



Repeatable patterns in the distribution of freshwater biodiversity indicators across contrasting landscapes

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Abstract

Context Freshwater biodiversity is declining at unparalleled rates, but fundamental questions remain over how it is distributed at the spatial scales most relevant for conservation management.

Objectives Here, we test the hypothesis that freshwater biodiversity is distributed across standing waterbody types in a pattern that is reproducible across disparate biota and contrasting landscapes, such that conservation efforts can be aligned across landscapes and taxa.

Methods We analysed the richness, composition and distribution of macrophytes, molluscs, beetles and odonates from 199 standing waterbodies (lakes, ponds, ditches and canals) nested within UK

landscapes with contrasting dominant land use (agricultural, upland and suburban).

Results We found a common pattern in the distribution of our biodiversity indicators across waterbody types in all landscapes that was largely repeated across biota; lakes consistently had the highest or equal alpha diversity and supported a greater proportion of the sampled species pool in each landscape (mean = 86%) in comparison to ponds (74%). Landscape-specific waterbody types (ditches and canals) also contributed significantly to the regional species pool (69 and 33% respectively). Each waterbody type contributed uniquely to landscape biodiversity and usually species of conservation concern, rather than simply supporting a subset of ubiquitous species found in lakes.

Conclusions Landscape-wide management strategies that encompass multiple habitats and biota should prove advantageous and generalisable.

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However, our study landscapes suggest that long-term biodiversity conservation should also recognise lakes as a priority for nature recovery, both to minimise further losses and to maintain the largest reservoir of biodiversity.

Keywords Biodiversity distribution · Invertebrate · Lake · Macrophyte · Pond

Introduction

Freshwater biodiversity is disproportionately high compared to marine and terrestrial environments but declining twice as fast (Darwall et al. 2018; Ferrer et al. 2019) due to overlapping impacts from an increasing variety of human-induced stressors, likely exacerbated by high inherent connectivity (Reid et al. 2018; Dudgeon 2019). Our ability to reverse the biodiversity decline in freshwaters depends on a suitable knowledge of large-scale patterns in biodiversity. Despite disagreements regarding underlying causes (Mittelbach et al. 2007; Pontarp et al. 2019), there is compelling evidence for strong and repeatable biodiversity patterns for marine and terrestrial systems (Hillebrand 2004). By contrast, other than fish in rivers, macroecological patterns in freshwater biodiversity are rather poorly characterised (Heino 2011; Domisch et al. 2016). This hinders the design of effective ecologically-underpinned landscape-scale conservation strategies aimed at mitigating declines in freshwater biodiversity (Heino 2009, 2011; Tisseuil et al. 2013).

We know that macroecological patterns vary substantially among taxonomic groups (Heino 2011) and that, at the landscape-scale, the importance of waterbody types varies among freshwater biota (Williams et al. 2004). Nevertheless, this knowledge has not been integrated to ask questions of fundamental macroecological and conservation relevance. For example, do patterns in the relative distribution of freshwater biodiversity between habitats repeat across landscapes with contrasting land uses? Such understanding is critical for designing biodiversity conservation strategies applicable at a broad scale. Even at the landscape-scale, knowledge of the comparative distribution of freshwater biodiversity is limited since research has focused on individual habitat types, sites or taxonomic groups within discrete geographic

units or similar land use types (Williams et al. 2004; Davies et al. 2008a; Bubíková and Hrivnák 2018; Hill et al. 2018; Oertli and Parris 2019).

Comparing published patterns of biodiversity across multiple habitat types and using multiple taxonomic groups, confirms that freshwater biodiversity is, indeed, distributed unevenly amongst habitats (De Bie et al. 2008; Davies et al. 2008b; Chester and Robson 2013; Williams et al. 2020). For example, in an 80 km² agricultural landscape in the UK, (Williams et al. 2004; Davies et al. 2008a) ponds contributed most to landscape-scale macrophyte and macroinvertebrate biodiversity, supporting greater richness and more unique species than lakes, ditches, rivers or streams. Similarly, for five agricultural landscapes in Europe, comparisons of macrophyte and macroinvertebrate diversity across ditches, ponds (plus lakes) and rivers (plus streams) found rivers were the most diverse habitat in terms of site-level alpha diversity, while ponds were most speciose at the landscape-level and were most important for rare species (Davies et al. 2008b). These and subsequent studies (see De Bie et al. 2008; Verdonschot et al. 2011; Bubíková and Hrivnák 2018) highlight important and unique contributions to landscape-scale biodiversity from different waterbody types emphasising the need to undertake conservation at spatial scales which encompass the full spectrum of freshwater habitats present (Sayer 2014). However, such studies have been largely restricted to lowland agricultural landscapes in which lakes have been either scarce and/or degraded due to nutrient loading from surrounding land use. Indeed, since the millennium, lakes have been generally less studied from a biodiversity perspective relative to other freshwater habitats, despite their widely recognised importance to local biodiversity (Stendera et al. 2012). Consequently, the generality of documented patterns and the conservation priorities that arise remain uncertain, particularly where connectivity (e.g. hydrological, human and aerial) and physical characteristics (e.g. habitat heterogeneity and surrounding land use) differ between waterbody types and landscapes.

Recently, studies of freshwater biodiversity patterns and processes have diversified across taxonomic groups (Ruhí et al. 2014; Dodemaide et al. 2018) and waterbody types (Hamerlík et al. 2014; Schriever and Lytle 2016; Bubíková and Hrivnák 2018) and have begun to incorporate a land use perspective, particularly urban versus rural (Hill et al. 2016; Thornhill

et al. 2018a). These comparative studies utilise survey methods where fixed areas within habitats are sampled, often for a fixed time, to control for species-area effects (Davies et al. 2008a; Bubíková and Hrivnák 2018). However, surveying biodiversity of a fixed area, irrespective of habitat size, will also systematically under-sample intrinsically larger habitats and over-sample smaller ones. Hence, given past limitations in data availability and the difficulty of comparing biodiversity in discrete (e.g. lakes and ponds) vs continuous habitats (e.g. ditches and canals), an incomplete picture prevails on exactly how freshwater biodiversity is distributed across a broad array of habitats and landscapes for different taxonomic groups.

Driven by official monitoring programmes, enthusiastic volunteer recorders and the publication of national online databases, there has been a revolution in the spatial and taxonomic coverage, resolution and frequency of records in biological databases, including for freshwater biota (Thornhill et al. 2018b). This has been accompanied by the emergence of biodiversity audits for assessing regional biodiversity and species occurrence patterns in which records are collated and compared for priority species to help direct species and/or habitat conservation efforts (Dolman et al. 2012). In this study we combine the collation of biological records with targeted semi-quantitative sampling to explore patterns in biodiversity (alpha, beta and gamma) across four key freshwater taxonomic groups (macrophytes, molluscs, water beetles and odonates) for four standing waterbody types (lakes, ponds, canals and ditches) nested within three landscapes in Great Britain (GB) characterised by contrasting land uses (predominantly agricultural, upland and suburban). We hypothesised that in each landscape, different waterbody types would share species, but also contain distinctive elements not found

elsewhere in the landscape, such that each habitat would uniquely contribute to landscape-scale biodiversity. However, we expected limited repeatability in the allocation of biodiversity among waterbody types across landscapes due to differences in the major land uses and the influence this might have on habitat connectivity and stressor type and intensity.

Methods

Field sites and data collection

Three landscapes within GB were chosen for their contrasting predominant land uses (Table 1) based on UKCEH land cover maps (Morton et al. 2024): north-east Norfolk (eastern England), characterised by low-land arable farming; Cumbria (north-west England), characterised by relatively high elevations, acid grassland, conifer plantations and livestock (cattle and sheep) grazing on permanent grasslands, and; Greater Glasgow (central Scotland), characterised by a high percentage of urban and suburban land, with waterbodies spanning the urban–rural gradient (Fig. 1). Some land uses were also shared across landscapes, e.g. improved grassland (i.e. typically managed as pasture, mown for silage or used for recreation and amenity) and, particularly, broadleaf woodland (Table 1). For convenience the three focal landscapes are, henceforth, referred to as agricultural, upland and suburban.

Within each of the landscapes, replicates of the common standing waterbody types (lakes and ponds) were sampled. Landscape-specific waterbody types were also included (ditches and canals in the agricultural and suburban landscapes, respectively) being both integral components of the standing water

Table 1 A summary of the main land use types (%) calculated from a 500 m buffer around each waterbody per landscape

Land use	Agricultural (N. Norfolk)	Upland (Cumbria)	Suburban (Glasgow)
Arable & Horticulture	40 ± 3 (0–97)	1 ± 1 (0–30)	7 ± 1 (0–60)
Acid Grassland	0 ± 0 (0–0)	38 ± 5 (0–100)	1 ± 1 (0–21)
Suburban	2 ± 1 (0–30)	1 ± 1 (0–45)	19 ± 2 (0–91)
Improved Grassland	30 ± 3 (0–100)	21 ± 3 (0–80)	28 ± 3 (0–80)
Broadleaf Woodland	14 ± 2 (0–56)	22 ± 3 (0–65)	20 ± 2 (0–68)
Coniferous Woodland	2 ± 1 (0–60)	13 ± 4 (0–100)	3 ± 1 (0–86)
Freshwater & Wetland	5 ± 1 (0–74)	2 ± 1 (0–12)	1 ± 1 (0–28)
Mean ± SE (min–max)			

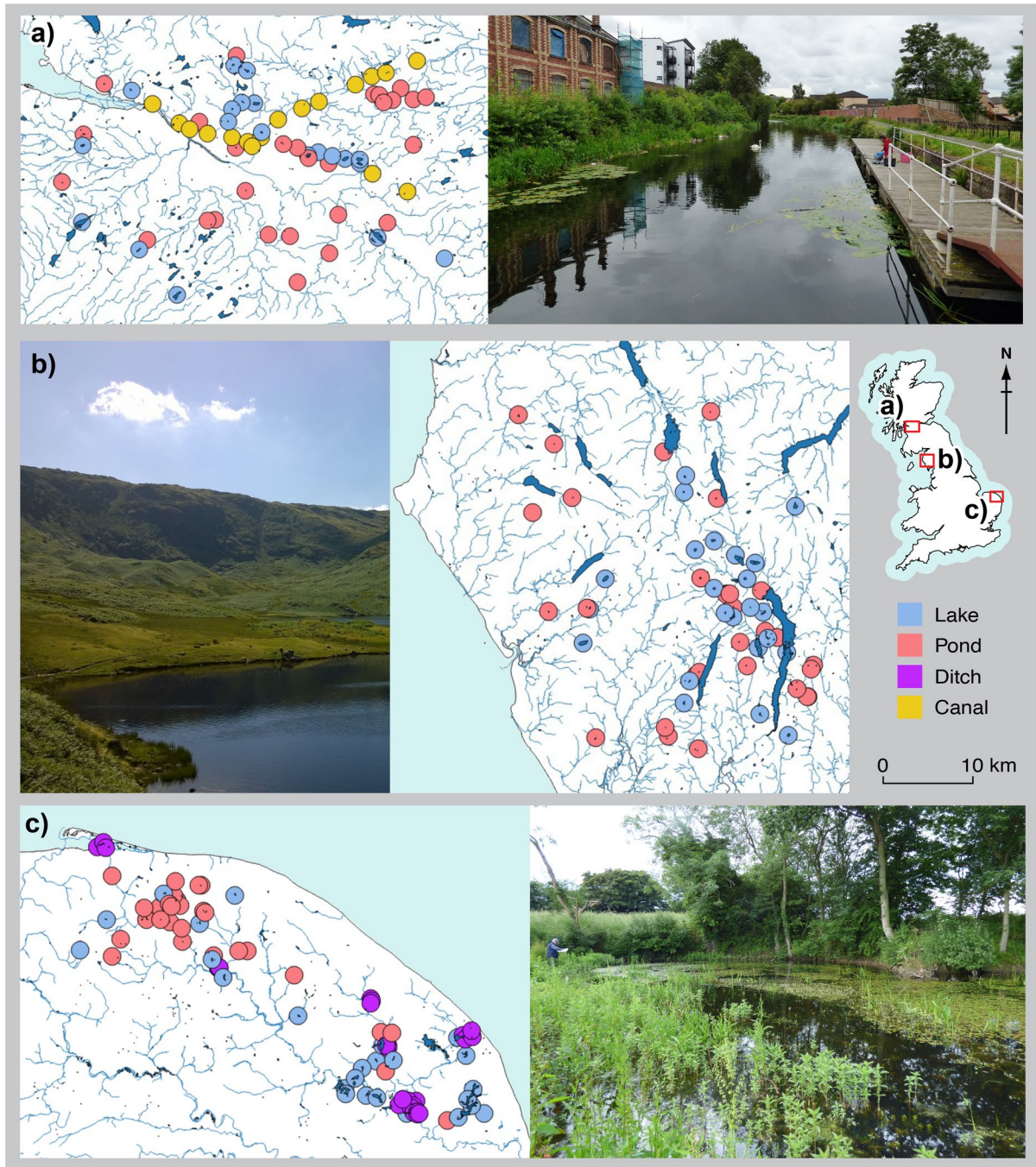


Fig. 1 Distribution of the waterbody types within each landscape, including a representative picture of the landscape; **a** Suburban landscape and canal, **b** Upland landscape and lake

and **c** Agricultural landscape and pond. Lakes—blue, ponds—red, canals—yellow, and ditches—purple

'hydroscape' and with the potential to support habitat specialists or interconnect sites. We aimed to sample 25 replicates of each waterbody type per landscape. With representativity in mind we chose sites distributed across each landscape to account for a broad range of geographic, environmental and land use conditions. Site choice was also partly guided by existing biological records, with the authors surveying sites spanning a gradient from low to high biodiversity for some or all taxonomic groups (Table S1). Lakes were defined as lentic waterbodies with a surface area > 1 ha (median: 7 ha), while ponds were defined as < 1 ha in area (median: 0.2 ha) and shallow (< 2 m max. depth). Both categories included examples of natural and human-made waterbodies. Canals and ditches were lentic, linear, artificial waterbodies designed for navigation or irrigation/drainage, respectively. The majority ($n=14$, 82%) of canal sites had low levels of recreational boat traffic, the rest being unnavigable and containing extensive emergent vegetation. On average, canals were 20 m wide and 1.8 m deep, whereas ditches were 3 m wide and 1 m deep. The ditches selected in the focal agricultural landscape were part of lowland grazing marsh systems and had a generally higher conservation value than the intermittent field drains typical of more intensive agricultural landscapes, which are often heavily polluted, intermittently dry and generally neglected in terms of conservation management (Davies et al. 2008b; Verdonschot et al. 2011; Clarke 2015). Although ditches can exhibit a range of flow regimes, ditches in this study had negligible water movement.

Four taxonomic groups relevant to all waterbody types were selected as indicators of freshwater biodiversity to cover a range of habitat requirements, pollutant sensitivities and dispersal abilities. These were: macrophytes (encompassing macroalgae, bryophytes and vascular plants), freshwater molluscs and water beetles (hereafter referred to as molluscs and beetles respectively) and odonates (dragonflies and damselflies). Extensive data on these four groups were obtained from databases created through national recording schemes (e.g. Aquatic Coleoptera Conservation Trust, British Conchological Society and British Dragonfly Society) with macrophyte commissioned survey data predominantly provided by U.K. environmental agencies or the Joint Nature Conservation Committee (JNCC) (details of further macrophyte survey data can be found in Table S1). All data

were closely scrutinised to ensure inter-compatibility, with comprehensive, structured, recent (within 10 years) surveys prioritised for all taxonomic groups. As most data were collected as part of systematic surveys or recording schemes, records were verified by national experts and conducted by trained operators. Where gaps in the data existed or a greater number of replicate waterbodies was needed, new data were collected during the summers of 2016 and 2017 by the authors. For several sites, data already existed for all four indicator groups based on past surveys, but 63% of the sites used in this study were visited by the authors to collect additional data for at least one taxonomic group to ensure comprehensive coverage of all four indicators across all sites (Supporting Information, Table S2).

During our field surveys, an exhaustive inventory was conducted for each taxon group, unless specified below. For macrophytes in all waterbody types, all plants from the marginal zone to the maximum growing depth were recorded, assisted by use of a grapnel, a double-headed rake and/or a bathyscope where necessary. In lakes and ponds, a boat was used to survey areas that were too deep to wade. For larger lakes (> 20 ha), we followed the UK standard survey methodology (JNCC 2015) compatible with the Water Framework Directive monitoring and reporting (Gunn et al. 2010). These structured surveys comprised multiple sectors per lake (typically three to four sectors, but up to seven depending on lake area and habitat complexity), each of 100 m shoreline length and positioned to account for variation in depth, littoral substrate and exposure. Within each sector, five transects were established perpendicular to the shore and four replicate points were sampled per transect at depths of 0.25, 0.50, 0.75 and > 0.75 m, giving a typical total of at least 60–80 points per lake. If the maximum depth of colonisation was not covered by the five transects, an additional transect of up to 20 points was established from the shore to the maximum depth of colonisation to ensure coverage of vegetation in deeper water. Despite not covering the full lake perimeter, this method has proved able to capture all known species at a site, including at species-rich sites (Gunn et al. 2010). For macrophytes in ponds, the entire water area and margins (average length $235\text{ m} \pm 186\text{ m SD}$) were surveyed, and for canals and ditches (i.e. continuous waterbodies) a 100 m stretch was surveyed covering both marginal and

open water habitats, consistent with standard river survey procedures (JNCC 2016). These surveys collectively resulted in a dataset on macrophytes that should be representative of the landscape and have a reasonable chance of detecting all but the rarest or most locally distributed species and should therefore ensure a representative sample of the plants present in each waterbody type at the time of survey.

Molluscs, beetles and larval odonates in all waterbodies were sampled using a standard 1 mm mesh GB pond net. For canals, ditches, lakes and ponds the number of mesohabitats (e.g. floating-leaved, short/tall emergent or submerged vegetation and, to a lesser extent, inorganic substrates) was visually assessed and all were then sampled by vigorously sweeping the pond net through the water column, any vegetation present and over the benthic substrate. This was repeated for each mesohabitat until no new species were found. For lakes, the entirety of lake margin was rarely sampled as much of the littoral zone was composed of naturally unsuitable habitat such as wave-exposed coarse substrates, therefore, sampling was focussed in sheltered, vegetated areas. For canals and ditches, inventory sampling was carried out within each 100 m stretch, as per the macrophyte sampling. Each sample was live sorted with individuals being either identified to species level in the field and released, or, when field identification was not feasible, preserved in 70% industrial methylated spirits (IMS) and identified later, to species-level, wherever possible. Where adult odonata were observed (e.g. ovipositing, flying/hawking, emerging or resting on

macrophytes) these individuals were identified visually in the field and assigned to the waterbody sampled. Where individuals within a taxonomic group were identified to mixed taxonomic resolution, the finest commonly available resolution was used across all records.

Statistical analyses

Species richness was defined as the number of species (or next highest taxonomic resolution) per waterbody within each indicator group. Non-native species, as defined by the GB non-native species secretariat (2023), were not removed from analyses as these form part of the species composition and can therefore potentially influence biodiversity patterns. A list of non-native macrophytes and molluscs species recorded in the study is given in Table S3. No vagrant odonates or non-native water beetles were encountered. Species of conservation concern (SoCC) were defined based on standardised IUCN criteria for macrophytes (Hodgetts 2011; Stroh et al. 2014), molluscs (Seddon et al. 2014), beetles (Foster 2010) and odonates (Daguet et al. 2008). SoCC per waterbody type and landscape are given in Table S4. From these criteria, we selected species that were classed as; Critically Endangered, Endangered, Vulnerable or Near Threatened as an indication of conservation importance. For each site i , we also calculated a multidiversity index (MD) where raw species richness per taxon group was rescaled by dividing by the mean of the five highest richness values recorded for that taxon within each landscape (Allan et al. 2014; Valdés et al. 2020), calculated as:

$$MD = \frac{1}{\text{mean}} \left[\left(\frac{Macrophyte_i}{Macrophyte_{5\text{highest}}} + \frac{Mollusc_i}{Mollusc_{5\text{highest}}} + \frac{Beetle_i}{Beetle_{5\text{highest}}} + \frac{Odonata_i}{Odonata_{5\text{highest}}} \right) \right]$$

A generalised linear model (GLM) was used to test for differences in species richness among waterbody types within each landscape and, as these data were over-dispersed, quasi-Poisson error distributions were used.

To determine if sufficient waterbodies were surveyed per landscape and to standardise comparison of species accumulation rates among fundamentally different waterbody types, rarefaction curves were calculated for each of the four taxonomic groups based on incidence data per waterbody type, Q0 raw species richness (Supporting Information, Figs. S1, S2, S3 and S4). Species accumulation curves based on Hill’s numbers (Q1—Shannon’s diversity and Q2—Simpson’s diversity) were also calculated (Chao et al. 2014), to allow the effective number of species to be compared after removing bias associated with rare or uncommon species. Hill’s numbers are also less sensitive to unit and area scale-dependence (Chase and Knight 2013). Furthermore, species richness was estimated using

a presence-absence based estimator (Chao et al. 2016) which allows for robust and detailed inferences about observed and expected species richness.

Finally, to explore species composition amongst waterbody types, unconstrained ordination was conducted using non-metric multidimensional scaling (NMDS) on twelve species x site matrices to compare composition amongst waterbody types per taxonomic group per landscape. A binomial dissimilarity index was applied within each NMDS as these data were presence only. Permutational analyses of variance were used to test for differences in species composition amongst waterbody types using the function ‘adonis2’ (Oksanen et al. 2019). Using these matrices, total beta diversity was partitioned into turnover and nestedness using the function ‘beta.sample’ (Baselga and Orme 2012).

All analyses were conducted using RStudio (Team 2021) with the packages: iNEXT (Hsieh et al. 2016), vegan (Oksanen et al. 2019) and betapart (Baselga and Orme 2012).

Table 2 Summary of biodiversity metrics for all taxon groups by waterbody type and landscape

Landscape	Waterbody type (no. surveyed)	Total richness	Multidiversity index Mean ± SE (min–max)	Total landscape richness supported (%)	Number of species unique to waterbody type	No. non-native species (% of sites with 1 non-native species)	No. of Species of Conservation Concern (% of sites with 1 SoCC)
Agricultural	Lake (25)	81-34-161-31	0.56 ± 0.09 (0.30–0.73)	63-95-80-97	17-2-30-4	9 (92%)	26 (64%)
	Pond (29)	83-25-121-28	0.31 ± 0.08 (0.13–0.50)	65-70-60-85	12-0-13-1	7 (45%)	11 (41%)
	Ditch (26)	80-27-142-22	0.37 ± 0.06 (0.28–0.54)	66-73-71-67	12-2-18-0	4 (58%)	19 (62%)
	All (80)	127-37-202-33				9 (64%)	29 (56%)
Upland	Lake (27)	83-21-90-20	0.50 ± 0.09 (0.39–0.72)	87-95-83-95	18-9-20-1	7 (59%)	6 (22%)
	Pond (27)	73-11-86-20	0.47 ± 0.08 (0.22–0.70)	78-50-79-95	9-1-19-1	5 (30%)	3 (19%)
	All (54)	95-22-109-21				7 (44%)	7 (20%)
Suburban	Lake (22)	103-27-70–10	0.61 ± 0.04 (0.55–0.71)	82-82-82-91	27-3-16-0	6 (86%)	0 (0%)
	Pond (26)	77-25-63-10	0.40 ± 0.05 (0.31–0.54)	62-76-74-91	15-5-14-0	6 (42%)	1 (4%)
	Canal (17)	40-16-29-7	0.34 ± 0.07 (0.19–0.51)	31-49-34-18	4-0-0-1	5 (100%)	2 (41%)
	All (65)	128-33-85-11				9 (72%)	2 (12%)

Where cells contain multiple numbers separated by hyphens, these represent macrophytes, molluscs, beetles and odonates, respectively

Results

Species richness

Across the 199 waterbodies studied, a total of 192 macrophyte, 48 mollusc, 242 beetle and 35 odonate species were recorded (a full list of species found per landscape and waterbody can be found in Supporting Information 2). For each taxon group and landscape, lakes supported the highest or at least a similar total (gamma) species richness followed by ponds (Table 2). In terms of the proportion of the total pool of species captured by the surveys in each landscape,

lakes also consistently ranked highest and consistently contributed the most unique species (Table 2). The high species richness of lakes was not unduly driven by the most speciose groups (i.e. macrophytes and beetles) since, when data were standardised (multidiversity index), lakes still had the highest index value in each landscape (Table 2). Within each of the three studied landscapes, some species were common to all waterbody types (agricultural 44%, upland 64%, and suburban 26%), but each waterbody type also contained unique species, i.e. those not shared with any other waterbody type (Table S4 lists the unique species per landscape and waterbody type). For the

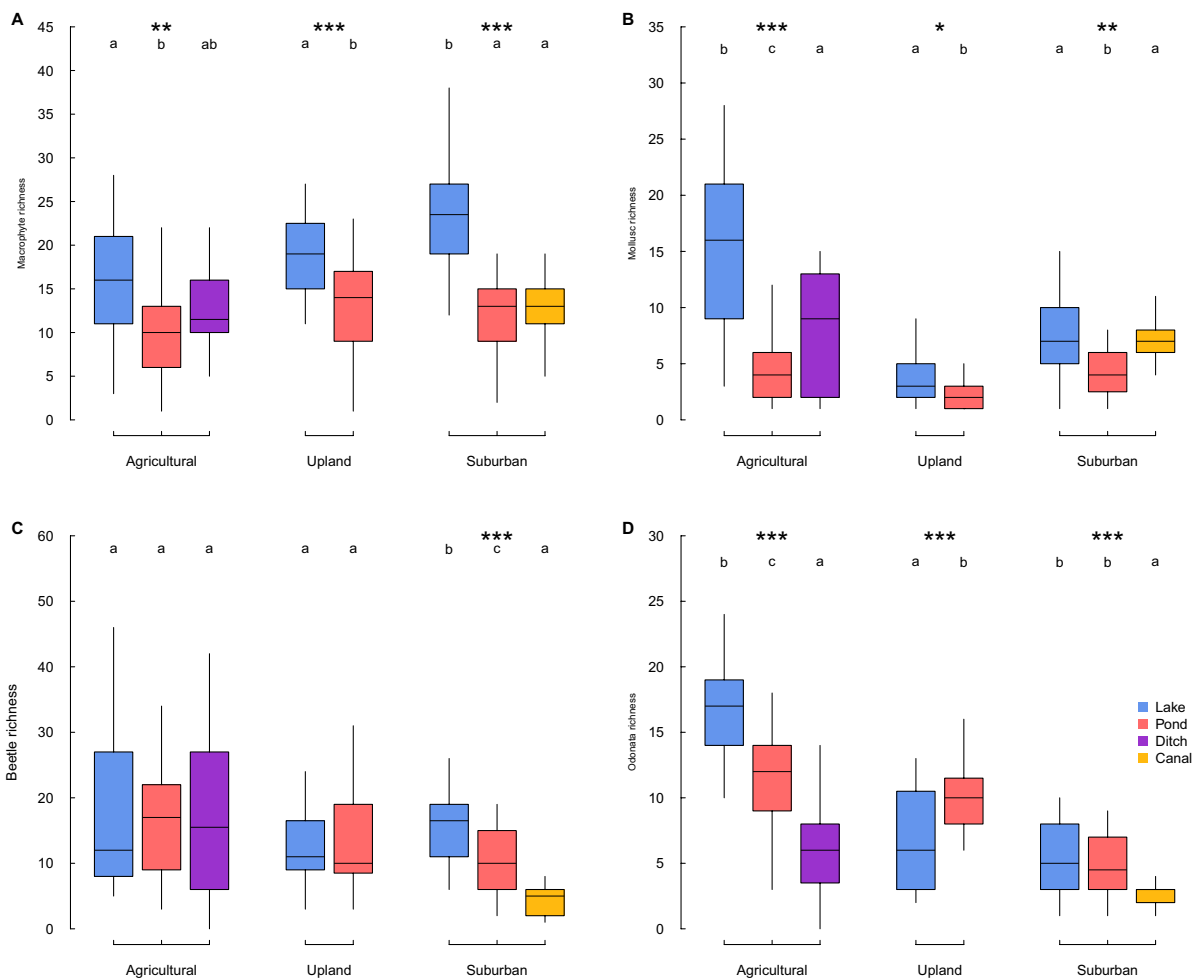


Fig. 2 Species richness (alpha diversity) per waterbody type and landscape for; **a** macrophytes, **b** molluscs, **c** beetles and **d** odonates. Boxes show median and enclose interquartile range and whiskers show 10th and 90th percentiles. Significance stars and letters are outputs from quasi-Poisson GLMs that

tested differences in richness among waterbody types within each landscape per species group (* $P=0.05$; ** $P=0.01$; *** $P<0.001$). Boxes sharing the same superscript letter were not significantly different from each other ($P>0.05$)

landscape-specific waterbodies (canals in suburban and ditches in agricultural landscapes) total species richness in ditches was similar to that of ponds in the agricultural landscape, but for canals, total species richness was low compared with the other suburban waterbody types (Table 2).

Across all landscapes and waterbodies, a total of 12 non-native and 35 SoCC were recorded (Tables S3 and S4, respectively). Lakes generally had high or the highest number of SoCC, but also contained a high number of non-native macrophytes and molluscs, regardless of landscape, with ponds containing the fewest non-native species. The suburban landscape had the highest percentage of all waterbodies (72%) in which non-native species were present, with the agricultural landscape having the highest number of SoCC.

For each taxonomic group, lakes contained the highest or comparable median richness (alpha diversity) regardless of landscape (Fig. 2). Group-specific patterns were also apparent, with some waterbody types being more important for particular taxa. For example, in all landscapes, ponds had high richness of beetles and odonates (Fig. 2c and d) yet a relatively low richness of macrophytes and molluscs (Fig. 2a and b), with lakes supporting higher median species richness for the latter taxonomic groups. Species richness in ditches was highly variable for molluscs and beetles, but relatively high for macrophytes and low for odonates.

Accumulation curves based on raw species richness (Q_0) estimated that sample coverage was generally high (mean = 94%), implying a systematically effective level of sampling replication (Fig. 3 and Supporting Information 1, Figs. S1, S2, S3 and S4). In general, accumulation curves illustrated that the highest species accumulation rates were found in lakes followed by ponds (Figs. S1, S2, S3 and S4). Ditches in the agricultural landscape displayed broadly comparable species accumulation trends to lakes and ponds, whereas canals in the suburban landscape had consistently lower species accumulation rates in comparison to lakes and ponds. When the effects of rare species were downweighted, i.e. using the effective number of common (Q_1 Shannon's diversity) or dominant (Q_2 Simpson's diversity) species, the aforementioned trends in species accumulation per waterbody type remained for each taxon group. However, curves plateaued earlier than raw species richness curves

(Q_0), indicating that common and dominant species were effectively accounted for within the number of waterbodies sampled (Figs. S1, S2, S3 and S4). This was further exemplified by rarefied species richness (Fig. S5) with the number of expected species often higher than we observed. However, the trend for lakes being the most or equally rich waterbody type for all taxon groups was preserved. Several rarefied estimates either could not be calculated (presumably due to species singletons) or were spuriously high (higher than the number of species that occur in GB), likely through high heterogeneity in species composition among sites, e.g. sites that were particularly species poor or rich. Due to these limitations, and because trends in rarefied estimates were similar to raw species richness, we used the latter in this study.

Species composition

The species composition of each taxon group differed significantly (all p values < 0.001) among waterbody types within each landscape, as is evident from the separation of centroids in Fig. 4. Therefore, even though species were often shared among waterbodies (Table S6), within each landscape each waterbody type had a distinctive composition. Lakes and ponds overlapped strongly and on average 57% of species found in lakes were also found in ponds (Table S6). Landscape-specific waterbody types (canals and ditches) also supported assemblages that were distinct from lakes and ponds for all taxon groups. This distinctiveness was more pronounced in canals compared to ditches. Overall, beta diversity for each taxon group per waterbody type and landscape was consistently better explained by species turnover (i.e. replacement) than nestedness (i.e. subset of the landscape species pool) (Fig. S6).

Subtle taxonomic trends were apparent among waterbody types and landscapes. For example, larger overlaps across waterbody types occurred in the agricultural landscape compared to the upland or suburban landscapes, for all groups except odonates (Fig. 4). Moreover, unusually species-rich sites in landscapes (e.g. beetles in ditches at Catfield Fen and the shallow lakes of Little Broad and Alderfen Broad in Norfolk, or molluscs in Windermere, Cumbria) strongly influenced compositional trends. Despite these outliers, significant compositional differences were apparent among waterbody types

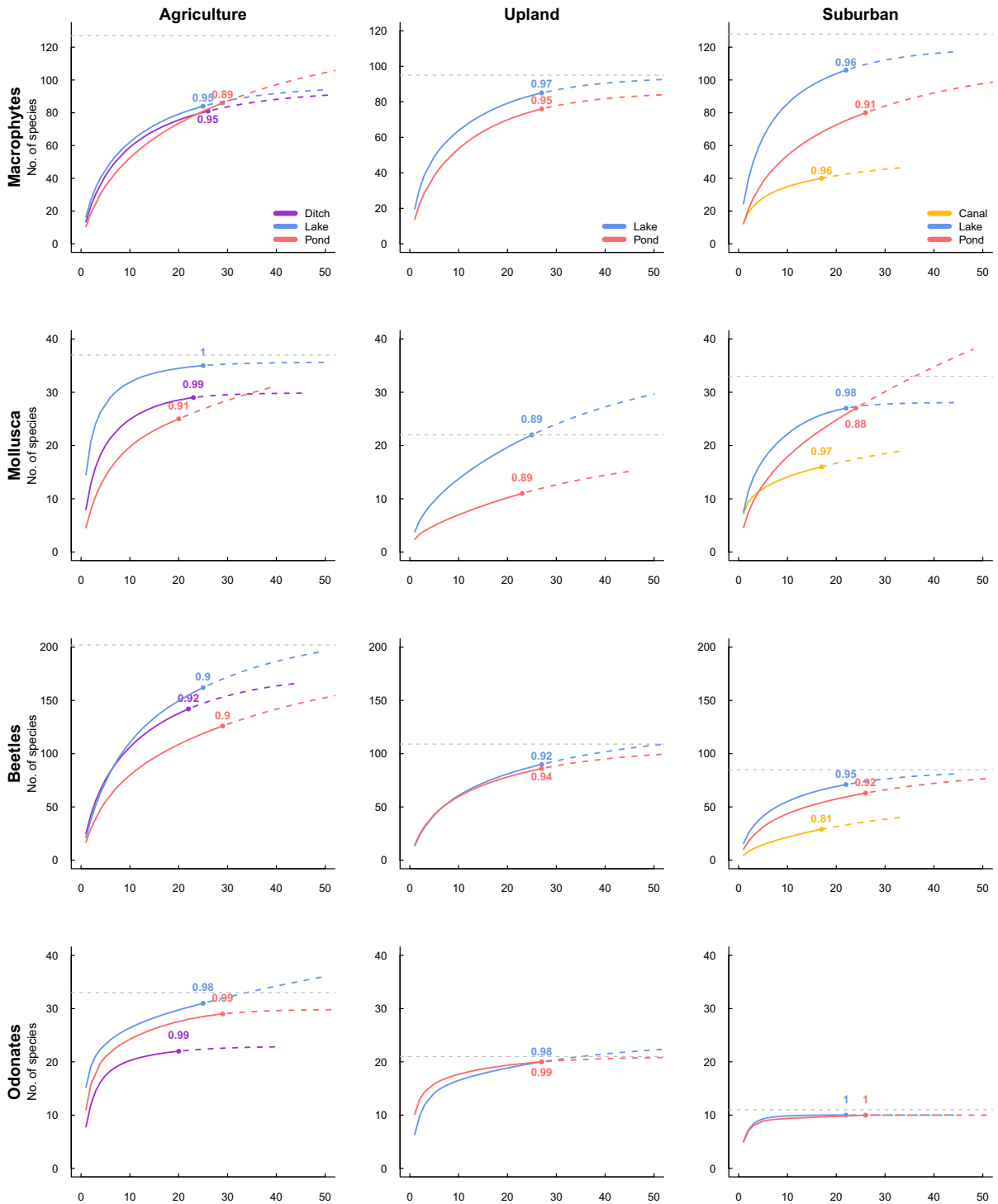


Fig. 3 Species accumulation curves with estimated coverage for each taxonomic group per standing waterbody type (lake, pond, ditch, canal) for agricultural, upland and suburban landscapes. Lines are extrapolated to estimate the effect of dou-

bling the sampling effort. Grey dashed lines represent the total species pool (gamma diversity) across waterbody types for each taxonomic group per landscape from our surveys

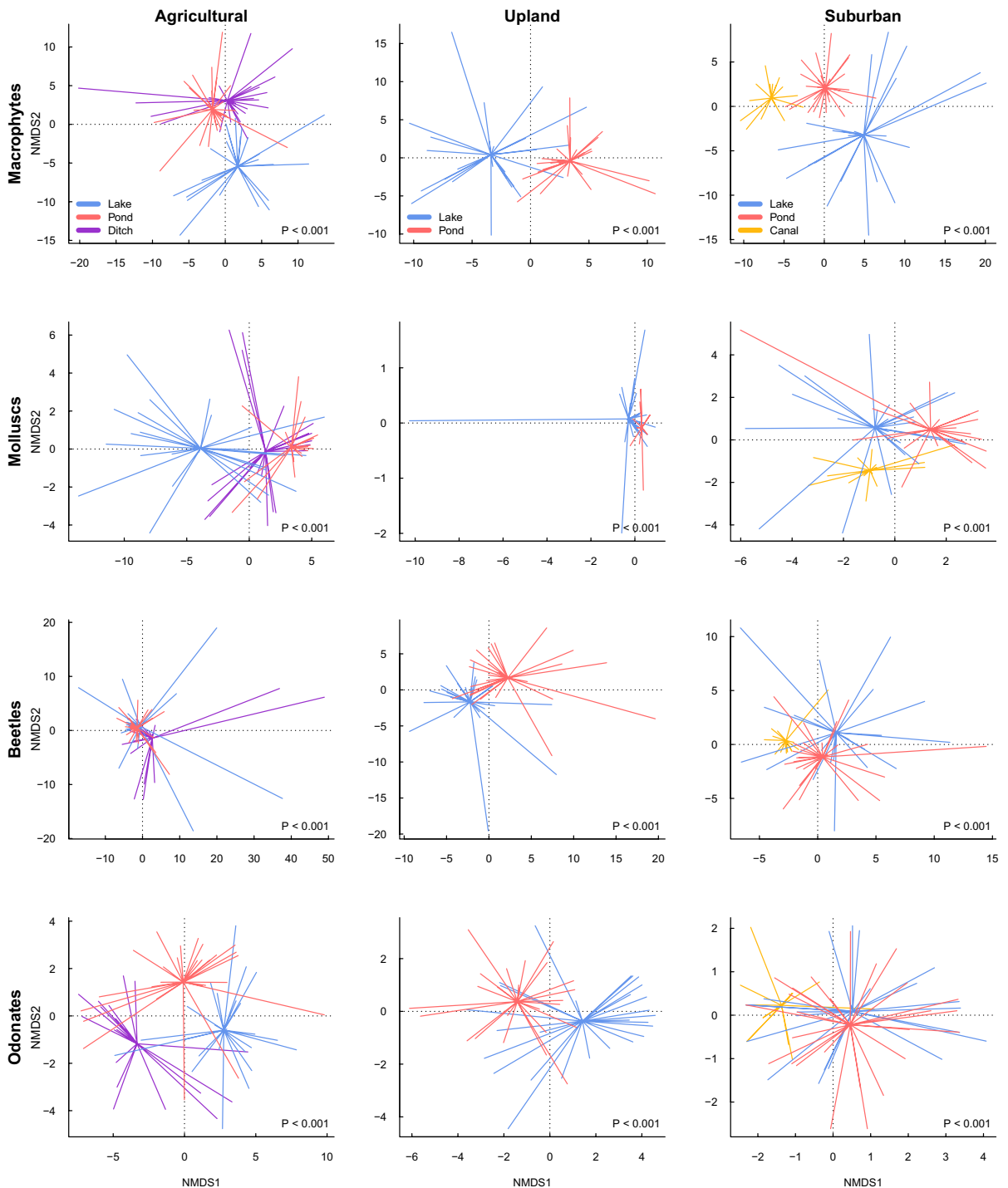


Fig. 4 Non-metric multidimensional scaling (NMDS) ordination plots. Each column represents a landscape (agricultural, upland and suburban) and each row represents a species group (macrophytes, molluscs, beetles and odonates). Each panel contains a spider plot for each waterbody type (lake, pond,

canal and ditch) with all sites connected by a line to their waterbody type centroid. *P*-values represent the output from permutational multivariate analyses of variance. All stress values were < 0.15

(which persisted after outliers were removed during data exploration). Differences in species composition among the two ubiquitous waterbody types were not driven by landscape-specific habitats, as the same trends were observed when analyses were re-run after removing canals and ditches (Fig. S7).

Discussion

Studies of global freshwater patterns that cover diverse biota are emerging (Pearson and Boyero 2009), alongside a steady flow of research on assemblage-environment responses in single or multiple landscapes with the same dominant land use for individual taxonomic groups (Williams et al. 2004; Davies et al. 2008a; Bubíková and Hrivnák 2018). However, assessments of landscape-scale patterns and their drivers in wider freshwater biodiversity remain elusive. Our study provides the first comparison of multiple-taxonomic groups, across multiple standing waterbody types, in contrasting landscapes and shows that the relative contributions of different waterbody types to freshwater biodiversity are largely generalisable at the landscape-scale.

Contrary to our hypothesis, we found that, despite major differences in topography and land use, the relative importance of different waterbody types was consistent across landscapes. Lakes made the greatest contribution to landscape biodiversity e.g. having the highest or equal highest alpha diversity, and highest multidiversity index, number of unique species and SoCC. Lakes may be species-rich due to their larger size which increases habitat heterogeneity, thereby, offering niches absent from smaller waterbodies (e.g. in the case of macrophytes, deep (3–5 m), clear waters for submerged species, or coarse, wave-disturbed shorelines suitable for isoetid species). This increased niche diversity should promote macrophyte richness and architectural complexity, thereby benefitting invertebrates, via increased food resources, mesohabitat diversity and refuge availability (Heino 2008; Law et al. 2019). Increased waterbody size also increases connectivity to the surrounding landscape, both via hydrological processes (large upstream catchments and downstream connections) and human and aerial vectors (being more accessible and attracting more people and waterfowl), potentially increasing site

richness via recruitment from surrounding populations (Turner 1989).

We found some evidence in our data of positive species–area relationships for molluscs, and to a lesser extent macrophytes, when ponds and lakes were aggregated (Fig. S8). However, this was not the case for beetles or odonates which may rely on specific mesohabitats within lakes, such as sheltered stands of emergent vegetation, that are less dependent on lake size. Several other studies have found inconsistent evidence for a species–area relationship in standing waterbodies (Oertli et al. 2002; Hof et al. 2008; Horváth et al. 2019). Evidently size can affect the biotic richness of waterbodies, but clearly does not solely account for the biodiversity importance of lakes that we observed.

Species composition differed significantly among waterbody types for all taxonomic groups, regardless of landscape. Small waterbodies (i.e. canals, ditches and ponds) may be more susceptible to stochastic events such as drought, pollution events, habitat destruction or fragmentation (Davies et al. 2008b). Small size, reduced hydrological connectivity and lower densities of avian vectors such as waterfowl (Green and Figuerola 2005) may also delay recovery after disturbances in small waterbodies, compared to lakes which have been shown to be buffered in the short-term when hydrological connectivity is high (Salgado et al. 2019). However, isolation may also bring advantages in terms of insulation from pressures such as water-borne pollution or biological invasion (Scheffer et al. 2006; Ishiyama et al. 2019). For example, we observed that incidence of non-native species in lakes was on average double that of ponds (Table 2). In addition, isolation should increase landscape heterogeneity among waterbodies (Hill et al. 2018), an expectation consistent with our finding that ponds had high or the highest dissimilarity (turnover) for the majority of species groups. We found that, for some species groups (beetles and odonata) in some landscapes, ponds had higher richness, supporting previous studies (Williams et al. 2004; Davies et al. 2008b). However, lakes were less abundant, more degraded or combined with ponds in these earlier studies, and thus under-represented, or under-sampled relative to their size.

Landscape-specific waterbody types (e.g. canals and ditches) are ubiquitous features of many human-influenced landscapes and our study indicated that

they were compositionally distinct from lakes and ponds. Ditches had high variability in species composition, with sites ranging from unmanaged, and heavily overgrown by emergent vegetation, to open-canopy channels with abundant submerged vegetation. Ditches in agricultural areas are often relatively species-poor habitats due to intensive land use (Davies et al. 2008b), but these differ physically and hydrologically from the low-lying, deeper, fen-type ditches in our study that are sustained by high groundwater and are managed less intensively (Painter 1999). For some taxa, under the right conditions and management (e.g. periodic, considerate dredging to prevent dominant species takeover) ditches can rival the best examples of other waterbody types (Verdonschot et al. 2011; Clarke 2015). Canals had an overall low dissimilarity among sites, but still were compositionally distinct from other waterbody types. This is most likely related to their physical uniformity, proximity to suburban land (e.g. influenced by urban run-off), longitudinal connectivity (including across watersheds) and management for navigation or drainage (Willby et al. 2001), leading to a lower alpha diversity. These findings support our hypothesis that all waterbody types will support distinctive communities that reflect varying abiotic attributes, but they also highlight that the biota of small waterbodies were not simply a subset of the waterbodies that contained the majority of species (i.e. lakes).

Sampling design and adequacy for comparative biodiversity studies

For comparative biodiversity studies, there is no study design that can equally encompass the scale and heterogeneity of different habitats, particularly in landscapes where discrete (lakes and ponds) and continuous (rivers, streams, canals and ditches, etc.) habitats co-occur. The current literature has predominantly adopted area- or time-standardised sampling of different waterbody types using the same survey method e.g. timed invertebrate sweep samples across different mesohabitats and/or macrophyte inventory surveys within a defined area (Verdonschot et al. 2011; Bubíková and Hrivnák 2018). Whilst this approach allows for fixed areas to be compared across waterbody types, it will also under-sample large waterbodies (lakes), oversample small waterbodies (ponds) and

exclude any habitats that are smaller than the fixed area surveyed (Davies et al. 2008b).

Our approach of inventory-type sampling whole discrete waterbodies and defined stretches of continuous waterbodies, in combination with utilising presence-only records, is likely to capture a waterbody's biodiversity more broadly, but detailed exploratory and statistical analysis was needed to support this. For example, to correct for sampling area, time and method we used rarefaction curves to check for asymptotes within taxon groups per landscape as an indication of sampling adequacy. As sampling coverage was consistently high (mean 94%), we have confidence that we consistently sampled the majority of common and dominant species despite differences in waterbody size and proportion of the resource surveyed. However, as several curves did not completely plateau, more rare species will occur in each landscape if more waterbodies were to be sampled (as demonstrated by the extrapolated endpoints, Fig. 3) with some potential for trends among some species groups and waterbodies to alter (e.g. ponds having a higher number of macrophytes in the agricultural landscape). Extrapolations are also inevitably highly uncertain, and the possibility also therefore exists that there would be minimal further gain in species with increased sampling effort.

Implications for freshwater biodiversity macroecology and conservation

It is clear that lakes make a unique contribution to freshwater biodiversity at the landscape-scale and the importance of protecting and improving exemplars should therefore not be ignored. Creating or restoring small waterbodies, such as ponds, is comparatively straightforward and can rapidly deliver multiple environmental gains at low cost (Lewis-Phillips et al. 2020; Sayer and Greaves 2020) with safety in numbers and isolation offering a strong rationale. Yet, focussing efforts solely on the creation or restoration of small waterbodies clearly cannot protect all elements of freshwater biodiversity in a landscape. Over the last two decades studies of lakes and their contribution to biodiversity have declined relative to other freshwater habitats (Stendera et al. 2012; Bolpagni et al. 2019) and there is a sense too that, the perennial, long-term challenges associated with lake

restoration, especially reducing catchment nutrient loading, alongside emerging stressors and climate change, can constrain progress against predicted timescales (Sharpley et al. 2013) which may dent enthusiasm for lake restoration. While different landscapes will introduce different combinations of conditions and stressors, and area/distribution of freshwater habitats our study suggests that these differences do not override the intrinsic spatial and abiotic attributes of the waterbody types within these landscapes, and that different biota respond in broadly similar ways. As such, incorporating principles of large-scale thinking (e.g. whole catchment-scale Stendera et al. 2012; Sayer 2014; Williams et al. 2020) and inclusiveness into management plans and policy should benefit freshwater habitats and their biodiversity across a range of landscapes.

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

Declarations

Conflict of interest The authors declare no competing interests.

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