

This is the peer reviewed version of the following article: Law, A, Baker, A, Sayer, C, et al. The effectiveness of aquatic plants as surrogates for wider biodiversity in standing fresh waters. *Freshwater Biol.* 2019; 64: 1664– 1675, which has been published in final form at <https://doi.org/10.1111/fwb.13369>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for self-archiving.

1 The effectiveness of aquatic plants as surrogates for wider biodiversity in standing fresh
2 waters

3
4 Alan Law^{1*}, Ambroise Baker^{2, 3}, Carl Sayer², Garth Foster⁴, Iain D. M. Gunn⁵, Philip Taylor⁵,
5 Zarah Pattison¹, James Blaikie¹, and Nigel J. Willby¹

6 ¹ Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA,
7 UK

8 ² Pond Restoration Research Group, Environmental Change Research Centre,
9 Department of Geography, University College London, London, WC1E 6BT, UK

10 ³ School of Science, Engineering and Design, Teesside University, Middlesbrough,
11 TS1 3BX, UK

12 ⁴ Aquatic Coleoptera Conservation Trust, 3 Eglinton Terrace, Ayr, KA7 1JJ, UK

13 ⁵ Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB,
14 UK

15

16 * Corresponding author:

17 alan.law1@stir.ac.uk

18 Biological and Environmental Sciences, Cottrell building, University of Stirling,
19 Stirling, FK9 4LA, UK.

20

21 **Keywords:** Lake, pond, macrophyte morpho-group, macroinvertebrates, structural equation
22 modelling.

23

24 **Summary**

- 25 1. Fresh waters are among the most globally threatened habitats and their biodiversity is
26 declining at an unparalleled rate. In an attempt to slow this decline, multiple
27 approaches have been used to conserve, restore or enhance waterbodies. However,
28 evaluating their effectiveness is time-consuming and expensive. Identifying species or
29 assemblages across a range of ecological conditions that can provide a surrogate for
30 wider freshwater biodiversity is therefore of significant value for conservation
31 management and planning.
- 32 2. For lakes and ponds in three contrasting landscapes of Britain (lowland agricultural,
33 eastern England; upland, north-west England; urban, central Scotland) we examined
34 the link between macrophyte species, macrophyte morpho-group diversity (an
35 indicator of structural diversity) and the richness of three widespread aquatic
36 macroinvertebrate groups (molluscs, beetles and odonates) using structural equation
37 modelling. We hypothesised that increased macrophyte richness and, hence, increased
38 vegetation structural complexity, would increase macroinvertebrate richness after
39 accounting for local and landscape conditions.
- 40 3. We found that macrophyte richness, via macrophyte morpho-group diversity, were an
41 effective surrogate for mollusc, beetle and odonate richness in ponds after accounting
42 for variation caused by physical variables, water chemistry and surrounding land use.
43 However, only mollusc richness could be predicted by macrophyte morpho-group
44 diversity in lakes, with no significant predicted effect on beetles or odonates.
- 45 4. Our results indicate that macrophyte morpho-group diversity can be viewed as a
46 suitable surrogate of macroinvertebrate biodiversity across diverse landscapes,
47 particularly in ponds and to a lesser extent in lakes. This has important implications
48 for the restoration, conservation and creation of standing water habitats and for

49 assessing their effectiveness in addressing the decline of global freshwater
50 biodiversity. Management actions prioritising the development of species-rich and
51 structurally diverse macrophyte assemblages will likely benefit wider freshwater
52 biodiversity.

53 **Introduction**

54 A biological surrogate, indicator or proxy is an individual or group of organisms that
55 can be used to identify a healthy, biodiverse or functional ecosystem, or to infer
56 environmental conditions existing now or in the past. Such surrogates are commonly used in
57 conservation decision making and offer a means of choosing and tracking the effectiveness of
58 management approaches, with the premise that, if the surrogate is protected and conserved,
59 there will be wider biodiversity and ecosystem benefits (Caro, 2010). A further advantage of
60 surrogates is reduced reliance on large-scale, multi-taxon surveys which are time-consuming,
61 expensive and often require specialist knowledge. Quantifying the link between surrogates
62 and wider biodiversity or functioning of an ecosystem is crucial for validation, yet numerous
63 studies conducted across several ecosystems and species have failed to identify consistent,
64 reliable surrogates of either biodiversity, ecosystem function or phylogenetic diversity
65 (Heino, 2015; Rapacciolo *et al.*, 2018). Despite this, improved ecological knowledge and
66 data accessibility, alongside advancing analytical tools, offer renewed promise in the search
67 for surrogates. This is particularly relevant in freshwater ecosystems as they are one of the
68 most globally threatened habitats due to the scale of humans impacts (Reid *et al.*, 2018;
69 WWF, 2018).

70 Numerous studies have sought to evaluate surrogacy in freshwaters, with
71 macroinvertebrates receiving most attention. For ponds and rivers there is broad consensus
72 that a few species-rich invertebrate groups (e.g. Coleoptera, Odonata, Mollusca and
73 Trichoptera) are broadly representative of wider macroinvertebrate assemblages (Briers &
74 Biggs, 2003; Bilton *et al.*, 2006; Sánchez-Fernández *et al.*, 2006; Ruhí & Batzer, 2014; Guan
75 *et al.*, 2018). However, where surrogacy across different taxonomic groups has been studied
76 e.g. plants or amphibians to macroinvertebrates, the results have been inconsistent, with
77 relationships variously non-existent (Santi *et al.*, 2010; Guareschi *et al.*, 2015), weak (Heino,

78 2010; Kirkman *et al.*, 2012; Rooney & Bayley, 2012; Ilg & Oertli, 2017), moderate (Santi *et*
79 *al.*, 2010; Gioria *et al.*, 2010) or strong (Janssen *et al.*, 2018). Most previous research has
80 concentrated on one or two taxonomic groups, focussing on a single habitat type, distributed
81 over a small geographical range. Therefore, even at small-scales, there is limited evidence of
82 effective surrogates for wider freshwater biodiversity.

83 Aquatic plants (macrophytes), encompassing bryophytes, macroalgae and vascular
84 plants, are a fundamental component of aquatic food webs and play a central role in nutrient
85 flux within freshwater habitats, linking atmosphere, soil and water. They influence the quality
86 of the surrounding aquatic environment by creating structurally-complex habitats comprised
87 of submerged, floating and emergent vegetation, where differences in leaf and stem
88 architecture (e.g. floating vs. simple linear vs. dendritic leaves) between species, diversifies
89 habitat complexity where it might otherwise be low (Jeppesen *et al.*, 1998). Furthermore, as
90 primary producers, macrophytes influence water chemistry, provide food for grazers, habitats
91 for egg-laying, whilst also mediating predator-prey interactions through provision of refugia
92 for prey and concealment for predators (Diehl & Kornijow, 1998; Jeppesen *et al.*, 1998). A
93 shared response to environmental conditions is often believed to be a key driver of species
94 surrogacy (Gioria, Bacaro & Feehan, 2011; Rooney & Bayley, 2012), but, given the key
95 structuring role of macrophytes, and their potential to operate as ecosystem engineers
96 (Gurnell *et al.*, 2013), it seems highly likely that their presence and richness will directly or
97 indirectly govern the availability of resources to, and environmental suitability for, other
98 species. Since they are taxonomically and ecologically well understood and occur in almost
99 all freshwater habitat types globally, macrophytes may thus be an ideal surrogate for wider
100 freshwater biodiversity.

101 To our knowledge, the influence of macrophyte richness on multiple aquatic biota,
102 across different freshwater habitats and covering environmentally diverse conditions has not

103 previously been examined. Therefore, current understanding of the potential value of
104 macrophytes as a surrogate is constrained. In this study, aquatic molluscs, aquatic beetles and
105 odonates were selected as focal biota due to their high taxonomic diversity, widespread
106 distribution in standing fresh waters and because all three groups include species of
107 conservation concern. Our primary objective was to test whether macrophytes act as
108 surrogates for wider freshwater biodiversity across three contrasting (agricultural, upland and
109 urban), but typical aquatic landscapes (so-called ‘hydrosapes’). We did this by assessing the
110 strength of chemical and physical drivers and surrounding land use in explaining waterbody-
111 scale richness of the biota. At the same time, we additionally tested if macrophyte species
112 richness, mediated through morpho-group diversity, could further explain macroinvertebrate
113 richness. We hypothesised that waterbodies with higher macrophyte richness, and, hence,
114 greater macrophyte morpho-group diversity (an indicator of structural diversity), would have
115 greater macroinvertebrate richness, with the former being a stronger predictor than chemical,
116 physical and surrounding land use. However, further macroinvertebrate assemblage-specific
117 effects are expected, reflecting either differences in the degree of dependence on macrophytes
118 for habitat support, or habitat type-specific (pond or lake) differences in the importance of
119 macrophytes as a component of habitat diversity.

120

121 **Methods**

122 *Study areas and data collection*

123 Three contrasting landscapes were chosen within Britain to account for different
124 combinations of stressors associated with different land use types; lowland agricultural
125 (north-east Norfolk, eastern England), upland (Cumbria, north-west England) and urban
126 (Greater Glasgow, central Scotland). Within each of these hydrosapes, 22-29 replicates of
127 both lakes and ponds were sampled. In this study, lakes were defined as waterbodies with

128 surface area > 1 ha, while ponds were < 1 ha in area and generally shallow (< 2 m max.
129 depth). Both categories included man-made and natural waterbodies. Within each of these
130 waterbodies four taxonomic groups were selected to cover a range of habitat requirements,
131 pollutant sensitivities and dispersal abilities, namely macrophytes (as surrogates), aquatic
132 molluscs, aquatic beetles (hereafter referred to as molluscs and beetles) and odonates (dragon
133 and damselflies). Extensive data on these taxonomic groups were obtained via national
134 recorders (i.e. Aquatic Coleoptera Conservation Trust, British Conchological Society and
135 British Dragonfly Society), while water chemistry, where available, and data on macrophytes
136 from commissioned surveys, was provided by UK environmental agencies or the Joint Nature
137 Conservation Committee (JNCC). All data were closely scrutinised to ensure inter-
138 compatibility, with multi-visit, full inventory surveys prioritised. Only records from the last
139 decade were retained. The availability of multiple recent records of adult odonates influenced
140 site selection because favourable weather conditions for surveying these could not be
141 guaranteed during field campaigns conducted for this study. Where gaps in the data existed or
142 when a greater number of replicate waterbodies were needed, new data were collected during
143 June to August of 2016-17. Several sites had data collected for all species assemblages and
144 88% of the sites used in the study were visited by the authors to gather additional data for at
145 least one species assemblage or to collect water samples for water chemistry analysis (Table
146 S1).

147 For each waterbody, the following physical variables were derived from the UK
148 Lakes Portal (<https://eip.ceh.ac.uk/apps/lakes/index.html>); altitude, area, catchment size,
149 perimeter, ratio of waterbody to catchment area and shoreline development index (indicating
150 shape complexity of the shoreline). For water chemistry data provided by UK environmental
151 agencies, a mean value was taken for each variable based on samples collected in summer
152 (June-September). In all other cases we collected a water sample from the middle of each site

153 and measured conductivity, dissolved oxygen, oxygen saturation, pH and temperature in the
154 field using a HACH HQ30d meter. Alkalinity was also measured in the field by titration
155 using sulphuric acid with a HACH AL-DT kit. A 500 ml subsample was filtered (47 mm
156 glass microfiber, 1.2 μm pore Whatman GF/C filters) within 12 hours of collection and
157 analysed for major nutrients and metals (see Table S2 for a list of determinands). Chlorophyll
158 *a* was determined by extraction by soaking filters in 90% methanol overnight and
159 quantification by spectrophotometry.

160 For surveys of biota, exhaustive inventory sampling was conducted for each taxon
161 group covering the complete margin of each waterbody. Macrophytes were recorded from the
162 marginal zone to the maximum growing depth, assisted by use of a double-headed rake
163 and/or a bathyscope for deeper water or where visibility was poor. For ponds, the entire water
164 area was surveyed. For lakes, three or four sectors, each covering 100 m of shoreline, were
165 surveyed to account for variation in exposure, shading, water depth and littoral substrate,
166 following the JNCC survey methodology (Interagency Freshwater Group 2015). Within each
167 sector, five transects were established perpendicular to the shore and four replicate quadrats
168 were sampled per transect at depths of 0.25 m, 0.50 m, 0.75 m and >0.75 m, respectively,
169 giving a total of 60 to 80 quadrats per lake. A boat was used to survey areas that were too
170 deep for survey by wading (>75 cm).

171 Molluscs, beetles and larval odonates were sampled using a 1 mm mesh pond net. For
172 each waterbody, the number of mesohabitats (e.g. rocky substrate, floating leaved, short/tall
173 emergent, or submerged vegetation) was visually assessed and all were then sampled by
174 sweeping the pond net through the water column and any vegetation present. This was
175 repeated in each mesohabitat until no more new species could easily be found. The sample
176 was live sorted and individuals were identified to species level in the field and released.
177 When individuals could not be identified in the field they were preserved in 70% industrial

178 methylated spirits (IMS) and identified to species-level, wherever possible. Adult odonates
179 were identified visually in the field, assisted by use of binoculars. Where individuals within a
180 taxonomic group were identified to mixed resolution, only the highest resolution records
181 were used.

182

183 *Land cover and connectivity*

184 Land Cover Maps (Rowland *et al.*, 2017) were used to assess land use within the
185 upstream catchment of each waterbody (representing hydrological connectivity), and within
186 buffers of 50 m, 100 m, 500 m and 1 km surrounding each waterbody (representing riparian
187 and aerial connectivity). To reduce the number of interrelated land cover categories, a series
188 of composites were created; agricultural (arable and horticulture + improved grassland);
189 urban (suburban + urban) and wetland (fen, marsh and swamp + bog). Within each
190 waterbody buffer or catchment, land cover classes were expressed as a percentage of the total
191 buffer or catchment area (minus the area occupied by the focal waterbody). Since freshwater
192 and wetland land cover classes exhibited a high number of zero or low values these classes
193 were transformed to absence (-1) and presence (1) to make their effect sizes directly
194 comparable with those of continuous predictors.

195

196 *Variable selection and statistical analyses*

197 Species richness was defined as the number of macrophyte or macroinvertebrate
198 species per waterbody (or highest taxonomic resolution). Macrophyte morpho-group
199 diversity was derived by assigning each species to one of 26 morpho-groups based on a
200 library of morphological and regenerative traits (Willby, Abernethy & Demars, 2000), but
201 expanded to incorporate bryophytes, macroalgae and a wide range of emergent species (Table
202 S3). To determine if a sufficient number of waterbodies were surveyed per hydroscape for the

203 four taxonomic groups, sample coverage was calculated based on incidence data per
204 waterbody using the iNEXT library (Hsieh, Ma & Chao, 2016). Prior to statistical analyses
205 all continuous explanatory variables (excluding pH) were log transformed, mean centred and
206 scaled by 1 SD, to improve comparability between variables and to reduce the effect of
207 outliers (full set of continuous variables given in Figure S1). 64% of ponds sampled
208 (especially those <0.1 ha) did not have definable catchments, so a binary ‘catchment present’
209 category was created for all ponds. Binary explanatory variables (e.g. catchment present for
210 ponds, outflow and inflow) were transformed to have values of -1 (absent) and 1 (present).

211 To reduce model complexity principal components analysis (PCA) was applied to
212 separate sets of water chemistry, physical and land use variables to identify those variables
213 that maximised variation amongst sites (Figure S1). All continuous explanatory variables
214 (excluding pH) were log transformed, mean centred and scaled by 1 SD, to improve
215 comparability between variables and to reduce the effect of outliers. Correlations between
216 predictor variables were then assessed in a correlation matrix (Figure S1) and checked for
217 variance inflation (VIF). Where variables were highly correlative ($VIF > 20$) they were
218 removed. The remaining variables were then used as explanatory variables for macrophyte
219 species richness in a linear model (LM) with model-averaging then implemented (Burnham
220 & Anderson, 2002). Variables that significantly explained macrophyte richness, based on the
221 sums of Akaike weights (Figure S1), were then retained.

222 A conceptual model was developed to incorporate expected relationships between
223 species richness and explanatory variables (Fig. 1). This model was based on the simple
224 hypothesis that connectivity, land use and waterbody physical and water chemistry variables
225 influence macrophyte species richness to a greater extent than macrophyte morpho-group
226 diversity or richness of the macroinvertebrate groups, and that it is predominantly via
227 macrophytes that these environmental effects are transmitted to macroinvertebrates. We also

228 hypothesised that macrophyte morpho-group diversity would be a more important
229 determinant of macroinvertebrate richness than macrophyte taxonomic richness due to the
230 increased structural complexity that a high richness of macrophyte morpho-groups provides.
231 We used structural equation modelling (SEM) to quantify the direct and indirect effects of
232 these explanatory variables on macrophyte richness, macrophyte morpho-group diversity and
233 macroinvertebrate richness. SEMs are a multivariate technique based on constituent LMs that
234 allow standardised comparisons of direct and indirect relationships. Constituent LMs were
235 created and residuals assessed to determine if they met linear model assumptions and
236 examined for spatial autocorrelation using Moran's I statistic. All constituent LMs met linear
237 model assumptions and no significant patterns in spatial autocorrelation were detected ($P >$
238 0.05). Bivariate relationships between each response and explanatory variable were explored
239 graphically to identify potential non-linear relationships. Where non-linear relationships were
240 found, the explanatory variable was converted to second degree orthogonal polynomials. No
241 multicollinearity was detected in constituent LMs with a VIF threshold of < 5 . During SEM
242 model evaluation, missing pathways (i.e. previously unconsidered significant relationships)
243 were identified and incorporated into the final SEM. Model fit was assessed using Fisher's C,
244 where values of $P > 0.05$ indicated that the model was supported by the observed data. The
245 term hydroscape ('Agricultural', 'Upland' and 'Urban') was added to each constituent LM,
246 but was never significant and often increased the VIF due to correlations with land use.
247 Hydroscape was then added as a random effect to each constituent LM, but did not improve
248 the AIC. Therefore, the term hydroscape was not included in the final SEMs.

249 All statistical analysis was conducted using RStudio (R Core Team, 2018) with the
250 libraries: piecewiseSEM (Lefcheck, 2016), sp (Bivand, Pebesma & Gomez-Rubio, 2013),
251 sjPlot (Lüdecke, 2018), MuMIn (Bartoń, 2018), ggbiplot (Vu, 2011), factoextra (Kassambara

252 & Mundt, 2017), FactoMineR (Le, Josse & Husson, 2008), iNEXT (Hsieh *et al.*, 2016) and

253 spdep (Bivand, Hauke & Kossowski, 2015).

254

255 **Results**

256 The *a priori* designation of the three hydrosapes as upland, urban or agricultural was
257 confirmed by analysis of the catchment characteristics of their constituent waterbodies (Table
258 1).

259 In total 176, 52, 249 and 35 species of macrophyte, mollusc, beetle and odonates
260 respectively were recorded across the 158 waterbodies, studied via a combination of our
261 surveys and archived data. Estimated sample coverage was generally high (mean = 94%)
262 indicating effective sampling of each taxonomic group per waterbody type per hydroscape
263 (Table 2). Further details of the sampling efficiency and completeness can be found in Figure
264 S2 in the supporting information.

265 For both lakes and ponds, correlations in raw species richness was compared amongst
266 the taxonomic groups (Figure S3), but none were found to be significant. Therefore,
267 environment variables have to be considered in order to deduce true correlative relationships
268 between the taxonomic groups.

269 Our conceptual model (Fig. 1) was poorly supported for both lakes and ponds, with
270 multiple missing significant pathways being identified. However, with the addition of these
271 pathways to the SEM (Table S4) the goodness-of-fit for both models reproduced the data
272 well (lakes: Fisher's $C = 162.3$, $df = 164$, $P = 0.523$; ponds: Fisher's $C = 121.2$, $df = 124$, $P =$
273 0.554). Unstandardised and standardised effect sizes of all explanatory variables for lakes and
274 ponds are provided in Table S5.

275 In lakes, macrophyte richness was explained principally by water chemistry and to a
276 lesser extent by nearby land use ($R^2 = 0.64$) (Fig. 2). Variables indicative of nutrient-
277 enrichment or poor water quality (nitrate, total phosphorus and water colour) negatively
278 affected macrophyte richness, with nearby agricultural land positively influencing
279 macrophyte richness. Macrophyte morpho-group diversity was, as expected, strongly related

280 to macrophyte richness. However, the subsequent effect on macroinvertebrates was varied;
281 macrophyte morpho-group diversity positively influenced mollusc richness, but had no effect
282 on beetle and odonate richness. For the latter groups, environmental conditions (i.e. land use
283 and waterbody physical variables) were more influential. Increasing altitude was a strong,
284 negative determinant of both mollusc and odonate richness, with reasonable variance
285 explained for both assemblages ($R^2 = 0.76$ and 0.36). The explained variance in beetle
286 richness was the lowest of all the taxonomic groups ($R^2 = 0.29$) with only wetlands in the
287 catchment and nearby agricultural land positively affecting richness and, to a lesser extent,
288 lakes with relatively large catchments having a negative effect.

289 For ponds, nearby surrounding land use had no significant impact on macrophyte
290 richness compared to the influence of water chemistry (principally conductivity and pH) and
291 presence of an outflow (Fig. 3). Macrophyte morpho-group diversity was again strongly
292 related to macrophyte richness, whilst ammonium and nearby urban land use also had minor
293 negative effects on morpho-group diversity. The degree of urbanisation within 500 m of a
294 pond had contrasting effects on macroinvertebrate biota, being positive for molluscs, but
295 highly negative for beetles and odonates. A negative effect of altitude was observed for
296 mollusc and beetle richness in ponds, as with lakes. Nevertheless, despite some variation
297 being explained by physical variables, water chemistry and land use, an increased
298 macrophyte morpho-group diversity had a significant positive effect on all macroinvertebrate
299 groups.

300

301

302 **Discussion**

303 Simple surrogates for freshwater biodiversity should help to inform choices over the
304 protection, restoration or creation of waterbodies, and in monitoring the effectiveness of
305 related actions. However, few studies have sought out a surrogate appropriate for multiple
306 freshwater habitats and disparate species assemblages over large spatial scales. We found
307 that, regardless of the landscape, high macrophyte richness, specifically via high morpho-
308 group diversity, was a suitable surrogate for a higher richness of multiple macroinvertebrate
309 species assemblages (molluscs, beetles and odonates) in ponds, but only mollusc richness
310 could be predicted by macrophyte morpho-group diversity in lakes.

311

312 *The drivers of species richness*

313 Land use is often assumed to be a major driver of species composition as it provides a
314 proxy for stressors (e.g. agriculturally-derived nutrients or pollutants originating from urban
315 areas) (Hassall, 2014) or affects spatial processes (altering connectivity both positively and
316 negatively) (Hill *et al.*, 2017). Urbanisation is assumed to be indicative of reduced
317 connectivity due to the density of roads and built-up areas that restrict dispersal between
318 waterbodies (Hassall, 2014). Moreover, previous studies of ponds and rivers indicate that
319 active dispersers were less restricted by habitat structure than passive dispersers (Hill *et al.*,
320 2017; Sarremejane *et al.*, 2017). In our study, urban land use had a negative effect on
321 actively-dispersing odonates and beetles in ponds, suggesting that an active dispersal ability
322 may be insufficient to counteract effects of urbanisation and the associated changes to local
323 habitat structure that urbanisation produces. However, urban land use was positively
324 associated with passively dispersing molluscs. This latter finding may reflect the increased
325 presence of vectors within the local landscape (for example waterfowl attracted by
326 supplementary feeding may increase bird-mediated dispersal (van Leeuwen *et al.*, 2012;

327 Simonová *et al.*, 2016)), combined with molluscs' tolerance of productive poorly oxygenated
328 conditions. Alternatively, the increased concentrations of some major ions due to rural and
329 urban run-off may also benefit molluscs since calcium is used for shell construction (Moss,
330 2017). It was expected that adjacent agricultural land use would negatively affect biodiversity
331 due to increased nutrient or fine sediment inputs, yet agriculture within 500 m of lakes had a
332 slight positive effect on lake macrophyte richness. However, the interpretation that
333 agriculture is positive for biodiversity should be taken with caution, since in the composite
334 LMs that underpin the SEM, agricultural land use in the catchment as a whole had a non-
335 linear relationship with macrophyte richness, becoming negative when agricultural extent
336 exceeded ~40% (though this was not significant in the final model). Freshwaters and
337 wetlands in the catchment or buffers were expected to positively affect biodiversity as they
338 potentially increase connectivity, and therefore resilience, by acting as stepping stones (Biggs
339 *et al.*, 2005). Although we observed a positive effect of nearby wetlands (within a 500 m
340 buffer), or wetlands in the catchment on lake beetles and molluscs, respectively, this was
341 secondary to waterbody-specific influences (e.g. altitude and water chemistry), consistent
342 with other studies (Hill *et al.*, 2017; Thornhill *et al.*, 2017). Water chemistry influenced
343 macrophyte richness in both lakes and ponds, with variables indicative of nutrient-enrichment
344 negatively affecting richness. Alkalinity had a negative effect on lake macrophytes, which
345 was unexpected as previous work has generally shown a positive influence of alkalinity on
346 macrophyte richness (Vestergaard & Sand-Jensen, 2000). The effect we observed was most
347 likely driven by a strong correlation between alkalinity and total oxidised nitrogen or
348 conductivity (Figure S1), indicative of declining water quality (Heegaard *et al.*, 2001).
349 Waterbody chemistry had few direct effects on the studied macroinvertebrate groups and it is
350 therefore likely that macrophytes mediate nutrient-enrichment effects (Declerck *et al.*, 2005).

351 Identifying a simple surrogate of diverse and complex species assemblages that
352 transcends multiple, potentially interacting variables which vary both temporally and
353 spatially is difficult, with few variables seemingly transferable across habitat types, regions
354 and species assemblages (Batzler, 2013). Macrophyte richness and composition have
355 previously been shown to positively affect macroinvertebrate assemblages in multiple
356 freshwater habitats; ponds (Palmer, 1981; Gioria *et al.*, 2011), wetlands (Kirkman *et al.*,
357 2012), lakes (Heino & Tolonen, 2017) and rivers (Holmes & Raven, 2014). However, the
358 drivers of species surrogacy are mostly speculative rather than explicitly studied. In our
359 study, the most plausible basis for the surrogacy we observed is that good water quality
360 allows for high macrophyte richness, which leads to a greater diversity of macrophyte
361 morpho-groups and macroinvertebrate richness benefits through provision of increased
362 architectural complexity. These benefits are probably group- or life stage-specific. For
363 example, molluscs may benefit from high macrophyte richness due to increased food
364 resources, reduced predation and increased microhabitat diversity (Brönmark, 1985). Beetles
365 may benefit from the heterogenous substrate available for egg-laying, refugia and through
366 increased prey availability (Bloechl *et al.*, 2010). Furthermore, adult odonates use emergent
367 macrophytes for perching, egg-laying and emergence (Le Gall *et al.*, 2018), whereas their
368 larvae use submerged macrophytes for shelter and foraging (Goertzen & Suhling, 2013). A
369 greater macrophyte morpho-group richness linked to asynchronous growth peaks may also
370 extend the duration of macrophyte cover (van Donk & Gulati, 1995; Sayer, Davidson &
371 Jones, 2010) which should benefit macroinvertebrates, but this area is relatively unexplored.

372 It is also possible that some macroinvertebrate groups may influence the richness of
373 others, for example, via predation. However, as positive or negative pathways between any of
374 the macroinvertebrate groups were not identified in our analysis, we can hypothesize that the
375 effect of predation on richness are low, relative to the effect of macrophytes. Differences in

376 explained variance amongst macroinvertebrates were reasonably consistent across waterbody
377 types, with mollusc richness highest followed by odonates and then beetles. The low
378 explained variance observed for beetles may in part reflect the high species richness found.
379 Beetles are one of the most speciose groups globally with a wide geographical and ecological
380 range (Bilton *et al.*, 2006); moreover, the balance between habitat specialists and generalists
381 will be masked when considering diversity only in terms of species richness.

382 The strength of the surrogacy between macrophytes and macroinvertebrates differed
383 between waterbody types, with macrophyte richness being a stronger driver of
384 macroinvertebrate richness in ponds than lakes. This pattern may arise because lakes are
385 more likely to support large populations of fish, which are known to exert strong predation
386 pressure on macroinvertebrates (Diehl, 1992; Jones & Sayer, 2003). Molluscs, for example,
387 are commonly consumed by fish with resulting reductions in density, although effects on
388 richness are less understood (Dillon, 2000). Fish could also influence macroinvertebrates
389 indirectly via various cascading effects on macrophyte diversity caused by herbivory
390 (Matsuzaki *et al.*, 2009), zooplanktivory (Jeppesen *et al.*, 1998) or benthivory, particularly in
391 shallow lakes (Kloskowski, 2011). Both abundance of macrophytes and macroinvertebrates
392 will also be affected by waterfowl herbivory and bioturbation (Rodríguez-Pérez & Green,
393 2012; Wood *et al.*, 2012), with lakes likely to support greater waterfowl densities than ponds.
394 A further factor affecting macroinvertebrate diversity in lakes may be physical disturbance of
395 the shoreline due to wave action, which is much more intense in lakes than ponds due to an
396 increased fetch (Fairchild, Faulds & Matta, 2000). Given that our focal macroinvertebrate
397 groups, molluscs in particular, are poorly stream-lined and prone to being dislodged by
398 currents, their link with macrophyte diversity may reflect a shared need for sheltered
399 marginal habitats. In this study, it is likely that the effects of fish predation or physical
400 disturbance on macroinvertebrate richness is mediated through macrophyte morpho-group

401 diversity, as found in Cladocera (Burks, Jeppesen & Lodge, 2007), but further study would
402 be useful to tease apart the multiple interacting processes involved (see Dillon (2000) for a
403 review). Moreover, future studies should endeavour to determine fish abundance. As fish can
404 be important drivers of aquatic community composition (Scheffer *et al.*, 2006), their
405 inclusion will undoubtedly improve the predictive power of models and therefore the
406 application of surrogates in other freshwater habitats.

407

408 *Surrogacy and available statistical tools*

409 The search for widely applicable and robust surrogates of freshwater biodiversity has
410 probably been somewhat confounded by the differing statistical approaches used to detect
411 surrogacy (Gioria *et al.*, 2011). The majority of studies have tested congruence between
412 species assemblages by using multivariate ordination to consider the influence of local
413 environmental variables (Declerck *et al.*, 2005; Bilton *et al.*, 2006; Santi *et al.*, 2010; Gioria
414 *et al.*, 2010; Guareschi *et al.*, 2015). Others have utilised Mantel tests (Heino, 2010; Rooney
415 & Bayley, 2012; Ruhí & Batzer, 2014; Ilg & Oertli, 2017), species correlations (Sánchez-
416 Fernández *et al.*, 2006; Slimani *et al.*, 2019) or a Species Accumulation Index (Kirkman *et*
417 *al.*, 2012). In addition to the range of analytical methods used, the choice of diversity index
418 for assessing surrogacy also influences outcomes, with alternative measures of alpha
419 diversity (e.g. richness, functional and phylogenetic alpha) varying in their sensitivity to
420 environmental drivers (Heino & Tolonen, 2017). To our knowledge SEMs have not been
421 previously utilised in the quest for surrogacy in freshwater ecology. The advantage of SEMs
422 is that disparate species assemblages can be analysed in relation to environmental variables,
423 unlike most community analyses that can only directly compare two assemblages at a time.
424 Moreover, SEMs standardise across environmental variables without the need for multiple

425 tests that risk false positives, and can, therefore, elucidate the relative strengths of
426 explanatory variables in driving observed relationships.

427

428 *Applications*

429 An effective surrogate should be transferable over a broad context and offer a
430 currency that is understandable to a range of stakeholders. According to our findings,
431 macrophytes could meet these criteria in providing an indirect surrogate for molluscs, beetles
432 and dragonflies in ponds and for molluscs in lakes. Macrophyte richness as a freshwater
433 biodiversity surrogate could be applicable from local to landscape scales, and simplify complex
434 patterns and processes. By isolating the effects of multiple environmental and spatial
435 explanatory variables in our dataset we demonstrate statistically that, via the diversity of
436 morpho-group diversity, a greater richness of macrophytes is also broadly indicative of
437 greater richness across disparate macroinvertebrate groups in ponds and molluscs in lakes.
438 From an applied perspective, as macrophytes act as ecosystem architects, our findings
439 suggest that researchers or practitioners can straightforwardly obtain a broad indication of the
440 overall habitat quality and macroinvertebrate biodiversity by monitoring the number of
441 macrophyte species and diversity of macrophyte morpho-groups, especially in the case of
442 ponds. Despite the advantages of surrogates, they cannot replace detailed surveys of
443 taxonomic groups particularly where species are rare, specialists or of conservation interest.
444 Therefore, although our results show that macrophyte morpho-group diversity can be useful
445 to indicate freshwater biodiversity, some caution is required as these results may not be
446 definitive in the broad sense.

447 It has been argued that declines in macrophyte richness should be viewed as an early
448 warning system for declines in overall macrophyte abundance and hence the quality of the
449 wider environment (Sayer *et al.*, 2010). Hence, we would recommend practitioners and

450 conservation managers need to be concerned for wider biodiversity if macrophyte richness
451 begins to decrease. The use of macrophytes as freshwater biodiversity surrogates can be
452 important for rapid and cost-effective assessment of conservation and restoration projects,
453 however, they will be most effective where constraints to biodiversity are diagnosed and
454 addressed at site, habitat and landscape-scales. For example, at the site-scale, high grazing
455 pressures may limit macrophyte regeneration from seedbanks and therefore wider
456 biodiversity will only benefit if areas of macrophytes are protected from over-grazing and
457 high disturbance. Additionally, at the habitat or landscape-scale, species translocations may
458 be needed to enhance structural complexity if there are significant barriers to colonisation.
459 However, in using macrophytes as a proxy for wider biodiversity, particularly when assessing
460 habitat restoration, it should be recognised that macrophyte responses to management are
461 complex and can be highly variable (Phillips, Willby & Moss, 2016).

462

463

464 **Acknowledgments**

465 This research was financially supported by the Natural Environmental Research Council
466 Highlight Topics grant NE/N006437/1: Hydroscape - connectivity x stressor interaction in
467 freshwater habitats. We also thank our many data providers (Aquatic Coleoptera
468 Conservation Trust, Biological Records Centre, British Conchological Society, British
469 Dragonfly Society, Broads Authority, Buglife, Cumbria Wildlife Trust, ENSIS, Environment
470 Agency, Froglife, Glasgow City Council, Norfolk Biodiversity Information Service, RSPB,
471 Scottish Environment Protection Agency and Upland Waters Monitoring Network) and pay
472 tribute to the numerous volunteers who contribute their data to recording schemes and to the
473 many landowners for allowing access to their sites. We are also grateful to two anonymous
474 reviewers for providing helpful comments on this manuscript.

475

476 **Data Availability Statement**

477 All data referred to in this article and code used in analyses are deposited in DataSTORRE -
478 the University of Stirling research data repository.

479

480 **Conflict of Interest Statement**

481 The authors declare that they have no conflicts of interest in presenting this work for
482 publication.

483

484 **References**

- 485 Bartoń K. (2018). *MuMIn: Multi-Model Inference*. R package version 1.42.1. Available at:
486 <https://CRAN.R-project.org/package=MuMIn>
- 487 Batzer D.P. (2013). The seemingly intractable ecological responses of invertebrates in North
488 American Wetlands: A review. *Wetlands*, 33, 1–15. [https://doi.org/10.1007/s13157-](https://doi.org/10.1007/s13157-012-0360-2)
489 012-0360-2
- 490 Biggs J., Williams P., Whitfield M., Nicolet P. & Weatherby A. (2005). 15 years of pond
491 assessment in Britain: results and lessons learned from the work of Pond
492 Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15, 693–
493 714. <https://doi.org/10.1002/aqc.745>
- 494 Bilton D.T., Mcabendroth L., Bedford A. & Ramsay P.M. (2006). How wide to cast the net?
495 Cross-taxon congruence of species richness, community similarity and indicator taxa
496 in ponds. *Freshwater Biology*, 51, 578–590. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2427.2006.01505.x)
497 2427.2006.01505.x
- 498 Bivand R.S., Hauke J. & Kossowski T. (2015). Comparing Implementations of Estimation
499 Methods for Spatial Econometrics. *Journal of Statistical Software*, 63, 1–36
- 500 Bivand R.S., Pebesma E. & Gomez-Rubio V. (2013). Applied spatial data analysis with R (2nd
501 edition). New York: Springer
- 502 Bloechl A., Koenemann S., Philippi B. & Melber A. (2010). Abundance, diversity and
503 succession of aquatic Coleoptera and Heteroptera in a cluster of artificial ponds in
504 the North German Lowlands. *Limnologica - Ecology and Management of Inland*
505 *Waters*, 40, 215–225. <https://doi.org/10.1016/j.limno.2009.08.001>

506 Briers R.A. & Biggs J. (2003). Indicator taxa for the conservation of pond invertebrate
507 diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 13, 323–330.
508 <https://doi.org/10.1002/aqc.576>

509 Brönmark C. (1985). Freshwater snail diversity: effects of pond area, habitat heterogeneity
510 and isolation. *Oecologia*, 67, 127–131. <https://doi.org/10.1007/BF00378463>

511 Burks R. L., Jeppesen E., & Lodge D. M. (2001). Littoral zone structures as *Daphnia* refugia
512 against fish predators. *Limnology and Oceanography*, 46, 230-237.

513 Burnham K.P. & Anderson D.R. (2002). Model selection and multi-model inference: a
514 practical information-theoretic approach. New York: Springer

515 Caro T. (2010). Conservation by proxy: indicator, umbrella, keystone, flagship, and other
516 surrogate species. Island Press

517 Declerck S., Vandekerkhove J., Johansson L., Muylaert K., Conde-Porcuna M., Van Der Gucht
518 K., et al. (2005). Multi-group biodiversity in shallow lakes along gradients of
519 phosphorus and water plant cover. *Ecology*, 86, 1905–1915

520 Diehl S. (1992). Fish Predation and Benthic Community Structure - the Role of Omnivory and
521 Habitat Complexity. *Ecology*, 73, 1646–1661. <https://doi.org/10.2307/1940017>

522 Diehl S. & Kornijow R. (1998). The influence of submerged macrophytes on trophic
523 interactions among fish and macroinvertebrates. In: The Structuring Role of
524 Submerged Macrophytes in Lakes. (Eds E. Jeppesen, M. Søndergaard, M.
525 Søndergaard & K. Christoffersen), pp. 24–46. New York: Springer.

526 Dillon R.T. (2000). The ecology of freshwater molluscs. Cambridge University Press

527 Fairchild G.W., Faulds A.M. & Matta J.F. (2000). Beetle assemblages in ponds: effects of
528 habitat and site age. *Freshwater Biology*, 44, 523–534.
529 <https://doi.org/10.1046/j.1365-2427.2000.00601.x>

530 Le Gall M., Fournier M., Chaput-Bardy A. & Husté A. (2018). Determinant landscape-scale
531 factors on pond odonate assemblages. *Freshwater Biology*, 63, 306-317.
532 <https://doi.org/10.1111/fwb.13065>

533 Gioria M., Bacaro G. & Feehan J. (2011). Evaluating and interpreting cross-taxon
534 congruence: Potential pitfalls and solutions. *Acta Oecologica*, 37, 187–194.
535 <https://doi.org/10.1016/j.actao.2011.02.001>

536 Gioria M., Schaffers A., Bacaro G. & Feehan J. (2010). The conservation value of farmland
537 ponds: Predicting water beetle assemblages using vascular plants as a surrogate
538 group. *Biological Conservation*, 143, 1125–1133.
539 <https://doi.org/10.1016/j.biocon.2010.02.007>

540 Goertzen D. & Suhling F. (2013). Promoting dragonfly diversity in cities: Major determinants
541 and implications for urban pond design. *Journal of Insect Conservation*, 17, 399–409.
542 <https://doi.org/10.1007/s10841-012-9522-z>

543 Guan Q, Liu J., Batzer D.P., Lu X. & Wu H. (2018). Snails (Mollusca: Gastropoda) as potential
544 surrogates of overall aquatic invertebrate assemblage in wetlands of Northeastern
545 China. *Ecological Indicators*, 90, 193-
546 200. <https://doi.org/10.1016/j.ecolind.2018.01.069>

547 Guareschi S., Abellan P., Laini A., Green A. J., Sanchez-Zapata J. A., Velasco J., & Millan A.
548 (2015). Cross-taxon congruence in wetlands: Assessing the value of waterbirds as
549 surrogates of macroinvertebrate biodiversity in Mediterranean Ramsar sites.
550 *Ecological Indicators*, 49, 204-215.

551 Gurnell A.M., O'Hare M.T., O'Hare J.M., Scarlett P. & Liffen T.M.R. (2013). The
552 geomorphological context and impact of the linear emergent macrophyte,
553 *Sparganium erectum* L.: A statistical analysis of observations from British rivers.

554 *Earth Surface Processes and Landforms*, 38, 1869–1880.
555 <https://doi.org/10.1002/esp.3473>

556 Hassall C. (2014). The ecology and biodiversity of urban ponds. *Wiley Interdisciplinary*
557 *Reviews: Water* 1, 187–206. <https://doi.org/10.1002/wat2.1014>

558 Heegaard E., Birks H.H., Gibson C.E., Smith S.J. & Wolfe-Murphy S. (2001). Species-
559 environmental relationships of aquatic macrophytes in Northern Ireland. *Aquatic*
560 *Botany*, 70, 175–223. [https://doi.org/10.1016/S0304-3770\(01\)00161-9](https://doi.org/10.1016/S0304-3770(01)00161-9)

561 Heino J. (2015). Approaches, potential and pitfalls of applying bioindicators in freshwater
562 ecosystems. In: *Indicators and Surrogates of Biodiversity and Environmental Change*.
563 (Eds D. Lindenmayer, P. Barton & J. Pierson), pp. 91–100. CRC Press.

564 Heino J. (2010). Are indicator groups and cross-taxon congruence useful for predicting
565 biodiversity in aquatic ecosystems? *Ecological Indicators*, 10, 112–117.
566 <https://doi.org/10.1016/j.ecolind.2009.04.013>

567 Heino J. & Tolonen K.T. (2017). Untangling the assembly of littoral macroinvertebrate
568 communities through measures of functional and phylogenetic alpha diversity.
569 *Freshwater Biology*, 62, 1168–1179. <https://doi.org/10.1111/fwb.12934>

570 Hill M.J., Heino J., Thornhill I., Ryves D.B. & Wood P.J. (2017). Effects of dispersal mode on
571 the environmental and spatial correlates of nestedness and species turnover in pond
572 communities. *Oikos* 126, 1575–1585. <https://doi.org/10.1111/oik.04266>

573 Holmes N. & Raven P. (2014). *Rivers: A natural and not-so-natural history*. British Wildlife
574 Publishing.

575 Hsieh T.C., Ma K.H. & Chao A. (2016). iNEXT: An R package for rarefaction and extrapolation
576 of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456.
577 <https://doi.org/10.1111/2041-210X.12613>

578 Ilg C. & Oertli B. (2017). Effectiveness of amphibians as biodiversity surrogates in pond
579 conservation. *Conservation Biology*, 31, 437–445.
580 <https://doi.org/10.1111/cobi.12802>

581 Interagency Freshwater Group. (2015). Common Standards Monitoring Guidance for
582 Freshwater Lakes. Joint Nature Conservation Committee

583 Janssen A., Hunger H., Konold W., Pufal G. & Staab M. (2018). Simple pond restoration
584 measures increase dragonfly (Insecta: Odonata) diversity. *Biodiversity and
585 Conservation*, 27, 2311–2328. <https://doi.org/10.1007/s10531-018-1539-5>

586 Jeppesen E., Søndergaard M., Søndergaard M. & Christoffersen K. (1998). The Structuring
587 Role of Submerged Macrophytes in Lakes. New York: Springer

588 Jones, J.I. & Sayer, C. D. (2003). Does the fish-invertebrate-periphyton cascade precipitate
589 plant loss in shallow lakes? *Ecology*, 84, 2155-2167. <https://doi.org/10.1890/02-0422>

590 Kassambara A. & Mundt F. (2017). factoextra: extract and visualize the results of
591 multivariate data analyses. R package version 1.0.5. Available at: [https://CRAN.R-
592 project.org/package=factoextra](https://CRAN.R-project.org/package=factoextra)

593 Kirkman L.K., Smith L.L., Quintana-Ascencio P.F., Kaeser M.J., Golladay S.W. & Farmer A.L.
594 (2012). Is species richness congruent among taxa? Surrogacy, complementarity, and
595 environmental correlates among three disparate taxa in geographically isolated
596 wetlands. *Ecological Indicators*, 18, 131–139.
597 <https://doi.org/10.1016/j.ecolind.2011.10.015>

598 Kloskowski J. (2011). Impact of common carp *Cyprinus carpio* on aquatic communities:
599 direct trophic effects versus habitat deterioration. *Fundamental and Applied
600 Limnology*, 178, 245–255. <https://doi.org/10.1127/1863-9135/2011/0178-0245>

601 Le S., Josse J. & Husson F. (2008). FactoMineR: An R package for multivariate analysis.
602 *Journal for Statistical Software*, 25, 1–18

603 Lefcheck J.S. (2016). piecewiseSEM: Piecewise structural equation modeling in R for ecology,
604 evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579

605 Lüdecke D. (2018). sjPlot: Data Visualization for Statistics in Social Science. R package
606 version 2.6.0. Available at: <https://CRAN.R-project.org/package=sjPlot>

607 Matsuzaki S.S., Usio N., Takamura N. & Washitani I. (2009). Contrasting impacts of invasive
608 engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia*,
609 158, 673–686.

610 Moss B. (2017). Ponds and small lakes. Pelagic Publishing.

611 Palmer M. (1981). Relationship between species richness of macrophytes and insects in
612 some water bodies in the Norfolk Breckland. *Entomologists Monthly Magazine*, 117,
613 35–46

614 Phillips G., Willby N.J. & Moss B. (2016). Submerged macrophyte decline in shallow lakes:
615 What have we learnt in the last forty years? *Aquatic Botany*, 135, 37–45.
616 <https://doi.org/10.1016/j.aquabot.2016.04.004>

617 R Core Team (2018). R: A language and environment for statistical computing. R Foundation
618 for Statistical Computing, Vienna

619 Rapacciuolo G., Graham C.H., Marin J., Behm J.E., Costa G.C., Hedges S.B., et al. (2018).
620 Species diversity as a surrogate for conservation of phylogenetic and functional
621 diversity in terrestrial vertebrates across the Americas. *Nature Ecology & Evolution*,
622 3, 53–61. <https://doi.org/10.1038/s41559-018-0744-7>

623 Reid A.J., Carlson A.K., Creed I.F., Eliason E.J., Gell P.A., Johnson P.T.J., et al. (2018).
624 Emerging threats and persistent conservation challenges for freshwater biodiversity.
625 *Biological Reviews*, 94, 849-873. <https://doi.org/10.1111/brv.12480>

626 Rodríguez-Pérez H., & Green A. J. (2012). Strong seasonal effects of waterbirds on benthic
627 communities in shallow lakes. *Freshwater Science*, 31, 1273-1288.

628 Rooney R. C., & Bayley, S. E. (2012). Community congruence of plants, invertebrates and
629 birds in natural and constructed shallow open-water wetlands: Do we need to
630 monitor multiple assemblages? *Ecological Indicators*, 20, 42-50.

631 Rowland C.S., Morton R.D., Carrasco L., McShane G., O'Neil A.W. & Wood C.M. (2017). Land
632 Cover Map 2015 (vector, GB)

633 Ruhí A. & Batzer D.P. (2014). Assessing Congruence and Surrogacy Among Wetland
634 Macroinvertebrate Taxa Towards Efficiently Measuring Biodiversity. *Wetlands*, 34,
635 1061–1071. <https://doi.org/10.1007/s13157-014-0566-6>

636 Sánchez-Fernández D., Abellán P., Mellado A., Velasco J. & Millán A. (2006). Are water
637 beetles good indicators of biodiversity in mediterranean aquatic ecosystems? The
638 case of the Segura River Basin (SE Spain). *Biodiversity and Conservation*, 15, 4507.
639 <https://doi.org/10.1007/s10531-005-5101-x>

640 Santi E., Mari E., Piazzini S., Renzi M., Bacaro G. & Maccherini S. (2010). Dependence of
641 animal diversity on plant diversity and environmental factors in farmland ponds.
642 *Community Ecology*, 11, 232–241. <https://doi.org/10.1556/ComEc.11.2010.2.12>

643 Sarremejane R., Mykrä H., Bonada N., Aroviita J. & Muotka T. (2017). Habitat connectivity
644 and dispersal ability drive the assembly mechanisms of macroinvertebrate
645 communities in river networks. *Freshwater Biology*, 62, 1073–1082.
646 <https://doi.org/10.1111/fwb.12926>

647 Sayer C.D., Davidson T.A. & Jones J.I. (2010). Seasonal dynamics of macrophytes and
648 phytoplankton in shallow lakes: a eutrophication-driven pathway from plants to
649 plankton? *Freshwater Biology*, *55*, 500–513. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2427.2009.02365.x)
650 [2427.2009.02365.x](https://doi.org/10.1111/j.1365-2427.2009.02365.x)

651 Scheffer M., van Geest G. J., Zimmer K., Jeppesen E., Sondergaard M., Butler M. G., Hanson
652 M. A., Declerck S., & De Meester L. (2006). Small habitat size and isolation can
653 promote species richness: second-order effects on biodiversity in shallow lakes and
654 ponds. *Oikos*, *112*, 227-231.

655 Simonova J., Simon O.P., Kapic S., Nehasil L., & Horsak M. (2016). Medium-sized forest snails
656 survive passage through birds' digestive tract and adhere strongly to birds' legs:
657 more evidence for passive dispersal mechanisms. *Journal of Molluscan Studies* *82*,
658 422-426.

659 Slimani N., Sánchez-Fernández D., Guilbert E., Boumaïza M., Guareschi S. & Thioulouse J.
660 (2019). Assessing potential surrogates of macroinvertebrate diversity in North-
661 African Mediterranean aquatic ecosystems. *Ecological Indicators*, *101*, 324–329.
662 <https://doi.org/10.1016/j.ecolind.2019.01.017>

663 Thornhill I., Batty L., Death R.G., Friberg N.R. & Ledger M.E. (2017). Local and landscape
664 scale determinants of macroinvertebrate assemblages and their conservation value
665 in ponds across an urban land-use gradient. *Biodiversity and Conservation*, *26*, 1065–
666 1086. <https://doi.org/10.1007/s10531-016-1286-4>

667 van Leeuwen C. H. A., van der Velde G., van Lith B., & Klaassen M. (2012). Experimental
668 quantification of long distance dispersal potential of aquatic snails in the gut of
669 migratory birds. *PLoS ONE* *7*(3): e32292. doi:10.1371/journal.pone.0032292

670 van Donk, E. & Gulati, R.D. (1995). Transition of a lake to turbid state six years after
671 biomanipulation: mechanisms and pathways. *Water Science and Technology*, 32,
672 197-206. [https://doi.org/10.1016/0273-1223\(95\)00699-0](https://doi.org/10.1016/0273-1223(95)00699-0)

673 Vestergaard O. & Sand-Jensen K. (2000). Aquatic macrophyte richness in Danish lakes in
674 relation to alkalinity, transparency, and lake area. *Canadian Journal of Fisheries and*
675 *Aquatic Sciences*, 57, 2022–2031. <https://doi.org/10.1139/f00-156>

676 Vu V.Q. (2011). ggbiplot: A ggplot2 based biplot. R package version 0.55. Available at:
677 <http://github.com/vqv/ggbiplot>

678 Willby N.J., Abernethy V.J. & Demars B.O.L. (2000). Attribute-based classification of
679 European hydrophytes and its relationship to habitat utilization. *Freshwater Biology*,
680 43, 43–74. <https://doi.org/10.1046/j.1365-2427.2000.00523.x>

681 Wood K. A., Stillman R. A., Clarke R. T., Daunt F., & O'Hare, M. T. (2012). The impact of
682 waterfowl herbivory on plant standing crop: a meta-analysis. *Hydrobiologia*, 686,
683 157-167.

684 WWF. 2018. Living Planet Report - 2018: Aiming Higher. Grooten, M. & Almond, R.E.A.(Eds).
685 WWF, Gland, Switzerland.

686

687 Table 1. A summary of environmental characteristics per waterbody type and hydroscape;
 688 mean \pm SE (min-max). Land use is representative from within catchments for lakes and the
 689 surrounding 500 m buffer for ponds.

Waterbody type	Hydroscape (No. waterbodies surveyed)	Size (ha.)	Altitude (m)	Urban (%)	Agriculture (%)	Freshwater (%)	Wetland (%)
Lake	Upland (n=27)	103.7 \pm 57.1 (1.5 – 1435.8)	166.9 \pm 20.5 (41.0 – 469.0)	0.4 \pm 0.2 (0.0 – 2.8)	14.0 \pm 4.1 (0.0 – 83.2)	7.0 \pm 0.9 (0.8 – 19.4)	0.1 \pm 0.1 (0.0 – 0.3)
	Urban (n=22)	15.3 \pm 4.8 (1.4 – 81.9)	93.3 \pm 11.6 (23.0 – 217.0)	17.1 \pm 5.1 (0.0 - 90.8)	33.2 \pm 4.1 (0.0 – 69.3)	7.5 \pm 1.3 (0.0 – 19.1)	4.2 \pm 1.8 (0.0 – 27.2)
	Agricultural (n=25)	14.5 \pm 3.4 (1.0 – 57.6)	14.6 \pm 4.5 (0.0 – 78.0)	4.2 \pm 1.0 (0.0 – 16.9)	61.7 \pm 5.1 (2.0 – 88.3)	7.9 \pm 2.4 (0.0 – 40.6)	4.9 \pm 2.8 (0.0 – 56.0)
Pond	Upland (n=27)	0.4 \pm 0.1 (0.1 - 1.6)	160.4 \pm 12.3 (64.0 – 306.0)	0.3 \pm 0.1 (0.0 – 2.2)	22.2 \pm 4.7 (0.0 – 75.5)	1.4 \pm 0.5 (0.0 – 12.2)	0.4 \pm 0.2 (0.0 – 5.5)
	Urban (n=26)	0.3 \pm 0.1 (0.1 - 1.2)	92.5 \pm 12.3 (9.0 – 233.0)	39 \pm 5.3 (0.0 – 98.9)	33.1 \pm 4.9 (0.0 – 94.6)	0.5 \pm 0.4 (0.0 – 12.2)	1.1 \pm 0.6 (0.0 – 16.6)
	Agricultural (n=30)	0.2 \pm 0.1 (0.1 - 1.2)	49.2 \pm 5.1 (0.0 – 82.0)	2 \pm 0.5 (0.0 – 13.4)	78.3 \pm 4.4 (14.4 – 99.4)	0.4 \pm 0.2 (0.0 – 4.1)	6.7 \pm 2.9 (0.0 – 58.5)

690

691

692

693

694

695

696

697 Table 2. Summary of species richness and sampling efficiency per waterbody type and
 698 hydroscape for each species assemblage. The estimated sample coverage gives an indication
 699 of the sampling completeness of each species group per waterbody type per hydroscape.

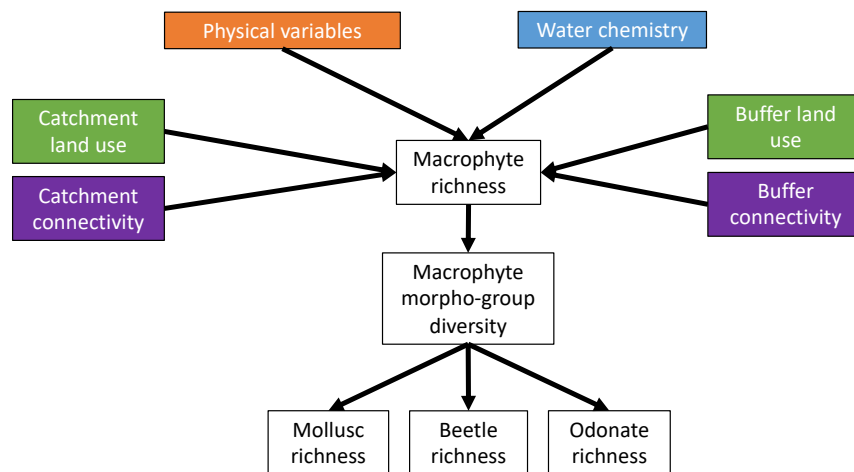
Waterbody type	Hydroscape (No. waterbodies surveyed)	Species group	Mean richness (range)	Total richness	Estimated sample coverage (%)
Lake	Upland (n=27)	Macrophytes	20 (11-34)	88	95
		Molluscs	4 (0-22)	22	80
		Beetles	13 (3-30)	86	90
		Odonates	6 (2-13)	19	98
	Urban (n=22)	Macrophytes	25 (12-39)	113	95
		Molluscs	8 (1-15)	28	97
		Beetles	16 (6-26)	68	95
		Odonates	5 (1-10)	10	100
	Agricultural (n=25)	Macrophytes	17 (3-29)	87	94
		Molluscs	16 (3-29)	46	99
		Beetles	20 (5-76)	157	87
		Odonates	16 (5-23)	34	98
Pond	Upland (n=27)	Macrophytes	15 (1-25)	86	95
		Molluscs	2 (0-5)	12	90
		Beetles	15 (3-35)	88	94
		Odonates	10 (6-16)	21	99
	Urban (n=26)	Macrophytes	12 (2-19)	84	90
		Molluscs	4 (0-16)	26	90
		Beetles	11 (2-30)	69	95
		Odonates	5 (1-9)	10	100
	Agricultural (n=29)	Macrophytes	11 (1-26)	95	89
		Molluscs	3 (0-12)	29	95
		Beetles	17 (3-50)	130	90

		Odonates	11 (1-25)	29	99
--	--	----------	-----------	----	----

700

701

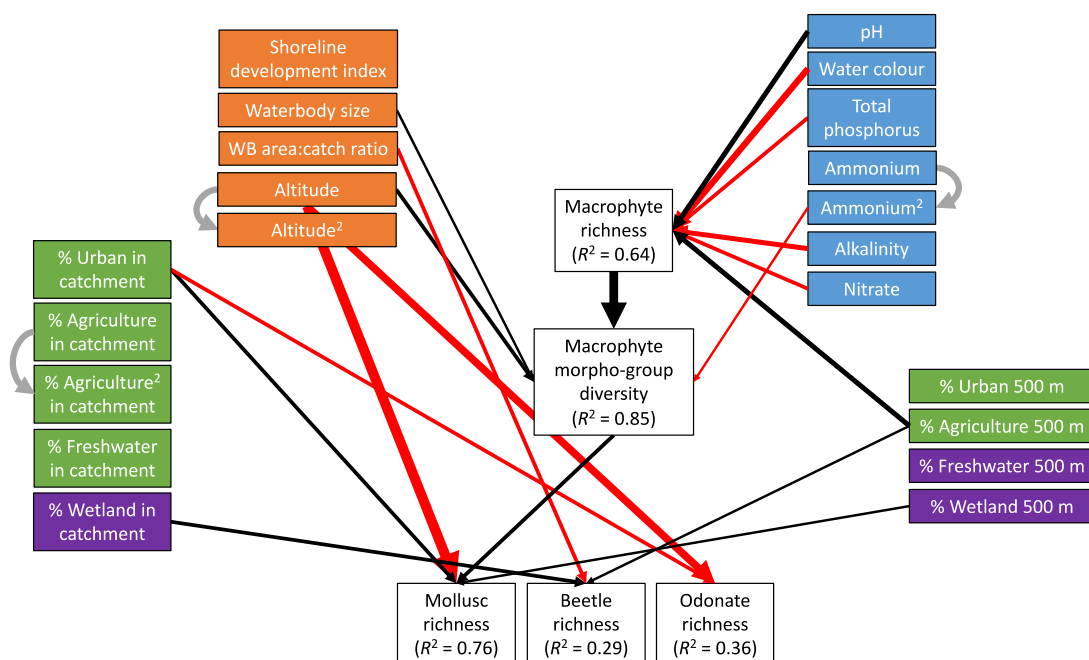
702 **Figures**



703

704 Figure 1. The conceptual model used to illustrate the direct and indirect relationships between
 705 response variables (macrophyte richness, macrophyte morpho-group diversity, mollusc,
 706 beetle and odonate richness) and explanatory variables (land use, connectivity, physical and
 707 water chemistry metrics).

708

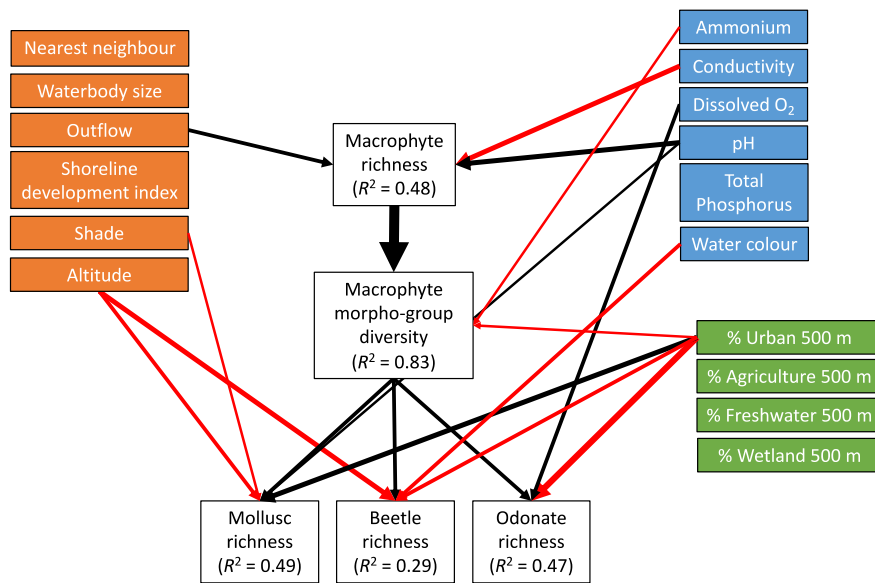


709

710 Fig. 2 Structural equation model (SEM) path diagram for lakes. Arrows are scaled according
 711 to standardised effect sizes, with black arrows indicating positive effects, red arrows negative

712 and grey arrows indicating specified correlated errors. Explanatory variables with no arrows
 713 indicate that they were included in the final SEM but were not significant. Boxes with a
 714 superscript represent parameters that had a non-linear relationship with the predictor.
 715 Coefficients of determination (R^2) are shown for each response variable. Non-significant
 716 relationships ($P > 0.05$) are omitted for clarity.

717



718

719 Fig. 3 Structural equation model (SEM) path diagram for ponds. Arrows are scaled according
 720 to standardised effect sizes, with black arrows indicating positive effects and red arrows
 721 negative. Explanatory variables with no arrows indicate that they were included in the final
 722 SEM but were not significant. Coefficients of determination (R^2) are shown for each response
 723 variable. Non-significant relationships ($P > 0.05$) are omitted for clarity.

724

725

726

727

728