sector needs. Numbered symbols represent where the information presented in this thesis (Chapters 2 to 9 - numbers) applies, and the type of impact (symbols) the information is having (green symbol) or is envisaged to have (white symbol). (Response options follow Vira et al, 2011 and impact type Meagher and Lyall 2013).

‘Instrumental use’ (direct impact of research on policy and practice) has been made of Chapter 6, as it has been identified to be of direct relevance in drawing-up sector guidance on woodland bird conservation in England and Scotland by conservation Advisors in both the forestry regulatory body and the public forest management body. Similarly, some of the species requirement information and the predictive model outputs from Chapter 7 have been written in to guidance for managers of the public forest estate in Scotland (Wildlife and Country Act, Schedule 8 lower plants- internal guidance documents), again demonstrating ‘instrumental use’.

Where research results are used to legitimise or lend credibility to decisions or policies that have already been taken or put in place, the impact is viewed as ‘symbolic use’ (Meagher and Lyall, 2013). Although a less well regarded form of impact, ‘symbolic use’ of my findings supports general principles already used in the policy narratives and the detail of the work itself could have an ‘instrumental use’ providing specific examples if and when policy documents are updated (Stevens 2011). For example, findings of Chapter 4 on coppice management and moth species, and Chapter 6 on woodland management for declining bird species are examples of the ‘symbolic use’ impact as the importance of managing neglected woodlands, creating temporary open space and diversity of woodland structures to benefit woodland biodiversity is stated in the forestry strategies (e.g. Forestry Commission England’s 2007 Wood Fuel strategy). Further, ‘symbolic use’ impacts are demonstrated by the findings of Chapter 5 as these do not challenge the ecological-benefits arguments supporting PAWS restoration targets which appear in the Forestry Strategies of all the countries (Welsh Assembly Government, 2009; Welsh Government, 2018; Defra 2007; Scottish Executive, 2006).

The Niches for Species model (Chapter 7) has been advocated by the conservation Advisor in the forestry regulatory body in Scotland as a method available to underpin woodland expansion decisions, indicating to nature NGOs that there is an objective process which they can scrutinise, being applied (Broome et al, 2018). Interchanges such as these demonstrate impacts of ‘conceptual use’ and ‘attitudinal change’. Whilst the findings of Chapter 3 and 9 have not resulted in changes to grants provided for juniper conservation, removing designation status from juniper sites which appear no longer to have the capacity to regenerate, has been discussed internally between public forest estate Conservation Advisors and Nature Agency Staff, indicating the ‘conceptual use’ impact of my research. I have identified one Chapter as being linked to ‘attitudinal use’ impact. The dependence of the Scottish endemic bird species, (Scottish crossbill) on lodgepole pine seed is demonstrated in Chapter 2. However, current forestry policy on forest resilience issued by the regulatory body for forestry in Scotland is to remove and not replace lodgepole pine, particularly from eastern conifer woodlands https://scotland.forestry.gov.uk/supporting/strategy-policy-guidance/resilient-forests/overview-of-forest-resilience#pine. Clearly the impact of Chapter 2 has not been demonstrated but this could be because the findings’ importance has been overshadowed by the need to protect the Scots pine woodland resource from Dothestroma Needle Blight, for which lodgepole pine removal is the main phytosanitory measure (Brown and Webber 2008).

10.4.2 Scale and detail of information to match end-user needs

In improving evidence-based conservation, it is important that the type of research carried out and the way it is disseminated considers the end user and addresses their evidence needs (Di Marco et al, 2017). The user’s needs will direct the spatial scale over which the information should apply and level of detail which it needs to contain (Sutherland et al, 2006). For woodland protected species in Britain, the evidence-users will range from forest policy makers requiring strategic level information with data summarised to the regional or national scale, forest planners making tactical decision at the forest or region scale, and forestry practitioners making decisions at the operational scale and requiring information at the forest or stand level. Most of the impacts described above (10.4.2) relate to strategic and national level decision-making. However, several of the Chapters in my thesis provide evidence which could support tactical and operational decision-making important to woodland protected species conservation. Such decisions may relate particularly to timing and location of woodland operations. For example:

- retaining patches of derelict coppice within a landscape of actively managed coppice for the rarer moth species it will support (Chapter 4);

- creating a diversity of stand structures suitable for declining woodland bird species with a focus on restructuring those stands which provide the least suitable habitat (Chapter 6);
- permitting clearfelling of conifers at PAWs sites when developing restoration plans (Chapter 5).

Evidence to support operational decision-making has been identified in several chapters:

- to help in avoiding damage during operations to important features in stands which could harbour protected species (Chapter 7),
- to help guide thinning operations (Chapter 8);
- in choosing between interventions to apply on different sites (Chapter 9).

Application of the above evidence is at the moment aspirational and may not be seen in the short or even medium term (1-3 years), although co-developing research (e.g. Chapter 7) with decision makers can assist in dissemination (e.g. Valls-Donderis et al, 2014), the processes allowing formal take-up of evidence often requires time.

10.5 Single versus multi species conservation approach

It is debateable which approach is more effective in supporting evidence-based conservation. In support for the efficacy of a single species approach several authors have reported that species recovery plans for a single species have been shown to perform better than plans attempting to cover multiple species, as measured by positive species recovery trends (Boersma et al, 2001; Lundquist et al, 2002; Taylor et al, 2005). Other authors have used modelling approaches to study the co-existence of species to investigate benefits of conservation of single/target species compared to multiple species (e.g. Roberge and Anglestram 2004; White et al, 2013; Tarjuelo et al, 2014; Laub and Budy 2015). They conclude that abundance of co-occurring species was consistently higher in sites where umbrella species were present, particularly where the umbrella species was a bird. More recent literature lends support to these findings but also indicate that divergent taxa may not be well represented by the umbrella or surrogate species (Senzaki et al, 2015; Barrientos and Arroyo 2014; Santangeli et al, 2015; Dorey et al, 2018). In Chapter 7, I attempt to collate habitat needs classified in to woodland niches for c. 200 protected species representing seven taxon groups. It is clear from the work presented in Chapter 7, that there is a diversity of habitat needs and that one management prescription to manipulate the habitat would not benefit all the species a habitat could potentially support. Model based studies which investigate the co-occurrence of species, are mostly directed towards planning, monitoring or refugia identification for target species. However, evidence is also needed on how species may respond to management of habitat.

In Chapters 4, 5 and 6, I focus on response of groups of species to habitat management. Overall, these Chapters show that management can be beneficial or neutral for the species group. However, to benefit all members of the birds and the coppice-moth groups, a diversity of habitat conditions are required which cannot always be delivered by a single management prescription (Hiers et al, 2016). A review of the broader literature on woodland interventions, whether they are aimed to benefit single species, species groups or habitat attributes, would be needed to understand at what level management should be targeted to deliver most effective species conservation. Until this work is completed, I suggest adopting a pragmatic approach based on the level of legal protection applied to a species. For example, single species research should be conducted to provide evidence to support guidance for species with a high level of legal protection and for which thresholds of management impact need to be set, but for taxa where compliance with legislation requires forestry decision-makers to demonstrate intent to conserve, research should be designed to provide evidence to guide a broader species group and habitat level approach to protected species conservation.

10.6 Conclusions

To aid in the conservation of biodiversity, researchers are challenged with providing evidence urgently needed by decision-makers. In my thesis I have attempted to demonstrate how I have conducted research to support conservation policy and management for protected woodland species in Britain. I have considered my success in supporting evidence-based conservation against how appropriate, sound and accessible is my research. Critically, I show that evidence I have generated is having an impact on policy and practice. Working closely with policy and practice does present challenges such as the need to adapt research direction to track the changing policy agenda (e.g. single to multi-species approaches). I suggest it is important that researchers understand the environments to which their studies relate (e.g. the management potential and past management histories), and the type of research that is appropriate based on what is already known (e.g. about a species). Further it is important researchers understand the policy and governance systems into which their evidence needs to fit, and how to factor-in decision-makers requirements to make the guidance tractable and tailored to end users needs.

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