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Complete List of Authors:	Law, Alan; University of Stirling School of Natural Sciences, Biological and Environmental Sciences Baker, Ambroise; Teesside University, School of Science; University College London, Department of Geography Sayer, Carl; University College London, Pond Restoration Research Group, Environmental Change Research Centre Foster, Garth; Aquatic Coleoptera Conservation Trust Gunn, Iain; Centre for Ecology and Hydrology Edinburgh Taylor, Philip; Centre for Ecology and Hydrology Edinburgh Pattison, Zarah; University of Stirling Blaikie, James; University of Stirling School of Natural Sciences Willby, Nigel; University of Stirling School of Natural Sciences
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Article title

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

Authors

Alan Law[1*], Ambroise Baker[2, 3], Carl Sayer[2], Garth Foster[4], Iain D. M. Gunn[5], Philip Taylor[5], Zarah Pattison[1], James Blaikie[1], and Nigel J. Willby[1]

[1] Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK

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

[3] School of Science, Engineering and Design, Teesside University, Middlesbrough, TS1 3BX, UK

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

[5] Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK

* Corresponding author:

alan.law1@stir.ac.uk

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

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Summary

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

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

Introduction

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

Numerous studies have sought to evaluate surrogacy in freshwaters, with macroinvertebrates receiving most attention. For ponds and rivers there is broad consensus that a few species-rich invertebrate groups (e.g. Coleoptera, Odonata, Mollusca and Trichoptera) are broadly representative of wider macroinvertebrate assemblages (Briers & Biggs, 2003; Bilton *et al.*, 2006; Sánchez-Fernández *et al.*, 2006; Ruhí & Batzer, 2014; Guan *et al.*, 2018). However, where surrogacy across different taxonomic groups has been studied e.g. plants or amphibians to macroinvertebrates, the results have been inconsistent, with relationships variously non-existent (Santi *et al.*, 2010; Guareschi *et al.*, 2015), weak (Heino, 2010; Kirkman *et al.*, 2012; Rooney & Bayley, 2012; Ilg & Oertli, 2017), moderate (Santi *et al.*, 2010; Gioria *et al.*, 2010) or strong (Janssen *et al.*, 2018). Most previous research has concentrated on one or two taxonomic groups, focussing on a single habitat type, distributed over a small geographical range. Therefore, even at small-scales, there is limited evidence of effective surrogates for wider freshwater biodiversity.

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

To our knowledge, the influence of macrophyte richness on multiple aquatic biota, across different freshwater habitats and covering environmentally diverse conditions has not previously been examined. Therefore, current understanding of the potential value of macrophytes as a surrogate is constrained. In this study, aquatic molluscs, aquatic beetles and odonates were selected as focal biota due to their high taxonomic diversity, widespread distribution in standing fresh waters and because all three groups include species of conservation concern. Our primary objective was to test whether macrophytes act as surrogates for wider freshwater biodiversity across three contrasting (agricultural, upland and urban), but typical aquatic landscapes (so-called 'hydroscapes'). We did this by assessing the strength of chemical and physical drivers and surrounding land use in explaining waterbody-scale richness of the biota. At the same time, we additionally tested if macrophyte species richness, mediated through morpho-group diversity, could further explain macroinvertebrate richness. We hypothesised that waterbodies with higher macrophyte richness, and, hence, greater macrophyte morpho-group diversity (an indicator of structural diversity), would have greater macroinvertebrate richness, with the former being a stronger predictor than chemical, physical and surrounding land use. However, further macroinvertebrate assemblage-specific effects are expected, reflecting either differences in the degree of dependence on macrophytes for habitat support, or habitat type-specific (pond or lake) differences in the importance of macrophytes as a component of habitat diversity.

Methods

Study areas and data collection

Three contrasting landscapes were chosen within Britain to account for different combinations of stressors associated with different land use types; lowland agricultural (north-east Norfolk, eastern England), upland (Cumbria, north-west England) and urban (Greater Glasgow, central Scotland). Within each of these hydroscapes, 22-29 replicates of both lakes and ponds were sampled. In this study, lakes were defined as waterbodies with surface area > 1 ha, while ponds were < 1 ha in area and generally shallow (< 2 m max. depth). Both categories included man-made and natural waterbodies. Within each of these waterbodies four taxonomic groups were selected to cover a range of habitat requirements, pollutant sensitivities and dispersal abilities, namely macrophytes (as surrogates), aquatic molluscs, aquatic beetles (hereafter referred to as molluscs and beetles) and odonates (dragon and damselflies). Extensive data on these taxonomic groups were obtained via national recorders (i.e. Aquatic Coleoptera Conservation Trust, British Conchological Society and British Dragonfly Society), while water chemistry, where available, and data on macrophytes from commissioned surveys, was provided by UK environmental agencies or the Joint Nature Conservation Committee (JNCC). All data were closely scrutinised to ensure inter-compatibility, with multi-visit, full inventory surveys prioritised. Only records from the last decade were retained. The availability of multiple recent records of adult odonates influenced site selection because favourable weather conditions for surveying these could not be guaranteed during field campaigns conducted for this study. Where gaps in the data existed or when a greater number of replicate waterbodies were needed, new data were collected during June to August of 2016-17. Several sites had data collected for all species assemblages and 88% of the sites used in the study were visited by the authors to gather additional data for at least one species assemblage or to collect water samples for water chemistry analysis (Table S1).

For each waterbody, the following physical variables were derived from the UK Lakes Portal (https://eip.ceh.ac.uk/apps/lakes/index.html); altitude, area, catchment size, perimeter, ratio of waterbody to catchment area and shoreline development index (indicating shape complexity of the shoreline). For water chemistry data provided by UK environmental agencies, a mean value was taken for each variable based on samples collected in summer (June-September). In all other cases we collected a water sample from the middle of each site and measured conductivity, dissolved oxygen, oxygen saturation, pH and temperature in the field using a HACH HQ30d meter. Alkalinity was also measured in the field by titration using sulphuric acid with a HACH AL-DT kit. A 500 ml subsample was filtered (47 mm glass microfiber, 1.2 µm pore Whatman GF/C filters) within 12 hours of collection and analysed for major nutrients and metals (see Table S2 for a list of determinands). Chlorophyll *a* was determined by extraction by soaking filters in 90% methanol overnight and quantification by spectrophotometry.

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

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

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

Land cover and connectivity

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

Variable selection and statistical analyses

Species richness was defined as the number of macrophyte or macroinvertebrate species per waterbody (or highest taxonomic resolution). Macrophyte morpho-group diversity was derived by assigning each species to one of 26 morpho-groups based on a library of morphological and regenerative traits (Willby, Abernethy & Demars, 2000), but expanded to incorporate bryophytes, macroalgae and a wide range of emergent species (Table S3). To determine if a sufficient number of waterbodies were surveyed per hydroscape for the four taxonomic groups, sample coverage was calculated based on incidence data per waterbody using the iNEXT library (Hsieh, Ma & Chao, 2016). Prior to statistical analyses all continuous explanatory variables (excluding pH) were log transformed, mean centred and scaled by 1 SD, to improve comparability between variables and to reduce the effect of outliers (full set of continuous variables given in Figure S1). 64% of ponds sampled (especially those <0.1 ha) did not have definable catchments, so a binary ‘catchment present’ category was created for all ponds. Binary explanatory variables (e.g. catchment present for ponds, outflow and inflow) were transformed to have values of –1 (absent) and 1 (present).

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

A conceptual model was developed to incorporate expected relationships between species richness and explanatory variables (Fig. 1). This model was based on the simple hypothesis that connectivity, land use and waterbody physical and water chemistry variables influence macrophyte species richness to a greater extent than macrophyte morpho-group diversity or richness of the macroinvertebrate groups, and that it is predominantly via macrophytes that these environmental effects are transmitted to macroinvertebrates. We also hypothesised that macrophyte morpho-group diversity would be a more important determinant of macroinvertebrate richness than macrophyte taxonomic richness due to the increased structural complexity that a high richness of macrophyte morpho-groups provides. We used structural equation modelling (SEM) to quantify the direct and indirect effects of these explanatory variables on macrophyte richness, macrophyte morpho-group diversity and macroinvertebrate richness. SEMs are a multivariate technique based on constituent LMs that allow standardised comparisons of direct and indirect relationships. Constituent LMs were created and residuals assessed to determine if they met linear model assumptions and examined for spatial autocorrelation using Moran's I statistic. All constituent LMs met linear model assumptions and no significant patterns in spatial autocorrelation were detected ($P > 0.05$). Bivariate relationships between each response and explanatory variable were explored graphically to identify potential non-linear relationships. Where non-linear relationships were found, the explanatory variable was converted to second degree orthogonal polynomials. No multicollinearity was detected in constituent LMs with a VIF threshold of < 5. During SEM model evaluation, missing pathways (i.e. previously unconsidered significant relationships) were identified and incorporated into the final SEM. Model fit was assessed using Fisher's C, where values of $P > 0.05$ indicated that the model was supported by the observed data. The term hydroscape ('Agricultural', 'Upland' and 'Urban') was added to each constituent LM, but was never significant and often increased the VIF due to correlations with land use. Hydroscape was then added as a random effect to each constituent LM, but did not improve the AIC. Therefore, the term hydroscape was not included in the final SEMs.

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

& Mundt, 2017), FactoMineR (Le, Josse & Husson, 2008), iNEXT (Hsieh *et al.*, 2016) and spdep (Bivand, Hauke & Kossowski, 2015).

Results

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

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

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

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

In lakes, macrophyte richness was explained principally by water chemistry and to a lesser extent by nearby land use (R^2 = 0.64) (Fig. 2). Variables indicative of nutrient-enrichment or poor water quality (nitrate, total phosphorus and water colour) negatively affected macrophyte richness, with nearby agricultural land positively influencing macrophyte richness. Macrophyte morpho-group diversity was, as expected, strongly related to macrophyte richness. However, the subsequent effect on macroinvertebrates was varied; macrophyte morpho-group diversity positively influenced mollusc richness, but had no effect on beetle and odonate richness. For the latter groups, environmental conditions (i.e. land use and waterbody physical variables) were more influential. Increasing altitude was a strong, negative determinant of both mollusc and odonate richness, with reasonable variance explained for both assemblages (R^2 = 0.76 and 0.36). The explained variance in beetle richness was the lowest of all the taxonomic groups (R^2 = 0.29) with only wetlands in the catchment and nearby agricultural land positively affecting richness and, to a lesser extent, lakes with relatively large catchments having a negative effect.

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

Discussion

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

The drivers of species richness

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

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

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

It is also possible that some macroinvertebrate groups may influence the richness of others, for example, via predation. However, as positive or negative pathways between any of the macroinvertebrate groups were not identified in our analysis, we can hypothesize that the effect of predation on richness are low, relative to the effect of macrophytes. Differences in explained variance amongst macroinvertebrates were reasonably consistent across waterbody types, with mollusc richness highest followed by odonates and then beetles. The low explained variance observed for beetles may in part reflect the high species richness found. Beetles are one of the most speciose groups globally with a wide geographical and ecological range (Bilton *et al.*, 2006); moreover, the balance between habitat specialists and generalists will be masked when considering diversity only in terms of species richness.

The strength of the surrogacy between macrophytes and macroinvertebrates differed between waterbody types, with macrophyte richness being a stronger driver of macroinvertebrate richness in ponds than lakes. This pattern may arise because lakes are more likely to support large populations of fish, which are known to exert strong predation pressure on macroinvertebrates (Diehl, 1992; Jones & Sayer, 2003). Molluscs, for example, are commonly consumed by fish with resulting reductions in density, although effects on richness are less understood (Dillon, 2000). Fish could also influence macroinvertebrates indirectly via various cascading effects on macrophyte diversity caused by herbivory (Matsuzaki *et al.*, 2009), zooplanktivory (Jeppesen *et al.*, 1998) or benthivory, particularly in shallow lakes (Kloskowski, 2011). Both abundance of macrophytes and macroinvertebrates will also be affected by waterfowl herbivory and bioturbation (Rodríguez-Pérez & Green, 2012; Wood *et al.*, 2012), with lakes likely to support greater waterfowl densities than ponds. A further factor affecting macroinvertebrate diversity in lakes may be physical disturbance of the shoreline due to wave action, which is much more intense in lakes than ponds due to an increased fetch (Fairchild, Faulds & Matta, 2000). Given that our focal macroinvertebrate groups, molluscs in particular, are poorly stream-lined and prone to being dislodged by currents, their link with macrophyte diversity may reflect a shared need for sheltered marginal habitats. In this study, it is likely that the effects of fish predation or physical disturbance on macroinvertebrate richness is mediated through macrophyte morpho-group diversity, as found in Cladocera (Burks, Jeppesen & Lodge, 2007), but further study would be useful to tease apart the multiple interacting processes involved (see Dillon (2000) for a review). Moreover, future studies should endeavour to determine fish abundance. As fish can be important drivers of aquatic community composition (Scheffer *et al.*, 2006), their inclusion will undoubtedly improve the predictive power of models and therefore the application of surrogates in other freshwater habitats.

Surrogacy and available statistical tools

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

Applications

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

It has been argued that declines in macrophyte richness should be viewed as an early warning system for declines in overall macrophyte abundance and hence the quality of the wider environment (Sayer *et al.*, 2010). Hence, we would recommend practitioners and conservation managers need to be concerned for wider biodiversity if macrophyte richness begins to decrease. The use of macrophytes as freshwater biodiversity surrogates can be important for rapid and cost-effective assessment of conservation and restoration projects, however, they will be most effective where constraints to biodiversity are diagnosed and addressed at site, habitat and landscape-scales. For example, at the site-scale, high grazing pressures may limit macrophyte regeneration from seedbanks and therefore wider biodiversity will only benefit if areas of macrophytes are protected from over-grazing and high disturbance. Additionally, at the habitat or landscape-scale, species translocations may be needed to enhance structural complexity if there are significant barriers to colonisation. However, in using macrophytes as a proxy for wider biodiversity, particularly when assessing habitat restoration, it should be recognised that macrophyte responses to management are complex and can be highly variable (Phillips, Willby & Moss, 2016).

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Data Availability Statement

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

Conflict of Interest Statement

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

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689 Table 1. A summary of environmental characteristics per waterbody type and hydroscape;
690 mean ± SE (min-max). Land use is representative from within catchments for lakes and the
691 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 ± 57.1 (1.5 – 1435.8)	166.9 ± 20.5 (41.0 – 469.0)	0.4 ± 0.2 (0.0 – 2.8)	14.0 ± 4.1 (0.0 – 83.2)	7.0 ± 0.9 (0.8 – 19.4)	0.1 ± 0.1 (0.0 – 0.3)
	Urban (n=22)	15.3 ± 4.8 (1.4 – 81.9)	93.3 ± 11.6 (23.0 – 217.0)	17.1 ± 5.1 (0.0 - 90.8)	33.2 ± 4.1 (0.0 – 69.3)	7.5 ± 1.3 (0.0 – 19.1)	4.2 ± 1.8 (0.0 – 27.2)
	Agricultural (n=25)	14.5 ± 3.4 (1.0 – 57.6)	14.6 ± 4.5 (0.0 – 78.0)	4.2 ± 1.0 (0.0 – 16.9)	61.7 ± 5.1 (2.0 – 88.3)	7.9 ± 2.4 (0.0 – 40.6)	4.9 ± 2.8 (0.0 – 56.0)
Pond	Upland (n=27)	0.4 ± 0.1 (0.1 - 1.6)	160.4 ± 12.3 (64.0 – 306.0)	0.3 ± 0.1 (0.0 – 2.2)	22.2 ± 4.7 (0.0 – 75.5)	1.4 ± 0.5 (0.0 – 12.2)	0.4 ± 0.2 (0.0 – 5.5)
	Urban (n=26)	0.3 ± 0.1 (0.1 - 1.2)	92.5 ± 12.3 (9.0 – 233.0)	39 ± 5.3 (0.0 – 98.9)	33.1 ± 4.9 (0.0 – 94.6)	0.5 ± 0.4 (0.0 – 12.2)	1.1 ± 0.6 (0.0 – 16.6)
	Agricultural (n=30)	0.2 ± 0.1 (0.1 - 1.2)	49.2 ± 5.1 (0.0 – 82.0)	2 ± 0.5 (0.0 – 13.4)	78.3 ± 4.4 (14.4 – 99.4)	0.4 ± 0.2 (0.0 – 4.1)	6.7 ± 2.9 (0.0 – 58.5)

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699 Table 2. Summary of species richness and sampling efficiency per waterbody type and
700 hydroscape for each species assemblage. The estimated sample coverage gives an indication
701 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

Figure captions

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

Fig. 2 Structural equation model (SEM) path diagram for lakes. Arrows are scaled according to standardised effect sizes, with black arrows indicating positive effects, red arrows negative and grey arrows indicating specified correlated errors. Explanatory variables with no arrows indicate that they were included in the final SEM but were not significant. Boxes with a superscript represent parameters that had a non-linear relationship with the predictor. Coefficients of determination (R^2) are shown for each response variable. Non-significant relationships ($P > 0.05$) are omitted for clarity.

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

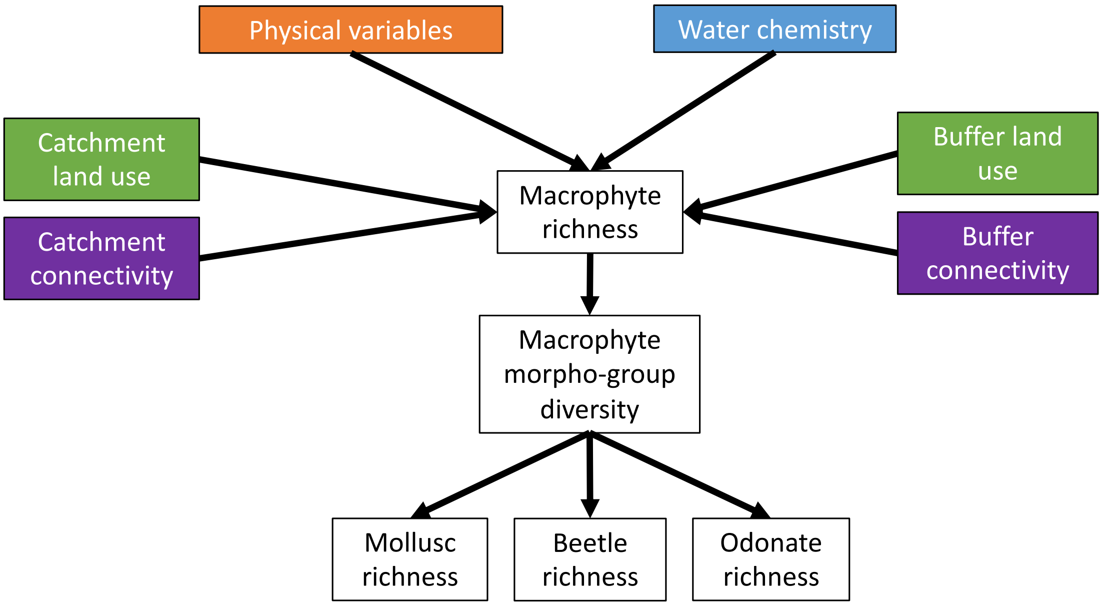

Figure 1. The conceptual model used to illustrate the direct and indirect relationships between response variables (macrophyte richness, macrophyte morpho-group diversity, mollusc, beetle and odonate richness) and explanatory variables (land use, connectivity, physical and water chemistry metrics).

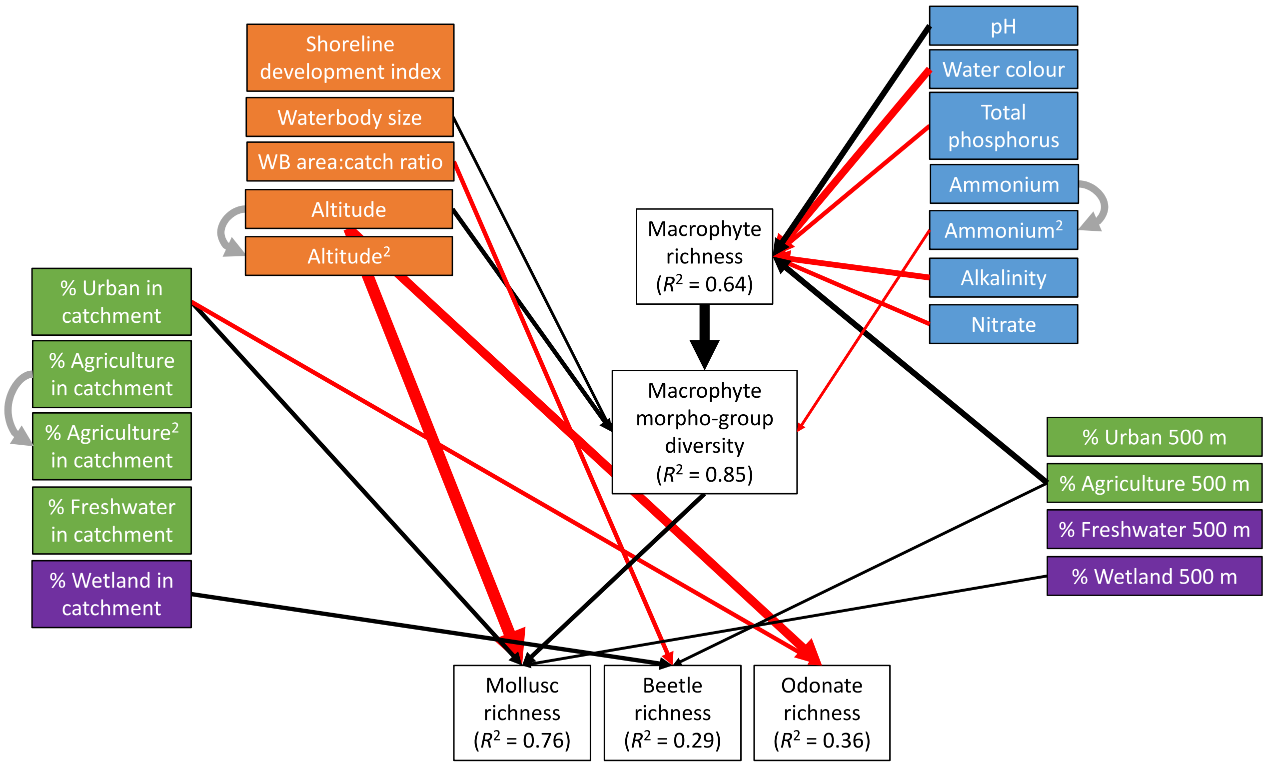

Fig. 2 Structural equation model (SEM) path diagram for lakes. Arrows are scaled according to standardised effect sizes, with black arrows indicating positive effects, red arrows negative and grey arrows indicating specified correlated errors. Explanatory variables with no arrows indicate that they were included in the final SEM but were not significant. Boxes with a superscript represent parameters that had a non-linear relationship with the predictor. Coefficients of determination (R^2) are shown for each response variable. Non-significant relationships (P > 0.05) are omitted for clarity.

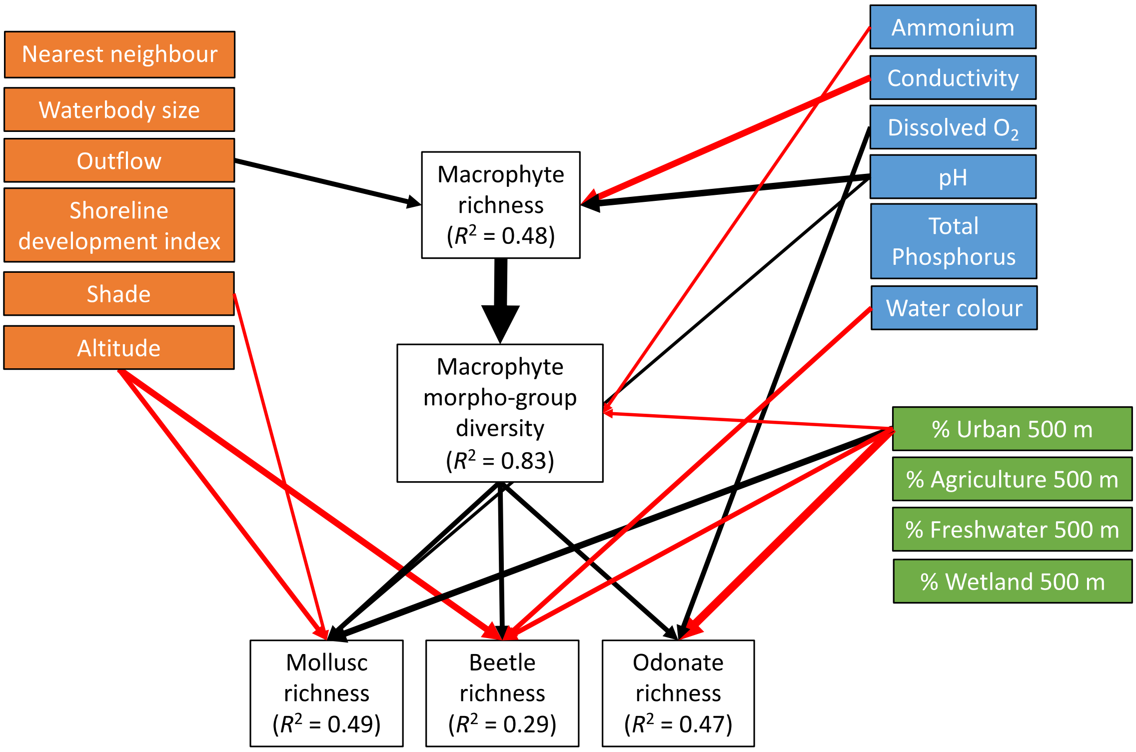

Fig. 3 Structural equation model (SEM) path diagram for ponds. Arrows are scaled according to standardised effect sizes, with black arrows indicating positive effects and red arrows negative. Explanatory variables with no arrows indicate that they were included in the final SEM but were not significant.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

Supporting Information

Table S1. Percentage and number of sites visited by the authors by waterbody type and taxonomic group.

Waterbody type	Water chemistry	Macrophyte	Mollusc	Beetle	Odonate
Lake (n = 74)	73% (n = 61)	57% (n = 48)	70% (n = 59)	70% (n = 59)	14% (n = 12)
Pond (n = 83)	98% (n = 81)	86% (n = 71)	90% (n = 75)	90% (n = 75)	0% (n = 0)

755 **Table S2**. List of major nutrients and metals derived from each 500ml water subsample.

Machine	Determinant
Thermo iCap 6000 Series	Ca
	K
	Mg
	Na
	Ag
	Al
	Ba
	Cd
	Fe
	Li
	Mn
	Ni
	Ti
	Cu
	Pb
	Zn
	TP
	OC
	TN
Dionex DX-120	Fl
	Cl
	NO2
	Br
	NO3
	PO4
	SO4
Thermo Helious Epsilion Spectrophotometer	Water colour
Bran + Luebbe Autoanalyzer 3	Ammonium

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Table S3. Table of macrophyte morpho-groups, their frequency and percentage of sites present. Adapted from Willby, Abernethy & Demars (2000) to accommodate a wider taxonomic and ecological range of taxa.

Morpho-group class	**Taxa**	**Notes**	**Frequency**	**% of sites present**
1	*Lemna minor*	Small and free-floating	73	46.2
1	*Lemna minuta*	Small and free-floating	9	5.7
1	*Lemna trisulca*	Small and free-floating	48	30.4
1	*Spirodela polyrhiza*	Small and free-floating	6	3.8
2	*Utricularia intermedia* agg.	Bladderworts	4	2.5
2	*Utricularia minor*	Bladderworts	16	10.1
2	*Utricularia stygia*	Bladderworts	2	1.3
2	*Utricularia vulgaris* agg.	Bladderworts	7	4.4
3	*Callitriche hermaphroditica*	Elodeids (aquatics with submerged long stems)	9	5.7
3	*Ceratophyllum demersum*	Elodeids (aquatics with submerged long stems)	23	14.6
3	*Ceratophyllum submersum*	Elodeids (aquatics with submerged long stems)	2	1.3
3	*Crassula helmsii*	Elodeids (aquatics with submerged long stems)	10	6.3
3	*Elodea canadensis*	Elodeids (aquatics with submerged long stems)	34	21.5
3	*Elodea nuttallii*	Elodeids (aquatics with submerged long stems)	35	22.2
3	*Ranunculus circinatus*	Elodeids (aquatics with submerged long stems)	4	2.5

4	*Callitriche* sp.	Starworts	12	7.6
4	*Callitriche hamulata*	Starworts	17	10.8
4	*Callitriche platycarpa*	Starworts	4	2.5
4	*Callitriche stagnalis*	Starworts	14	8.9
5	*Apium inundatum*	Myriophyllids (aquatics with long stems reaching the surface)	13	8.2
5	*Hippuris vulgaris*	Myriophyllids (aquatics with long stems reaching the surface)	13	8.2
5	*Hottonia palustris*	Myriophyllids (aquatics with long stems reaching the surface)	2	1.3
5	*Myriophyllum alterniflorum*	Myriophyllids (aquatics with long stems reaching the surface)	40	25.3
5	*Myriophyllum spicatum*	Myriophyllids (aquatics with long stems reaching the surface)	12	7.6
6	*Baldellia ranunculoides*	Submerged graminoids	1	0.6
6	*Butomus umbellatus*	Submerged graminoids	2	1.3
6	*Luronium natans*	Submerged graminoids	1	0.6
6	*Sparganium angustifolium*	Submerged graminoids	15	9.5
6	*Sparganium emersum*	Submerged graminoids	14	8.9
6	*Sparganium natans*	Submerged graminoids	7	4.4
7	*Ranunculus aquatilis*	thin-leaved water crowfoots	6	3.8
8	*Chara* sp.	Stoneworts	11	7.0
8	*Chara aculeolata*	Stoneworts	1	0.6

8	*Chara aspera*	Stoneworts	1	0.6
8	*Chara baltica*	Stoneworts	2	1.3
8	*Chara connivens*	Stoneworts	2	1.3
8	*Chara contraria*	Stoneworts	4	2.5
8	*Chara globularis*	Stoneworts	14	8.9
8	*Chara hispida*	Stoneworts	7	4.4
8	*Chara intermedia*	Stoneworts	2	1.3
8	*Chara virgata*	Stoneworts	29	18.4
8	*Chara vulgaris*	Stoneworts	13	8.2
8	*Nitella* sp.	Stoneworts	4	2.5
8	*Nitella flexilis* agg.	Stoneworts	32	20.3
8	*Nitella confervacea*	Stoneworts	1	0.6
8	*Nitella flexilis*	Stoneworts	5	3.2
8	*Nitella mucronata*	Stoneworts	2	1.3
8	*Nitella opaca*	Stoneworts	5	3.2
8	*Nitella translucens*	Stoneworts	25	15.8
8	*Nitellopsis obtusa*	Stoneworts	2	1.3
9	*Eleocharis acicularis*	Isoetids (submerged rosette-forming aquatics)	2	1.3
9	*Isoetes lacustris*	Isoetids (submerged rosette-forming aquatics)	17	10.8
9	*Juncus bulbosus*	Isoetids (submerged rosette-forming aquatics)	47	29.7
9	*Littorella uniflora*	Isoetids (submerged rosette-forming aquatics)	41	25.9
9	*Lobelia dortmanna*	Isoetids (submerged rosette-forming aquatics)	18	11.4
9	*Subularia aquatica*	Isoetids (submerged rosette-forming aquatics)	1	0.6

10	*Elatine hexandra*	Diminutive and living on substrate	4	2.5
10	*Elatine hydropiper*	Diminutive and living on substrate	2	1.3
10	*Hypericum elodes*	Diminutive and living on substrate	2	1.3
10	*Lythrum portula*	Diminutive and living on substrate	1	0.6
10	*Montia fontana*	Diminutive and living on substrate	3	1.9
10	*Ranunculus hederaceus*	Diminutive and living on substrate	1	0.6
10	*Ranunculus omiophyllus*	Diminutive and living on substrate	2	1.3
11	*Menyanthes trifoliata*	Rooted and medium floating leaves	44	27.8
11	*Nymphoides peltata*	Rooted and medium floating leaves	1	0.6
11	*Persicaria amphibia*	Rooted and medium floating leaves	20	12.7
12	*Nuphar lutea*	Rooted and large floating leaves	34	21.5
12	*Nymphaea alba*	Rooted and large floating leaves	35	22.2
12	*Nymphaea marliacea*	Rooted and large floating leaves	12	7.6
12	*Sagittaria sagittifolia*	Rooted and large floating leaves	1	0.6

13	*Najas marina*	Thin and flat leaved pondweeds and similar habits	6	3.8
13	*Potamogeton berchtoldii* OR *Potamogeton pusillus*	Thin and flat leaved pondweeds and similar habits	24	15.2
13	*Potamogeton berchtoldii*	Thin and flat leaved pondweeds and similar habits	34	21.5
13	*Potamogeton friesii*	Thin and flat leaved pondweeds and similar habits	4	2.5
13	*Potamogeton obtusifolius*	Thin and flat leaved pondweeds and similar habits	20	12.7
13	*Potamogeton pusillus*	Thin and flat leaved pondweeds and similar habits	15	9.5
13	*Potamogeton trichoides*	Thin and flat leaved pondweeds and similar habits	4	2.5
14	*Eleogiton fluitans*	Thin and cylindrical pondweeds and similar habits	19	12.0
14	*Potamogeton filiformis*	Thin and cylindrical pondweeds and similar habits	1	0.6

14	*Potamogeton pectinatus*	Thin and cylindrical pondweeds and similar habits	27	17.1
14	*Zannichellia palustris*	Thin and cylindrical pondweeds and similar habits	17	10.8
15	*Potamogeton alpinus*	Submerged/floating broad-leaved pondweeds	10	6.3
15	*Potamogeton gramineus*	Submerged/floating broad-leaved pondweeds	1	0.6
15	*Potamogeton natans*	Submerged/floating broad-leaved pondweeds	62	39.2
15	*Potamogeton polygonifolius*	Submerged/floating broad-leaved pondweeds	44	27.8
16	*Potamogeton crispus*	Submerged-only broad-leaved pondweeds	19	12.0
16	*Potamogeton gramineus* x *perfoliatus = P.* x *nitens*	Submerged-only broad-leaved pondweeds	2	1.3
16	*Potamogeton perfoliatus*	Submerged-only broad-leaved pondweeds	9	5.7
16	*Potamogeton praelongus*	Submerged-only broad-leaved pondweeds	1	0.6
17	*Apium nodiflorum*	Semi-submerged	10	6.3
17	*Berula erecta*	Semi-submerged	9	5.7
17	*Hydrocharis morsus-ranae*	Semi-submerged	8	5.1
17	*Oenanthe aquatica*	Semi-submerged	1	0.6
17	*Oenanthe crocata*	Semi-submerged	2	1.3
17	*Oenanthe fistulosa*	Semi-submerged	1	0.6
17	*Sium latifolium*	Semi-submerged	1	0.6

17	*Stratiotes aloides*	Semi-submerged	2	1.3
18	*Acorus calamus*	Large (>1m), emergent, rhizomatous graminoid emergents	4	2.5
18	*Bolboschoenus maritimus*	Large (>1m), emergent, rhizomatous graminoid emergents	2	1.3
18	*Carex acutiformis*	Large (>1m), emergent, rhizomatous graminoid emergents	18	11.4
18	*Carex aquatilis*	Large (>1m), emergent, rhizomatous graminoid emergents	1	0.6
18	*Carex lasiocarpa*	Large (>1m), emergent, rhizomatous graminoid emergents	5	3.2
18	*Carex pseudocyperus*	Large (>1m), emergent, rhizomatous graminoid emergents	6	3.8
18	*Carex riparia*	Large (>1m), emergent, rhizomatous graminoid emergents	23	14.6
18	*Carex rostrata*	Large (>1m), emergent, rhizomatous graminoid emergents	72	45.6
18	*Carex vesicaria*	Large (>1m), emergent, rhizomatous graminoid emergents	22	13.9

18	*Cladium mariscus*	Large (>1m), emergent, rhizomatous graminoid emergents	6	3.8
18	*Equisetum fluviatile*	Large (>1m), emergent, rhizomatous graminoid emergents	51	32.3
18	*Glyceria maxima*	Large (>1m), emergent, rhizomatous graminoid emergents	9	5.7
18	*Iris pseudacorus*	Large (>1m), emergent, rhizomatous graminoid emergents	50	31.6
18	*Phalaris arundinacea*	Large (>1m), emergent, rhizomatous graminoid emergents	34	21.5
18	*Phragmites australis*	Large (>1m), emergent, rhizomatous graminoid emergents	55	34.8
18	*Schoenoplectus lacustris*	Large (>1m), emergent, rhizomatous graminoid emergents	22	13.9
18	*Schoenoplectus tabernaemontani*	Large (>1m), emergent, rhizomatous graminoid emergents	4	2.5
18	*Sparganium erectum*	Large (>1m), emergent, rhizomatous graminoid emergents	62	39.2

18	*Typha angustifolia*	Large (>1m), emergent, rhizomatous graminoid emergents	22	13.9
18	*Typha latifolia*	Large (>1m), emergent, rhizomatous graminoid emergents	61	38.6
18	*Typha latifolia* x *angustifolia = T.* x *glauca*	Large (>1m), emergent, rhizomatous graminoid emergents	1	0.6
19	*Carex elata*	Tussock forming emergents	4	2.5
19	*Carex paniculata*	Tussock forming emergents	4	2.5
20	*Eleocharis palustris*	Other graminoid emergents	74	46.8
20	*Glyceria declinata*	Other graminoid emergents	2	1.3
20	*Glyceria fluitans*	Other graminoid emergents	37	23.4
20	*Juncus articulatus*	Other graminoid emergents	15	9.5
21	*Alisma lanceolatum*	Broad-leaved emergents	3	1.9
21	*Alisma plantago-aquatica*	Broad-leaved emergents	29	18.4
21	*Bidens cernua*	Broad-leaved emergents	2	1.3
21	*Caltha palustris*	Broad-leaved emergents	21	13.3
21	*Cicuta virosa*	Broad-leaved emergents	6	3.8
21	*Lysimachia thyrsiflora*	Broad-leaved emergents	4	2.5
21	*Lythrum salicaria*	Broad-leaved emergents	8	5.1
21	*Mentha aquatica*	Broad-leaved emergents	69	43.7
21	*Mimulus guttatus*	Broad-leaved emergents	6	3.8
21	*Myosotis laxa*	Broad-leaved emergents	13	8.2
21	*Myosotis scorpioides*	Broad-leaved emergents	38	24.1
21	*Myosotis secunda*	Broad-leaved emergents	11	7.0
21	*Persicaria hydropiper*	Broad-leaved emergents	4	2.5
21	*Potentilla palustris*	Broad-leaved emergents	38	24.1

21	*Ranunculus flammula*	Broad-leaved emergents	60	38.0
21	*Ranunculus lingua*	Broad-leaved emergents	7	4.4
21	*Ranunculus sceleratus*	Broad-leaved emergents	10	6.3
21	*Rorippa nasturtium-aquaticum*	Broad-leaved emergents	21	13.3
21	*Rumex hydrolapathum*	Broad-leaved emergents	3	1.9
21	*Veronica anagallis-aquatica*	Broad-leaved emergents	2	1.3
21	*Veronica beccabunga*	Broad-leaved emergents	21	13.3
21	*Veronica catenata*	Broad-leaved emergents	1	0.6
21	*Veronica scutellata*	Broad-leaved emergents	12	7.6
22	*Bacillariophyta*	Amorphous growth	4	2.5
22	Blue-green algal scum/pelts	Amorphous growth	1	0.6
23	*Batrachospermum* sp.	Filamentous algae	5	3.2
23	*Cladophora glomerata*	Filamentous algae	17	10.8
23	Filamentous green algae	Filamentous algae	13	8.2
23	*Hydrodictyon reticulatum*	Filamentous algae	2	1.3
23	*Klebsormidium* sp.	Filamentous algae	1	0.6
23	*Microspora* sp.	Filamentous algae	1	0.6
23	*Mougeotia* sp.	Filamentous algae	1	0.6
23	*Spirogyra* sp.	Filamentous algae	22	13.9
23	*Ulothrix* sp.	Filamentous algae	1	0.6
23	*Ulva flexuosa*	Filamentous algae	10	6.3
23	*Vaucheria* sp.	Filamentous algae	7	4.4
23	Zygnematalean algae	Filamentous algae	4	2.5
24	*Brachythecium rivulare*	Pleurocarpous mosses (bryophyte)	3	1.9
24	*Calliergonella cuspidata*	Pleurocarpous mosses (bryophyte)	14	8.9

24	*Cratoneuron filicinum*	Pleurocarpous mosses (bryophyte)	2	1.3
24	*Drepanocladus aduncus*	Pleurocarpous mosses (bryophyte)	10	6.3
24	*Fontinalis antipyretica*	Pleurocarpous mosses (bryophyte)	21	13.3
24	*Fontinalis squamosa*	Pleurocarpous mosses (bryophyte)	2	1.3
24	*Leptodictyum riparium*	Pleurocarpous mosses (bryophyte)	7	4.4
24	*Platyhypnidium riparioides*	Pleurocarpous mosses (bryophyte)	1	0.6
24	*Scorpidium scorpioides*	Pleurocarpous mosses (bryophyte)	3	1.9
24	*Sphagnum* sp.	Pleurocarpous mosses (bryophyte)	21	13.3
24	*Sphagnum cuspidatum*	Pleurocarpous mosses (bryophyte)	10	6.3
24	*Sphagnum denticulatum*	Pleurocarpous mosses (bryophyte)	7	4.4
24	*Thamnobryum alopecurum*	Pleurocarpous mosses (bryophyte)	1	0.6
24	*Warnstorfia fluitans*	Pleurocarpous mosses (bryophyte)	2	1.3
25	*Bryum pseudotriquetrum*	Acrocarpous mosses (bryophyte)	2	1.3
25	*Philonotis fontana*	Acrocarpous mosses (bryophyte)	1	0.6

25	*Racomitrium aciculare*	Acrocarpous mosses (bryophyte)	1	0.6
26	*Chiloscyphus polyanthos*	Liverworts (byophytes)	1	0.6
26	*Jungermannia sp.*	Liverworts (byophytes)	3	1.9
26	*Marsupella emarginata*	Liverworts (byophytes)	3	1.9
26	*Pellia* sp.	Liverworts (byophytes)	3	1.9
26	*Pellia epiphylla*	Liverworts (byophytes)	1	0.6
26	*Scapania undulata*	Liverworts (byophytes)	2	1.3

Table S4. Missing pathways added to the SEM per waterbody.

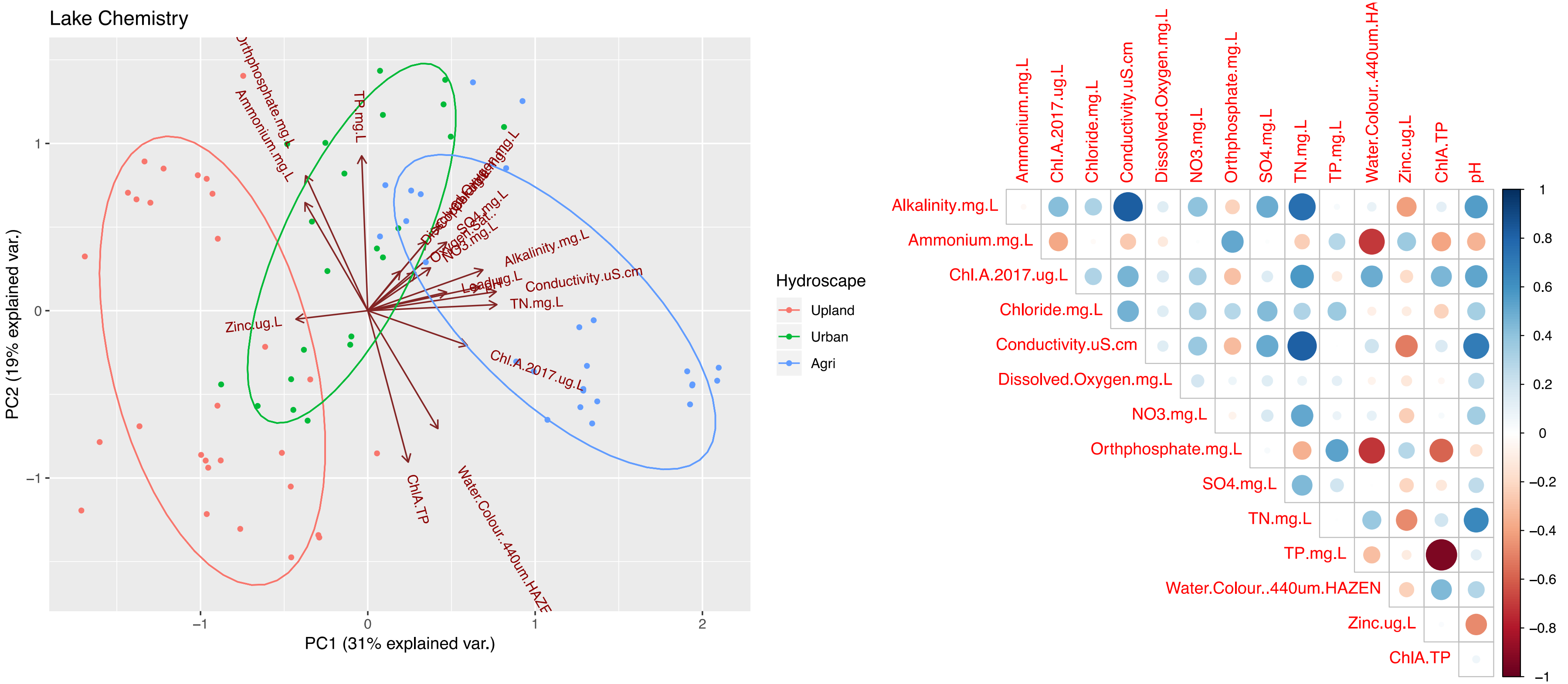
Waterbody type	Response	Explanatory added
Lake	Macrophyte richness	NA
	Macrophyte morpho-group richness	Alkalinity
		Altitude
		WB_area
		AmmoniumPoly
		AmmoniumPoly2
	Mollusc richness	Altitude
		UrbanCcatchment
		WetlandPresence500m
	Beetle richness	WetlandCatchment
		WBArea.catchment.ratio
		ArableC500m
	Odonate richness	Altitude
		UrbanCcatchment
Pond	Macrophytes	NA
	Macrophyte morpho-group richness	UrbanC500m
		Ammonium.mg.L
	Mollusc richness	Altitude
		UrbanC500m
		Shade
		pH
	Beetle richness	Altitude
		UrbanC500m
		Water.Colour..440um.HAZEN
	Odonate richness	UrbanC500m
		Dissolved.Oxygen.mg.L

766 **Table S5**. Unstandardised and standardised pathway coefficients for lake and pond SEMs.

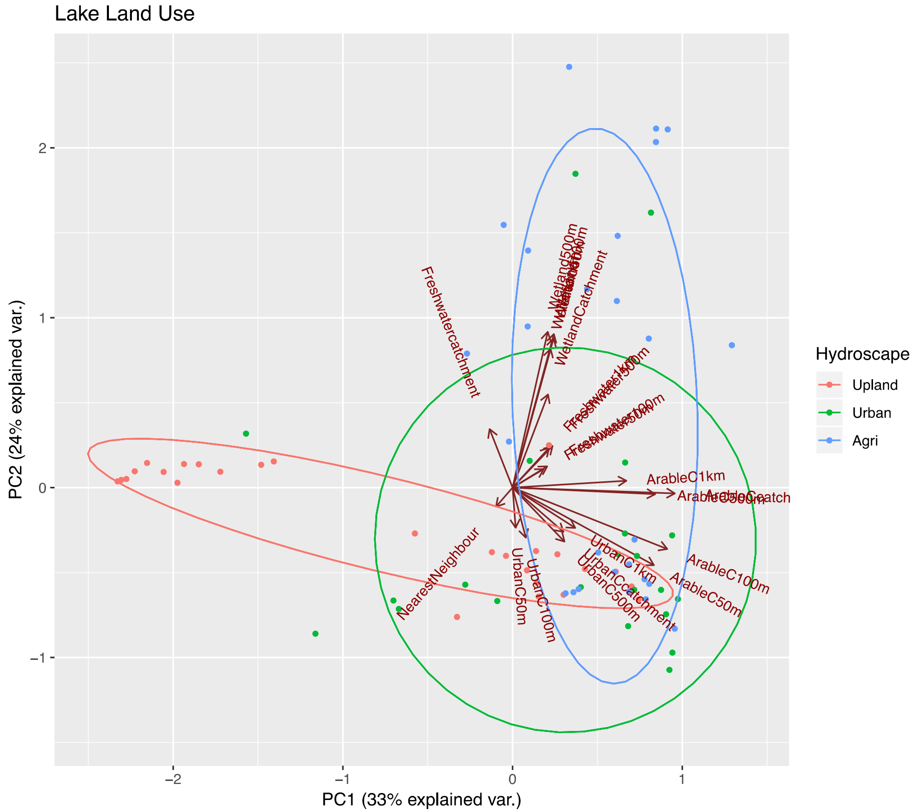
Waterbody type	Response	Explanatory	Estimate	DF	P.Value	Std.Estimate	Sig
Lake	mphyte.rich	AmmoniumPoly	7.1542	52	0.2918	0.1165	
	mphyte.rich	AmmoniumPoly2	-8.9608	52	0.1822	-0.1459	
	mphyte.rich	Alkalinity.mg.L	-2.7624	52	0.0273	-0.3846	*
	mphyte.rich	NO3.mg.L	-2.4456	52	0.0016	-0.3469	**
	mphyte.rich	pH	2.815	52	0.0194	0.3978	*
	mphyte.rich	TP.mg.L	-2.244	52	0.0047	-0.3149	**
	mphyte.rich	Water.Colour..440um.HAZEN	-3.5937	52	0.0017	-0.487	**
	mphyte.rich	ArableCcatchmentPoly	-13.3993	52	0.2056	-0.2182	
	mphyte.rich	ArableCcatchmentPoly2	2.5966	52	0.7211	0.0423	
	mphyte.rich	Freshwatercatchment	-0.638	52	0.5818	-0.0836	
	mphyte.rich	UrbanCcatchment	0.423	52	0.7149	0.0717	
	mphyte.rich	WetlandCatchment	-0.1215	52	0.8973	-0.0164	
	mphyte.rich	AltitudePoly	4.6184	52	0.6525	0.0752	
	mphyte.rich	AltitudePoly2	-13.3673	52	0.06	-0.2177	
	mphyte.rich	SDI.m	0.8424	52	0.4249	0.1109	
	mphyte.rich	WB_area	-1.5534	52	0.2076	-0.2129	
	mphyte.rich	WBArea.catchent.ratio	1.793	52	0.1036	0.2509	
	mphyte.rich	FreshwaterPresence	2.0114	52	0.1262	0.2713	
	mphyte.rich	WetlandPresence	-0.3962	52	0.7331	-0.0476	
	mphyte.rich	ArableC500m	1.9012	52	0.0435	0.3509	*
	mphyte.rich	UrbanC500m	-0.9449	52	0.3836	-0.1571	
	mphyte.morpho	mphyte.rich	0.3184	67	0	0.6998	***
	mphyte.morpho	Alkalinity.mg.L	-0.2642	67	0.2795	-0.0809	
	mphyte.morpho	Altitude	1.0381	67	1.00E-04	0.3138	***
	mphyte.morpho	WB_area	0.4831	67	0.0111	0.1456	*
	mphyte.morpho	AmmoniumPoly	-0.5259	67	0.7193	-0.0188	
	mphyte.morpho.fun	AmmoniumPoly2	-2.9691	67	0.0456	-0.1063	*
	mollusc.rich.log	mphyte.morpho	0.0717	69	3.00E-04	0.2874	***
	mollusc.rich.log	UrbanCcatchment	0.2024	69	0	0.3023	***
	mollusc.rich.log	WetlandPresence	0.1704	69	0.0178	0.1806	*
	mollusc.rich.log	Altitude	-0.6266	69	0	-0.7598	***
	beetle.rich.log	mphyte.morpho	-2.00E-04	69	0.9894	-0.0014	
	beetle.rich.log	WetlandCatchment	0.1658	69	0.013	0.2779	*
	beetle.rich.log	WBArea.catchent.ratio	-0.1981	69	0.0025	-0.3436	**
	beetle.rich.log	ArableC500m	0.1078	69	0.0285	0.2466	*
	odonate.rich.log	mphyte.morpho	-0.011	70	0.674	-0.0514	
	odonate.rich.log	Altitude	-0.4179	70	0	-0.5885	***

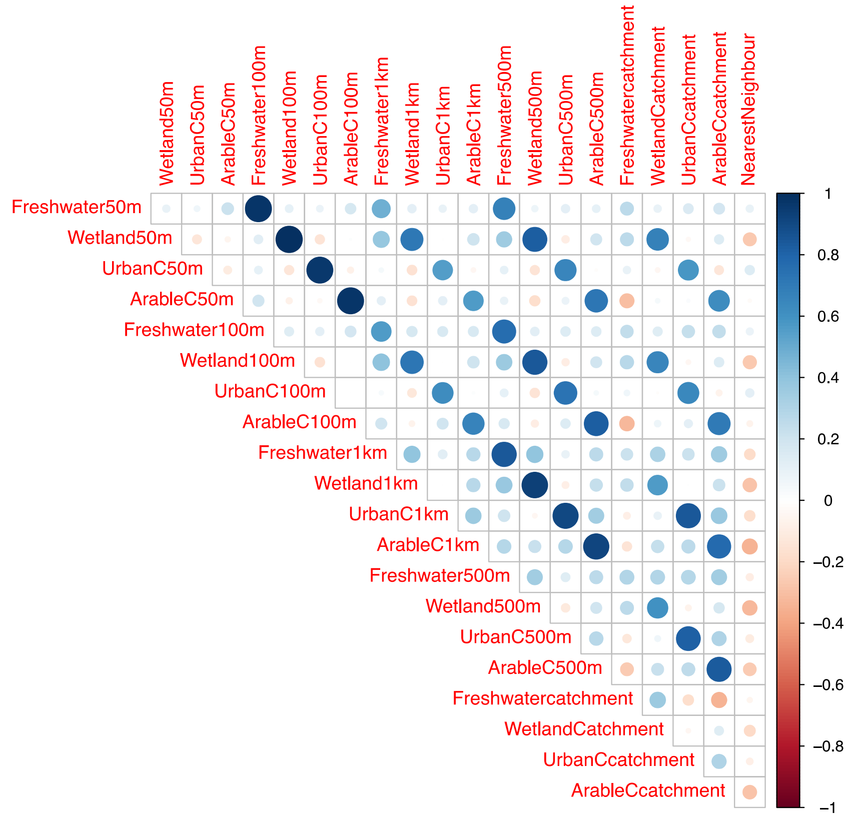
	odonate.rich.log	UrbanCcatchment	-0.1644	70	0.0069	-0.2851	**
Pond	mphyte.rich	Ammonium.mg.L	0.0887	64	0.9006	0.0144	
	mphyte.rich	Conductivity.uS.cm	-2.5184	64	0.0187	-0.4394	*
	mphyte.rich	Dissolved.Oxygen.mg.L	1.0003	64	0.1503	0.1719	
	mphyte.rich	pH	2.2842	64	0.0032	0.3981	**
	mphyte.rich	TP.mg.L	-0.8439	64	0.2363	-0.1495	
	mphyte.rich	Water.Colour..440um.HAZEN	0.2076	64	0.7587	0.0359	
	mphyte.rich	ArableC500m	1.1487	64	0.0612	0.2717	
	mphyte.rich	FreshwaterPresence	0.7617	64	0.3074	0.1239	
	mphyte.rich	UrbanC500m	-0.1161	64	0.8012	-0.031	
	mphyte.rich	WetlandPresence	0.1381	64	0.8671	0.018	
	mphyte.rich	Altitude	-0.2317	64	0.7718	-0.0389	
	mphyte.rich	Outflow	1.7905	64	0.0096	0.3076	**
	mphyte.rich	SDI.m	0.3581	64	0.5584	0.0636	
	mphyte.rich	WB_area	1.5258	64	0.0729	0.2619	
	mphyte.rich	Shade	0.0915	64	0.9016	0.0154	
	mphyte.rich	Catchment.present	-0.7676	64	0.3051	-0.1288	
	mphyte.rich	NearestNeighbour	0.5141	64	0.614	0.0551	
	mphyte.morpho	mphyte.rich	0.461	78	<0.001	0.8232	***
	mphyte.morpho	UrbanC500m	-0.4762	78	<0.001	-0.2272	***
	mphyte.morpho	Ammonium.mg.L	-0.4318	78	0.0139	-0.1253	*
	mollusc.rich.log	mphyte.morpho	0.0641	76	0.0024	0.2832	**
	mollusc.rich.log	Altitude	-0.2029	76	0.0038	-0.2687	**
	mollusc.rich.log	UrbanC500m	0.1988	76	<0.001	0.4193	***
	mollusc.rich.log	Shade	-0.18	76	0.006	-0.2389	**
	mollusc.rich.log	pH	0.171	76	0.011	0.2351	*
	beetle.rich.log	mphyte.morpho	0.0427	77	0.0263	0.2301	*
	beetle.rich.log	Altitude	-0.2263	77	<0.001	-0.3658	***
	beetle.rich.log	UrbanC500m	-0.122	77	0.0048	-0.3138	**
	beetle.rich.log	Water.Colour..440um.HAZEN	-0.1508	77	0.0178	-0.2509	*
	odonate.rich.log	mphyte.morpho	0.0566	78	0.0014	0.3071	**
	odonate.rich.log	UrbanC500m	-0.178	78	<0.001	-0.4611	***
	odonate.rich.log	Dissolved.Oxygen.mg.L	0.1515	78	0.0065	0.2524	**

Figure S1. Principal components analysis (PCA), correlations & dredge outputs for lakes and ponds.

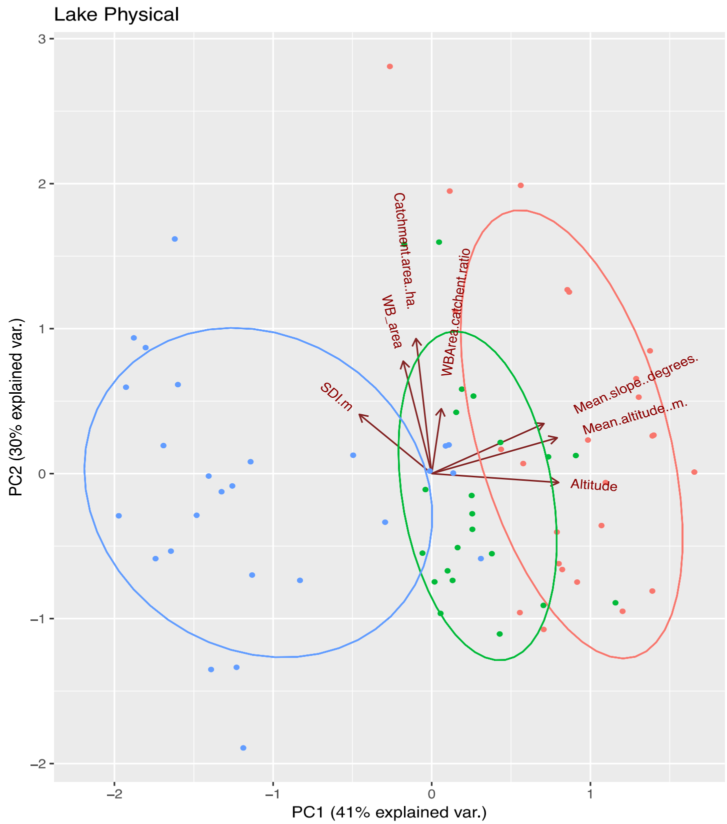


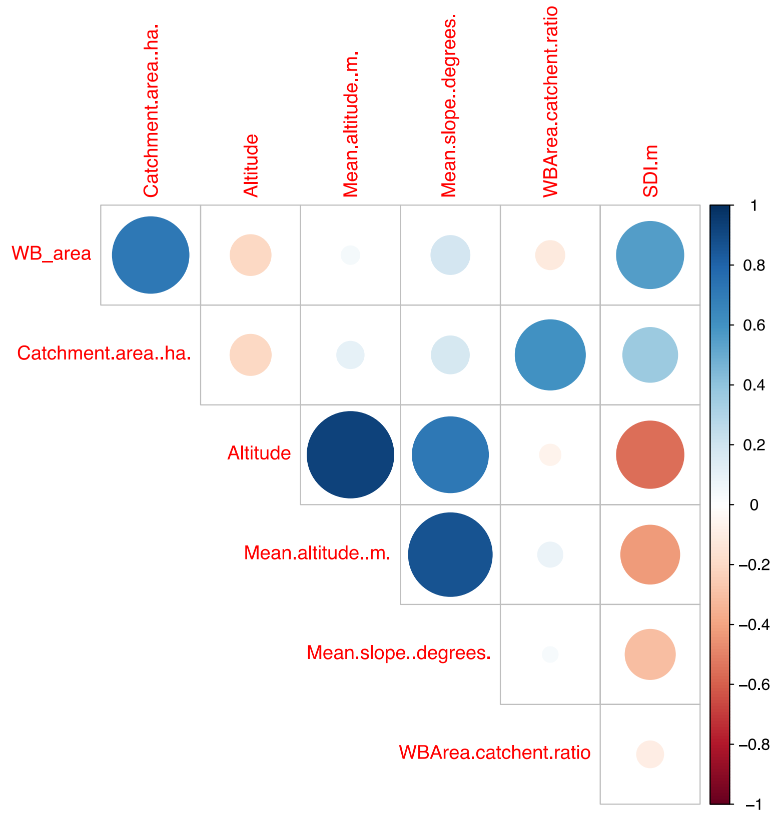
	Ammonium	NO3	pH	Water colour	Alkalinity	TP	Ortho	TN	DO	Zinc	Chloride	SO4	Cond	ChlA
Importance	1	1	1	0.95	0.91	0.8	0.44	0.18	0.1	0.1	0.09	0.09	0.08	0.08
N containing models	28	28	28	26	25	21	15	6	3	3	3	3	3	3
P-val mean	0.017	0.003	<0.001	0.028	0.027	0.003	0.138	0.316	0.452	0.575	0.541	0.589	0.568	0.962



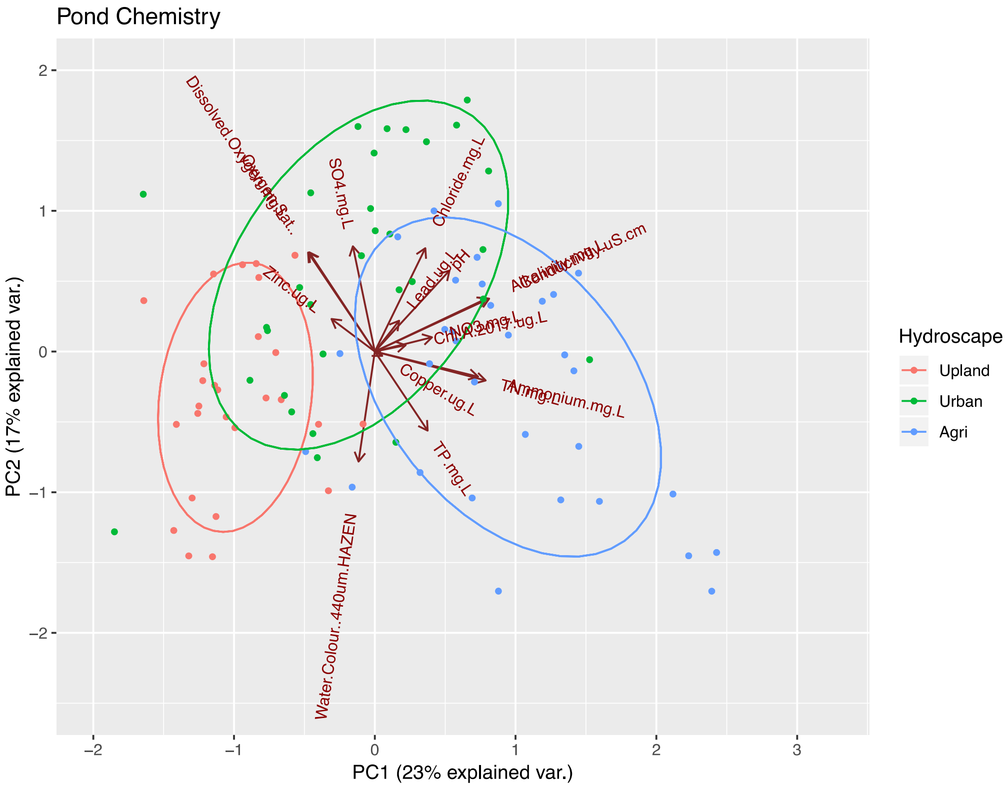


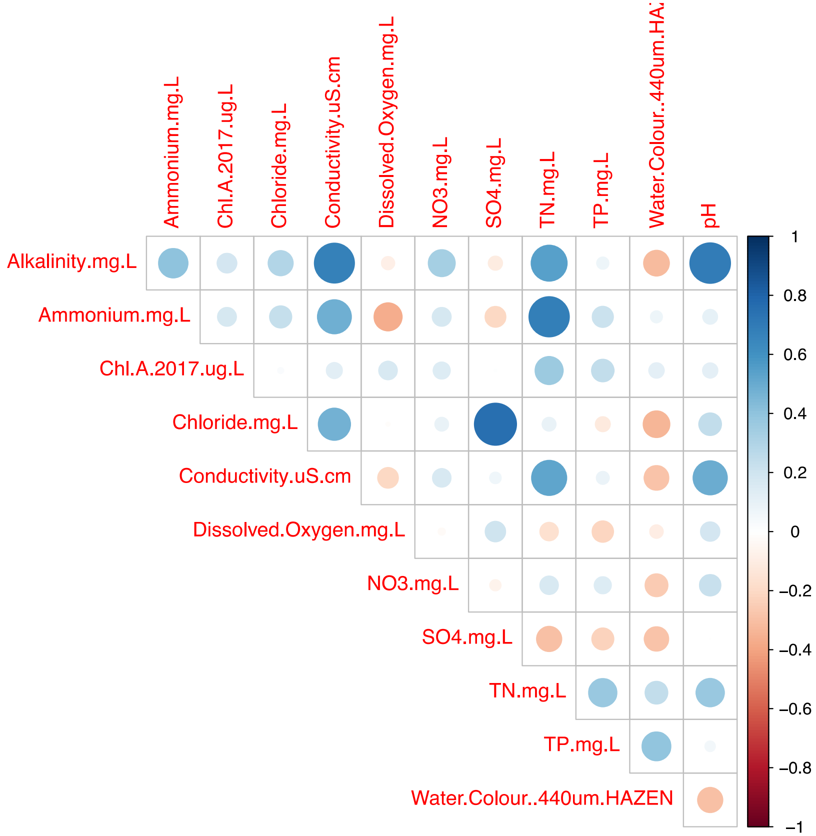
	Wetland 500m	Arable 500m	Wetland Catch	Arable Catch	FW catch	FW 500m	Urban Catch	Urban 500m	NN
Importance	1	0.88	0.84	0.18	0.17	0.13	0.07	0.07	0.07
N containing models	13	11	10	3	3	2	1	1	1
P-val mean	0.005	0.051	0.045	0.847	0.421	0.445	0.769	0.919	0.942



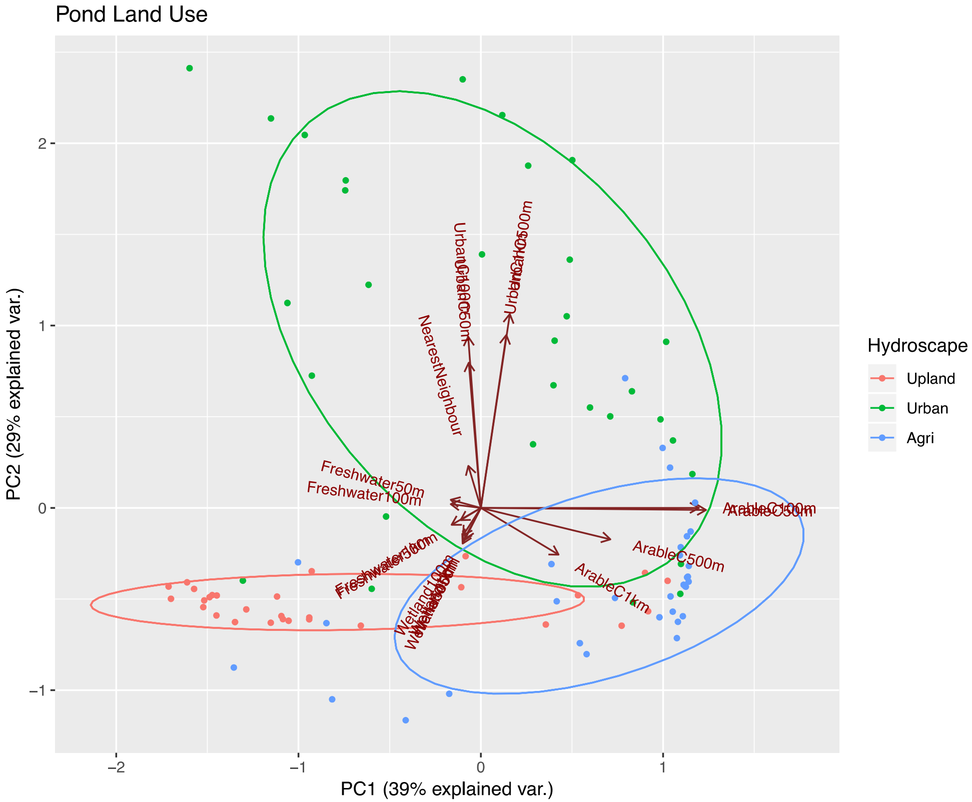


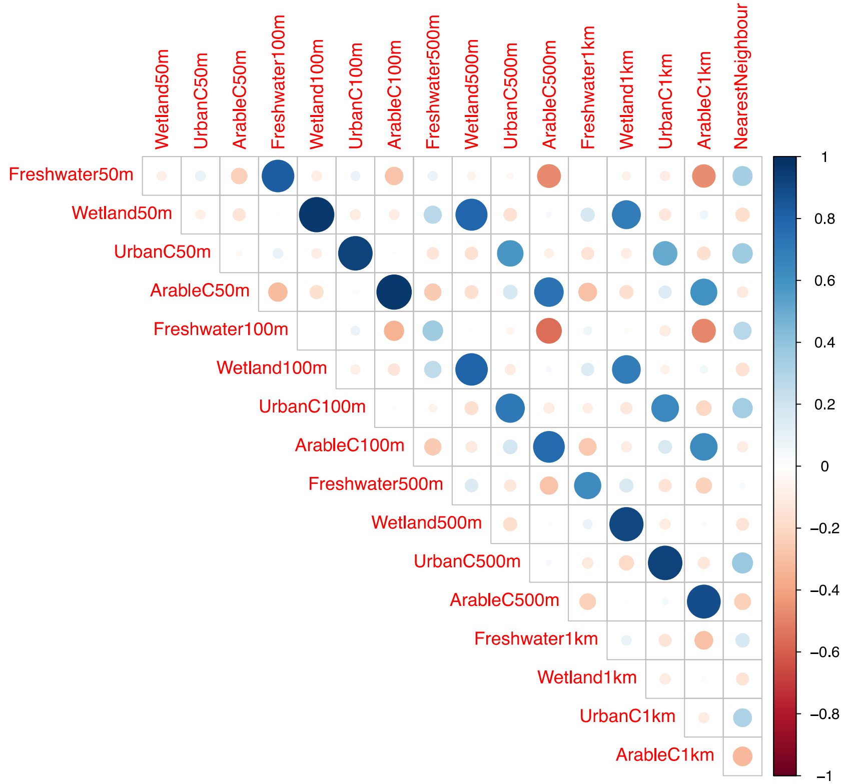
	Altitude	Mean catch alt	Mean slope	WB area	WB area: catch	Catch area	SDI
Importance	0.6	0.49	0.38	0.3	0.27	0.19	0.16
N containing models	20	20	13	14	12	10	7
P-val mean	0.061	0.216	0.093	0.265	0.493	0.870	0.519



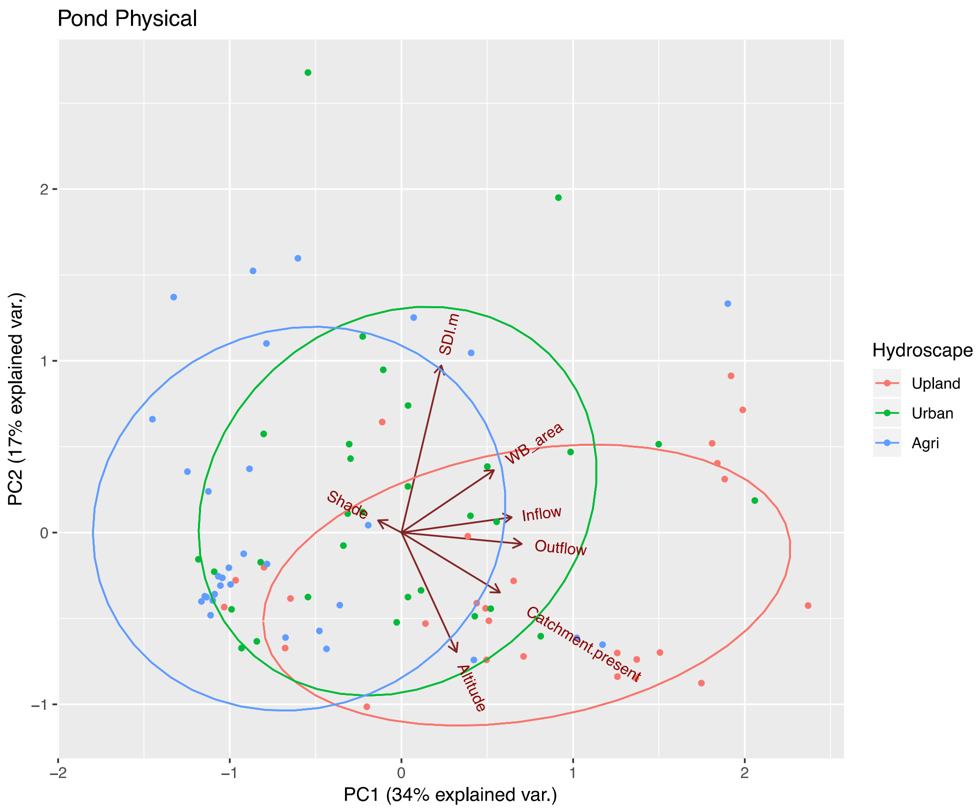


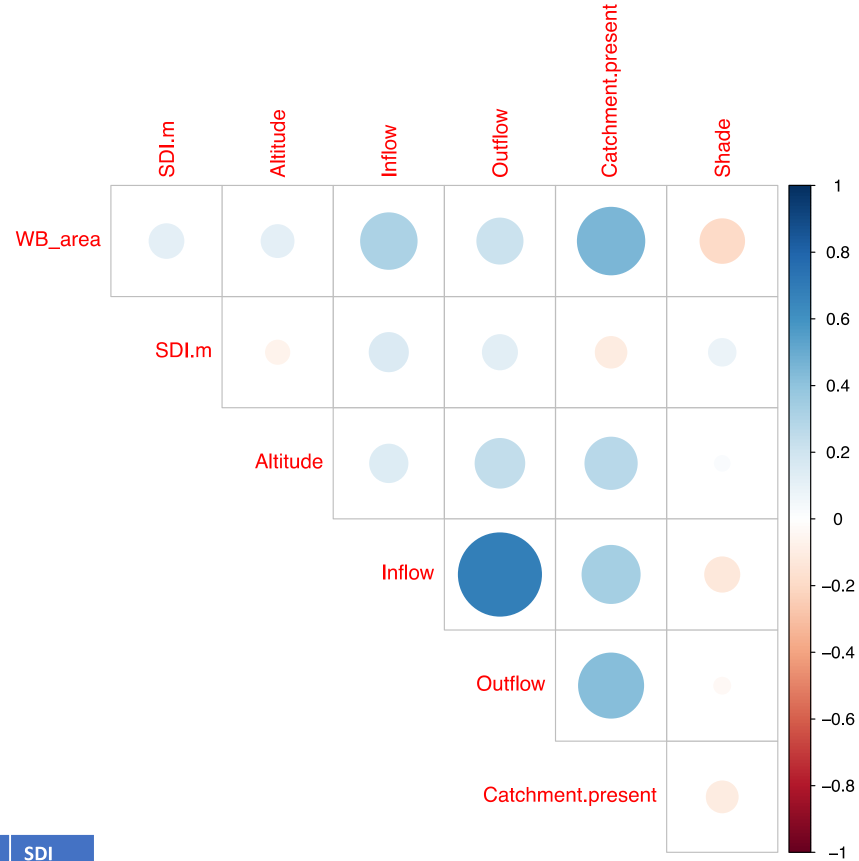
	Conductivity	pH	Chloride	DO	TP	SO4	TN	Alk	NO3	Ammonium	Water Colour	ChlA
Importance	1	1	0.68	0.44	0.38	0.38	0.28	0.23	0.21	0.13	0.11	0.09
N containing models	152	152	101	67	55	58	49	44	42	26	22	19
P-val mean	<0.001	0.002	0.148	0.162	0.172	0.230	0.274	0.364	0.388	0.644	0.672	0.915





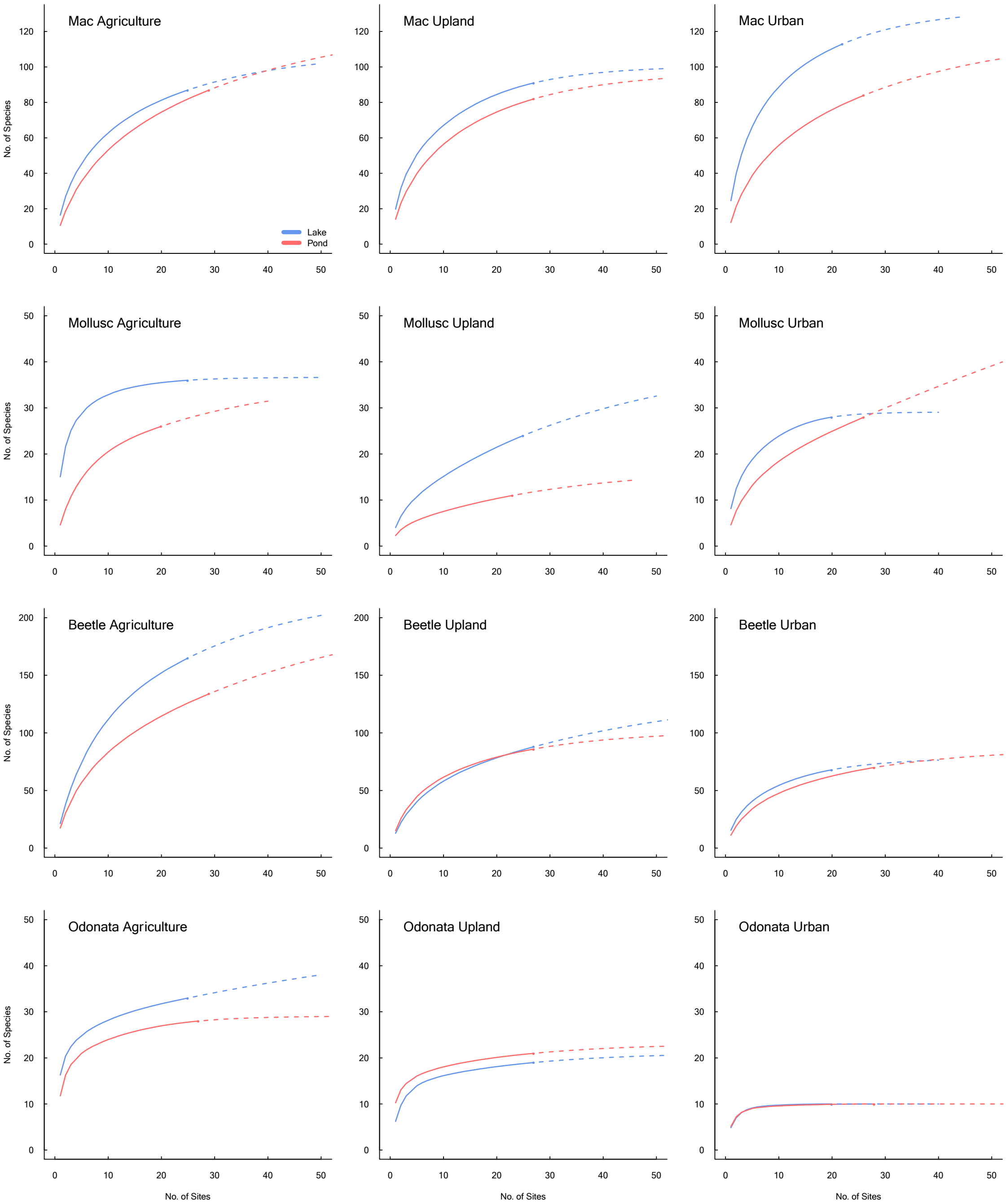
	Nearest neighbour	Urban 500m	Freshwater 500m	Wetland 500m	Arable 500m
Importance	0.35	0.3	0.24	0.24	0.24
N containing models	8	8	6	6	6
P-val mean	0.276	0.385	0.444	0.469	0.464



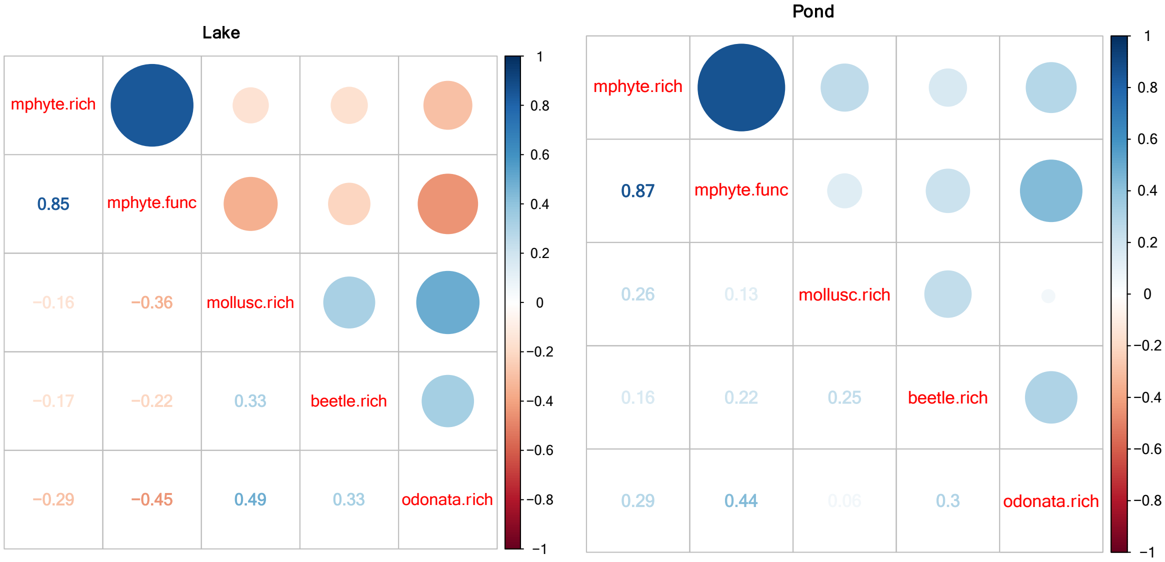


	Outflow	WB area	Shade	Inflow	Altitude	Catchment present	SDI
Importance	1	1	0.95	0.3	0.18	0.15	0.15
N containing models	9	9	8	4	2	2	2
P-val mean	0.008	0.007	0.017	0.394	0.508	0.729	0.851

Figure S2. Species accumulation curves for all taxonomic groups per waterbody type (lakes – blue lines, and ponds – red lines) and hydroscape (agricultural, upland and urban). Lines are extrapolated to estimate the effect of doubling sampling effort.



784 **Figure S3.** The correlation coefficients between taxonomic groups for lakes and ponds.



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