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Elements of lake macrophyte metacommunity structure: Global variation and community-environment relationships

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Abstract

Documenting the patterns of biological diversity on Earth has always been a central challenge in macroecology and biogeography. However, we are only beginning to generate an understanding of the global patterns and determinants of macrophyte diversity. Here, we studied large-scale variation and community-environment relationships of lake macrophytes along climatic and geographical gradients using regional data from six continents. We applied statistical routines typically used in the context of metacommunity studies to provide novel insights into macrophyte community compositional patterns within regions worldwide. We found that lake macrophyte metacommunities followed clumped species replacement structures, suggesting that two or more species groups were responding similarly to the environment within regions. Underlying such general convergence, our results also provided evidence that community-environment relationships were largely context-dependent, stressing that no single mechanism is enough to account for the complex nature of compositional variation. Surprisingly, we found no general relationships between functional or phylogenetic composition and main metacommunity types, suggesting that linking multi-trait and evolutionary information to the elements of metacommunity structure is not straightforward. Our findings highlight that global conservation initiatives and biodiversity protection need to capture environmental variation at the metacommunity level, and acknowledge the highly context-dependent patterns in the community-environment relationships of lake macrophytes. Overall, we emphasize the need to embrace the potential complexity of ecological inferences in metacommunity organization across the globe.

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Regional biotas develop under influences of environmental, climatic and geographical factors (Willig et al. 2003). However, much uncertainty remains in our understanding of their role in affecting local biotic assemblages over large spatial extents, due in part to the lack of comparable and well-curated data over large areas (Wüest et al. 2020). Consequently, examining the relative importance of these factors on geographical patterns of community compositional variation is still central to macroecology and biogeography (Heino 2011) and a prerequisite for understanding the distribution of biodiversity on Earth (Kreft and Jetz 2007). Recently, considerable progress has been made toward documenting large-scale patterns in the biodiversity of terrestrial ecosystems, including woody plants, insect, birds, and mammals (e.g., Swenson et al. 2012; Cooke et al. 2019). By contrast, organisms inhabiting inland waterbodies have been far less studied from the macroecological perspective (see Heino 2011 and Hortal et al. 2014 for comprehensive reviews). Given that freshwater ecosystems are typically more isolated and fragmented than most terrestrial and marine systems, the underlying factors controlling the ecogeographical patterns of freshwater biodiversity should differ from those found in the other two realms of life (Kinlock et al. 2018). In this regard, generalizations about ecogeographical rules evidenced using terrestrial plants can rarely be used to explain distributional patterns and their underlying mechanisms in freshwater macrophytes (Alahuhta et al. 2020). These inconsistencies originate from differences in accessibility to water and atmospheric gases between terrestrial and aquatic plants, the latter of which also experience less extreme temperatures in inland waters (Iversen et al. 2019). However, we are only beginning to generate an understanding of the global patterns and determinants of freshwater macrophyte diversity (Grimaldo et al. 2016; Alahuhta et al. 2017; Alahuhta et al. 2018*a*; Murphy et al. 2019). Such a research program should not only be of interest to macroecologists and biogeographers, but also to environmental managers and conservation practitioners seeking to delineate biogeographical regions for environmental assessment and conservation (Bailey 2010).

Given the strong associations between the theoretical foundations of metacommunity ecology (Leibold et al. 2004) and modern biogeography (Jocque et al. 2010), understanding the mechanistic basis of large-scale biogeographical patterns also necessitates use of hypotheses and analytical approaches that have been more typically applied in the analysis of metacommunities at the landscape level (Heino et al. 2015*a*). Metacommunities (i.e., a set of interacting communities linked by dispersal; Leibold et al. 2004) show multiple patterns and models in space and time, ranging from those assuming strong species interactions to those suggesting idiosyncratic responses to the environment (Heino et al. 2015*a*). Indeed, these ideas intrigued plant ecologists in the first half of the 20th century, when Clements (1916) and Gleason (1926) debated the discrete vs. continuous nature of community boundaries along underlying environmental gradients. More recently, Leibold and Mikkelson (2002) devised a stepwise routine based on the three "elements of metacommunity structure" (hereafter, EMS)—coherence, species range turnover and range boundary clumping—to examine such community patterns. In this approach, random distributions of species are contrasted with four main idealized models: nested subsets (Patterson and Atmar 1986), evenly spaced gradients (Tilman 1982), Clementsian gradients (Clements 1916), and Gleasonian gradients (Gleason 1926). These main metacommunity types are broad idealizations of nature and, hence, multiple subtypes (i.e., quasi-structures) can also be distinguished (Presley et al. 2010, see Table 1 for a glossary).

Although the EMS approach was originally aimed at testing for multiple patterns across a set of local communities (Leibold and Mikkelson 2002), the same analytical routine can be adopted to examine distributional patterns across regions at large biogeographical scales (Heino and Alahuhta 2015; Schlemmer-Brasil et al. 2017). Nonetheless, this approach is not without its problems, as outlined recently by Ulrich and Gotelli (2013) and Schmera et al. (2018). Their criticism mainly concentrated on the likely unreliable mathematical mechanisms that give rise to some idealized structures (Schmera et al. 2018). While we agree that the EMS framework may be burdened by anomalies in detecting some empirical patterns (e.g., checkerboard distributions, Presley et al. 2019), we argue that its careful non-mechanistic interpretation and subsequent combination with alternative analytical approaches should lead to a better understanding of main macroecological patterns and community-environment relationships (Meynard et al. 2013; Heino and Alahuhta 2015). For example, a simultaneous comparison of multiple study regions may help to elucidate whether compositional variation is molded predictably by a set of ecological settings or if that compositional variation is context-dependent (Tonkin et al. 2016). Those settings could be revealed using ecological correlates of metacommunity structure similar to functional traits and phylogenetic distances of species in other contexts (Heino et al. 2015*b*; García-Girón et al. 2019*a*). Surprisingly, to our knowledge, no single study has assessed both the best fit patterns of community variation and the ecological features of regional metacommunities simultaneously at global scale.

Here, we present an analysis of geographical variation, context dependency and community-environment relationships of macrophytes using data from 16 regions worldwide (Fig. 1a). We specifically examined the following questions: (1) Which idealized metacommunity model best fits the empirical data of lake macrophyte metacommunities within study regions? (2) Are community-environment

Table 1. A glossary of the main elements of metacommunity structure and idealized models dealt with in this paper.

Concept	Description
Coherence	A measure of the degree to which a distributional pattern can be collapsed into a single ordination axis (Leibold and Mikkelson 2002)
Species range turnover	A measure that reflects the tendency for species to replace each other from site to site along an ordination axis (Leibold and Mikkelson 2002)
Range boundary clumping	A measure of the degree to which the boundaries of different species' ranges are clustered together along an ordination axis (Leibold and Mikkelson 2002).
Random distribution	A random structure exists when there are no gradients or discernible patterns in species distributions among sites (Leibold and Mikkelson 2002)
Nested subsets	A metacommunity structure where species poor sites form proper subsets of species from progressively richer communities (Patterson and Atmar 1986)
Evenly spaced	A metacommunity structure where gradients result in no discrete communities, but species ranges are arranged more evenly than expected by random chance (Tilman 1982)
Clementsian	A metacommunity structure where species respond to environmental gradients as groups, resulting in discrete communities (Clements 1916)
Gleasonian	A metacommunity structure where species respond individualistically to underlying environmental gradients (Gleason 1926)
Quasi-structure	Quasi-structures are intermediate metacommunity types. *Quasi-nested* metacommunities (i.e., *quasi-hyperdispersed species loss*, *quasi-random species loss*, and *quasi-clumped species loss*) is the name for cases of significant positive coherence and non-significant (negative) range turnover. By contrast, *quasi-evenly spaced*, *quasi-Gleasonian*, and *quasi-Clementsian* structures are the names for cases with positive coherence and non-significant (positive) range turnover. They can be distinguished based on range boundary clumping (Presley et al. 2010)

Table adapted from Leibold and Mikkelson (2002), Presley et al. (2010), and Heino et al. (2015*b*).

relationships consistent or variable among different regions? (3) What ecological correlates describing metacommunity characteristics (i.e., elevation range, spatial extent, latitude, longitude, age of the oldest lake within each region, matrix fill, species richness, functional composition, and phylogenetic composition) best determine variation in coherence, species range turnover and range boundary clumping? Based on evidence from previous studies (Henriques-Silva et al. 2013; Heino et al. 2015*b*), we expected to find clear geographical variation in metacommunity structuring, with a change from Gleasonian to Clementsian gradients from the equator to the poles (H1). This is because we expected that two or more groups of species would respond similarly to the typically harsher environmental conditions in boreal regions, leading to clumped range boundaries in their geographical distributions (Heino et al. 2015*b*). We also hypothesized (H2) that a strong context dependency would be observed in the community-environment relationships, not least because the structuring of lake metacommunities can be highly variable among different regions (Alahuhta et al. 2017, 2018*a*; Heino and Tolonen 2017). In addition, we predicted (H3) that variables describing the ecological features of metacommunities would be good predictors of the three elements of metacommunity structure, because multi-trait and evolutionary information should be related to the predictability of the underlying distributional patterns (Meynard et al. 2013; García-Girón et al. 2019*a*).

Methods

Macrophyte data sets and regional characteristics

We analyzed a data set of 16 different study regions covering six continents across the Earth (Fig. 1a, Supporting Information Appendix S1 and Fig. S1). The study regions and field methods have been described previously (Alahuhta et al. 2018*a*) and are here outlined briefly to aid understanding of the ecological context of individual regions. We had strict quality control for selecting each data set: (1) each study region had to include ca. 30 lakes with similar geographical distribution from the pool of candidate lakes; (2) all lakes had to be mostly natural lentic systems (i.e., reservoirs were excluded); and (3) all macrophyte communities within each data set had to have been empirically surveyed using similar methods to maintain data comparability. The selected lakes ranged from glacial-origin and relatively stable lakes situated in temperate and boreal zones (e.g., Finland, Sweden, Norway, Estonia, Denmark, Poland, New Zealand and US states of Minnesota and Wisconsin) to semi-arid shallow Mediterranean lakes (e.g., Morocco and Spain). Most of the study lakes suffered from various anthropogenic pressures such as water

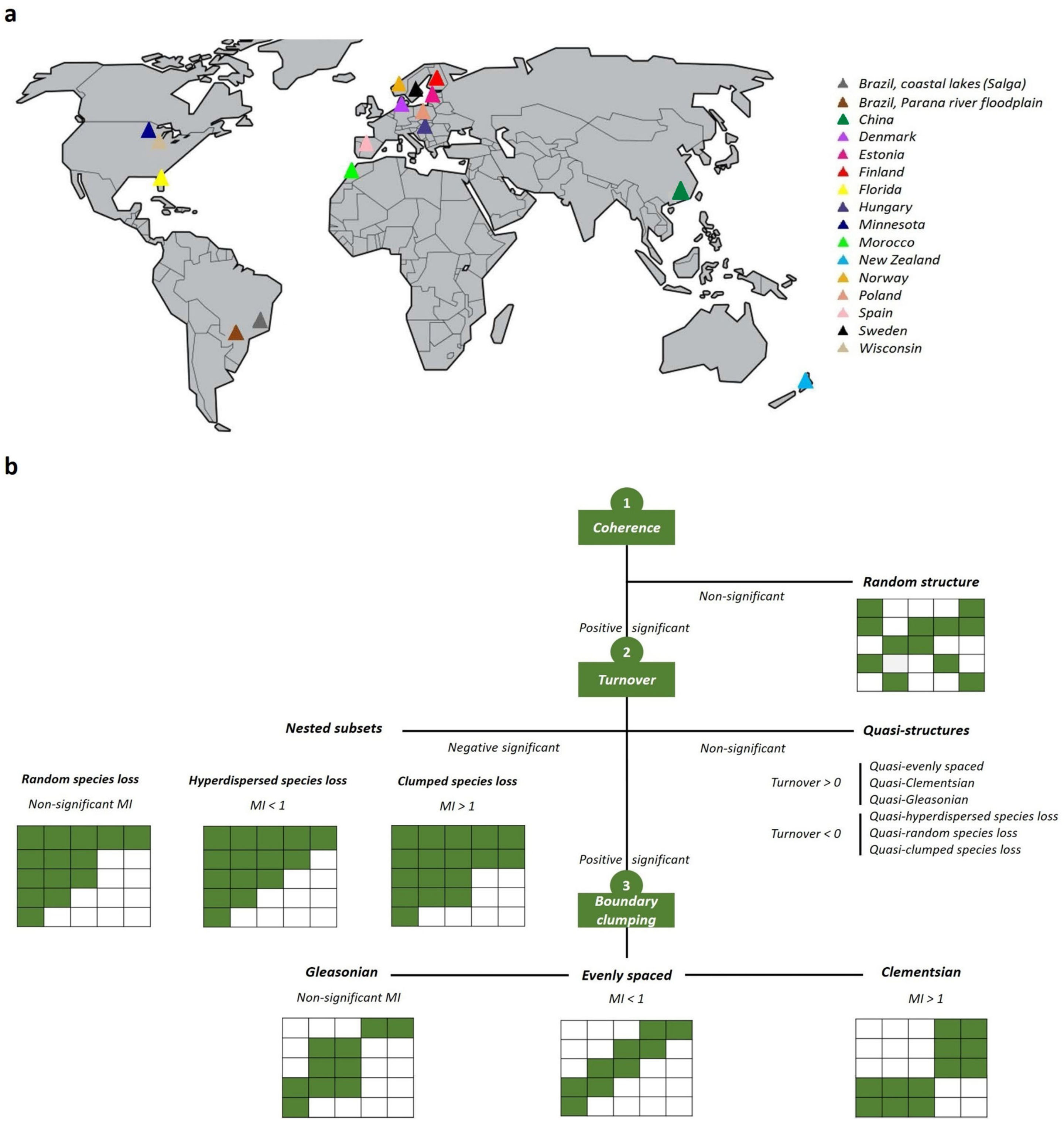

Fig 1. (**a**) Our study system comprised ca. 30 lakes surveyed in each of the 16 regions (colored triangles) across the world. (**b**) Schematic representation describing Leibold and Mikkelson's (2002) elements of metacommunity structure (i.e., coherence, species range turnover and range boundary clumping). The combination of coherence, species range turnover and range boundary clumping results in seven main metacommunity types (i.e., random, random species loss, hyperdispersed species loss, clumped species loss, evenly spaced, Clementsian and Gleasonian; bold font) and six quasi-structures (i.e., quasi-evenly spaced, quasi-Clementsian, quasi-Gleasonian, quasi-hyperdispersed species loss, quasi-random species loss and quasi-clumped species loss; italic font). Species × sites distributions corresponding to the principal metacommunity types are represented as follows: *columns* represent different species and *rows* represent sites. Figure modified from Presley et al. (2010) and Henriques-Silva et al. (2013). *MI*, Morisita's index.

extraction, invasive species, nutrient enrichment, and decreased connectivity, which cannot be avoided in an increasingly human-dominated world.

Our data set consisted of presence-absence observations of aquatic macrophyte species (i.e., species that are strongly bound to aquatic environments; see Kosten et al. 2009). These species included submerged (elodeids and isoetids), floating-leaved, free-floating (ceratophyllids and lemnids) and emergent forms (Cook 1999). The species list from each region was carefully checked to guarantee that inconsistencies were minimal. To do this, non-aquatic helophytes, shore species, aquatic bryophytes and charophytes were removed from the final data sets. Similarly, we excluded hybrids, subspecies, and genus level identifications when species from the same genus were recorded from the data.

Elements of metacommunity structure (EMS) analysis using site-by-species incidence matrices

Following the metacommunity framework originally proposed by Leibold and Mikkelson (2002), and thereafter expanded by Presley et al. (2010) and Henriques-Silva et al. (2013), we analyzed which metacommunity structure best fitted lake macrophyte data in each study region across the globe. To do this, we adopted the "range perspective" in our analyses (Presley et al. 2010). The metacommunity types were assessed by analyzing aspects of coherence, species range turnover and range boundary clumping of site-by-species presence-absence matrices. Incidence matrices were first ordinated via reciprocal averaging (CA). This procedure allowed us to obtain a latent gradient in which sites were ordered according to species composition and species were ordered according to site occurrences. After rearranging the data matrix, we tested the different metacommunity elements in a hierarchical way, that is, (i) coherence, (2) species range turnover, and (3) range boundary clumping (Fig. 1b; Table 1).

Coherence is based on calculating the number of embedded absences (i.e., gap in a species range) in the ordinated empirical incidence matrix and then comparing the observed value to a null distribution of embedded absences from 1000 simulated matrices. A metacommunity is considered to be coherent when the number of observed embedded absences is lower than expected by chance. Significantly positive coherence thus suggests that species distributions are responding similarly to a common environmental gradient represented by the ordinated site-by-species presence-absence matrix. Non-significant coherence means that species are distributed at random, suggesting that species are not responding to a common environmental gradient (Leibold and Mikkelson 2002). For metacommunities with positive and significant coherence, the range turnover component was tested (Fig. 1b). *Species range turnover* was measured as the number of empirical replacements for each possible pair of species and for each possible pair of sites in the ordinated matrix. Then, the number of observed replacements was compared to a null distribution that randomly shifts the entire ranges of species (Leibold and Mikkelson 2002). Significantly negative turnover (i.e., the observed replacement is lower than expected by chance) is consistent with a nested structure (i.e., hyperdispersed species loss, random species loss, and clumped species loss), whereas significantly positive turnover (i.e., the number of observed replacements are higher than expected by chance) indicates evenly spaced, Gleasonian or Clementsian metacommunity types. The cases of significant positive coherence and non-significant turnover can be interpreted as quasi-structures (Presley et al. 2010). We further analyzed *range boundary clumping* using Morisita's index of dispersion and a subsequent χ^2 test that compares the empirical distribution of range boundaries to an expected uniform distribution. Index values significantly larger than "1" indicate clumped range boundaries (i.e., Clementsian and clumped species loss structures) and values significantly less than "1" suggest hyperdispersed range boundaries (i.e., evenly spaced distribution and hyperdispersed species loss structures). Species distributions that occur independently and idiosyncratically with respect to each other (i.e., Gleasonian and random species loss structures) are indicated by a non-significant χ^2 test. Correspondingly, quasi-evenly spaced, quasi-Gleasonian, quasi-Clementsian structures, quasi-hyperdispersed species loss, quasi-random species loss, and quasi-clumped species loss can be separated by boundary clumping (Presley et al. 2010; see Fig. 1b).

The significance of the index values for coherence and range turnover was tested using the fixed-proportional null model (Gotelli 2000), where the species richness of each site is maintained (i.e., row sums are fixed) but species ranges (i.e., columns) are filled based on their marginal probabilities. Random matrices for the fixed-proportional null model were produced by the "r1" method as implemented in the vegan package (Oksanen 2016). Although the fixed-proportional null model makes sense ecologically and is not highly sensitive to type I or type II errors (Presley et al. 2009), this modeling approach does not involve shifting of ranges and therefore our findings need to be treated with caution. We also used a strict and conservative fixed–fixed null model based on the "quasi-swap" method in the R package vegan to find out if the null model used affected the results. In the fixed–fixed null model, both species richness of each site and species frequencies are maintained. We used 1000 simulations to provide random matrices for testing coherence and species range turnover. Elements of metacommunity structure were evaluated for each study region along the first reciprocal averaging (i.e., correspondence analysis) axis because we were interested in the most important species compositional gradient. Analyses of coherence, species range turnover and range boundary clumping were performed using the metacom package (Dallas 2013) in the R environment (R Core Team 2018).

We also used a Z-score or standardized effect size (SES) for the indices of coherence and species range turnover for each individual metacommunity:

$$\mathrm{SES} = \frac{obs - rnd.mean}{rnd.sd}$$

where *obs* is the observed index value, *rnd.mean* the mean index value of the null distribution, and *rnd.sd* the standard deviation of simulated index values (see Gotelli and McCabe 2002).

Z-scores allow comparisons among data sets and can thus subsequently be used in comparative analyses (see Heino et al. 2015*b*). Basically, Z-scores between -1.96 and 1.96 are non-significant at $\alpha = 0.05$ and, thus, Z-scores of coherence and species range turnover can also be used to infer metacommunity structures. We also applied the traditional approach to delineate metacommunity types based on statistical significance from the randomization tests of coherence and species range turnover (see above).

Community-environment relationships

Community-environment relationships within the study regions were compared based on a set of a priori determined lake-level variables. Physico-chemical variables consisted of lake area (km^2), Secchi depth (m) and water total phosphorus concentration ($\mathrm{mg\ L}^{-1}$). These three physico-chemical variables were chosen because they often account for significant variation in community structure of lake macrophytes (see Alahuhta et al. 2018*b*), and correlate with other hydromorphological and water chemistry variables that were not available for all study regions (e.g., Kosten et al. 2009). Physico-chemical variables were surveyed and determined following similar procedures within each study region (Supporting Information Appendix S1). Climate variables included atmospheric annual mean temperature (°C), annual temperature range (°C), and annual precipitation (mm) defined for each study lake based on 30 years average values (1 km resolution data) obtained from the WorldClim (Hijmans et al. 2005). Climate variables were not only a surrogate for thermal energy availability (Alahuhta et al. 2017) and water-level fluctuation (Carpenter et al. 2011), but also for nutrient and material loading from the catchment (Sahoo et al. 2015).

Our main statistical method to explore community-environment relationships within regions was canonical correspondence analysis (CCA), which is a constrained extension of reciprocal averaging (Legendre and Legendre 2012), thus providing a link to the EMS analysis. We used the intraset correlations between environmental variables and site scores along the first two ordination axes to infer which factors were best related to variation in community composition and compare whether the same environmental drivers were important in each study region (see Heino et al. 2015*b*). Note, however, that we cannot associate a given metacommunity type specifically to environmental drivers, not least because there is no evidence that a particular mechanism can map onto a particular structure. CCAs were run with the "cca" function using the R package vegan.

Comparative analyses

We used simple linear regression to analyze variation in the Z-scores of coherence, the Z-scores of species range turnover or the index of range boundary clumping with a set of ecological correlates (i.e., predictor variables) describing metacommunity characteristics (see below). Standardized effect sizes of each metacommunity element (Y_i) were log-transformed [$\min (Y_{max} + a = 1) \rightarrow \log (Y_i + a)$] before analyses to improve normality and reduce skewness.

We first summarized regional environmental information within convex hulls encompassing the minimum area containing all surveyed lakes within each region. For each study region, we defined *elevation range within the convex hull* (m), *area of the convex hull* (km^2), *latitude of the convex hull* (from centroid), *longitude of the convex hull* (from centroid), and estimated the *maximum lake age within a particular region* (see Supporting Information Appendix S1 and Table S1 for variable information). These variables can indirectly affect lake macrophytes by indicating variation in habitat suitability (Alahuhta et al. 2017), dispersal limitation (García-Girón et al. 2019*b*), environmental heterogeneity (Downing and Rath 1988), and temporal availability for colonization sources (Alahuhta et al. 2018*a*). Second, we used *matrix fill* (i.e., the proportion of "1 s" in the site-by-species incidence matrix) and *species richness* because data set characteristics may have strong effects in comparative analyses of metacommunities (Heino et al. 2015*b*). Third, we considered several key functional traits (Supporting Information Appendix S2, Table S2 and Fig. S2) to provide information on multiple ecological aspects of each metacommunity (Heino et al. 2015*b*) and to give a broad characterization of the realized niche of the species. We then used the mixed-variables coefficient of distance (i.e., a generalization of Gower's distance; Borcard et al. 2011) to extract a functional distance matrix across the 16 data sets using the "daisy" function in the R library cluster (Maechler et al. 2014). The phylogenetic composition of each study region was addressed using the phylogenetic fuzzy-weighting method implemented in the PCPS package (Debastiani 2018). To do this, we used a molecular-based phylogeny for aquatic macrophytes recently developed by García-Girón et al. (2020) (for details on phylogenetic reconstruction, see Supporting Information Appendix S3 and Fig. S3). Thereafter, the pairwise output values for the functional distance matrix were synthesized into principal coordinate analysis (PCO) following Duarte et al. (2012). The scores of each single metacommunity along *PCO1*, *PCO2*, *PCPS1*, and *PCPS2* components were then used to indicate the combined *functional* (i.e., PCO) *and phylogenetic* (i.e., PCPS) *features of each metacommunity* (Supporting Information Appendix S4 and Fig. S4).

Results

The Z-scores of coherence from fixed-proportional (i.e., “r1”) or fixed–fixed (i.e., “quasi-swap”) null models were strongly correlated ($r_p = 0.93$, $p < 0.001$), and the same was true for the Z-scores of species range turnover ($r_p = 0.73$, $p < 0.01$). Accordingly, we focused on the results based on the fixed-proportional method because most previous studies have used it in the context of the EMS analysis (Heino et al. 2015*b*; Gascón et al. 2016; Schlemmer-Brasil et al. 2017). There was wide variation in the Z-scores of coherence, the Z-scores of species range turnover, and the index of range boundary clumping among the metacommunities (Table 2). However, the EMS analysis showed consistent patterns among study regions, resulting in three observed metacommunity types (Fig. 2 and Table 2). We found that Clementsian structure ($n = 8$) was the most common, followed by quasi-Clementsian ($n = 7$) and clumped species loss ($n = 1$) metacommunity types. In other words, most metacommunities were responding to latent environmental gradients, here represented by the first CA axis; groups of species had coincident range boundaries in each metacommunity; and species composition changed consistently in similar places of the underlying environmental gradient.

Community-environment relationships varied among individual metacommunities and did not allow us to single out a few environmental drivers among the set of available predictor variables (Fig. 3), suggesting that specific details of community-environment relationships were largely context dependent. For instance, Secchi depth had the highest effect on variation in community composition in China (CCA1), whereas temperature range and precipitation were strongly

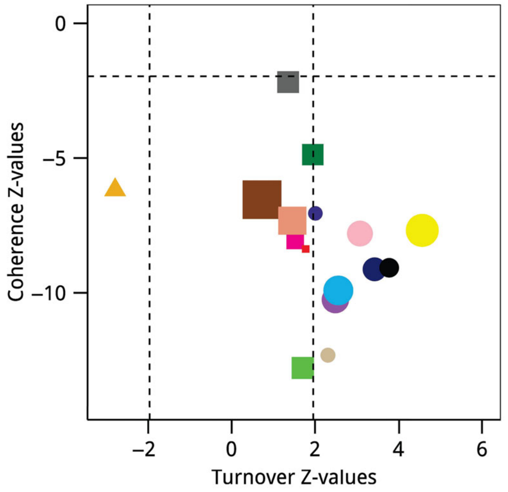

Fig 2. Metacommunity structures (*Clementsian*, circle; *quasi-Clementsian*, square; *clumped species loss*, triangle) of the 16 study regions plotted in the space of the Z-scores of coherence and species range turnover. Bubble size denotes the index of range boundary clumping. Dashed lines indicate Z-scores between – 1.96 and 1.96. See Fig. 1a for color scales corresponding to the study regions.

Table 2. Results of the EMS analysis for each individual study region. These results were based on the fixed-proportional null model. Interpretations followed Presley et al. (2010). Significant results (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$) are marked in bold font.

	Coherence				Species range turnover				Boundary clumping	
	Abs	Coh Z	Sim mean	Sim sd	Rep	Tur Z	Sim mean	Sim sd	Index	Interpretation
Brazil, coastal lakes	122	**−6.54*** **	200	12	1480	0.73	1183	405	**3.06*** **	Q-Clementsian
Brazil, Parana river floodplain	300	**−2.18*** **	468	77	2140	1.36	1843	219	**1.65***	Q-Clementsian
China	131	**−4.87*** **	204	15	2356	1.95	1459	458	**1.63** **	Q-Clementsian
Denmark	495	**−10.24*** **	874	37	19,357	**2.49***	14,406	1988	**1.97*** **	Clementsian
Estonia	426	**−8.05*** **	619	24	10,238	1.53	7921	1513	**1.47*** **	Q-Clementsian
Finland	566	**−8.37*** **	792	27	18,936	1.78	14,302	2606	**1.28** **	Q-Clementsian
Florida	247	**−7.68*** **	439	25	8765	**4.57*** **	4460	942	**2.47*** **	Clementsian
Hungary	336	**−7.04*** **	505	24	11,462	**2.01***	8267	1592	**1.37***	Clementsian
Minnesota	472	**−9.11*** **	718	27	17,643	**3.43*** **	10,688	2027	**1.75*** **	Clementsian
Morocco	158	**−12.78*** **	567	32	8599	1.71	7414	694	**1.67*** **	Q-Clementsian
New Zealand	156	**−9.91*** **	384	23	7587	**2.56***	5205	929	**2.19*** **	Clementsian
Norway	168	**−6.18*** **	273	17	1911	**−2.79** **	3608	607	**1.42*** **	Nested*
Poland	370	**−7.32*** **	575	28	7878	1.46	6137	1193	**2.06*** **	Q-Clementsian
Spain	338	**−7.79*** **	595	33	13,473	**3.08** **	8657	1564	**1.88*** **	Clementsian
Sweden	564	**−9.05*** **	890	36	27,480	**3.78*** **	17,343	2683	**1.54*** **	Clementsian
Wisconsin	543	**−12.3*** **	912	30	26,894	**2.31***	19,990	2985	**1.38*** **	Clementsian

Abs, the number of embedded absences; Coh, coherence; Q, quasi; Sim mean, mean of the simulated null matrix; Sim sd, standard deviation of the simulated null matrix; Rep, number of species replacements; Tur, species range turnover.

*Nested, clumped species loss (sensu Presley et al. 2010).

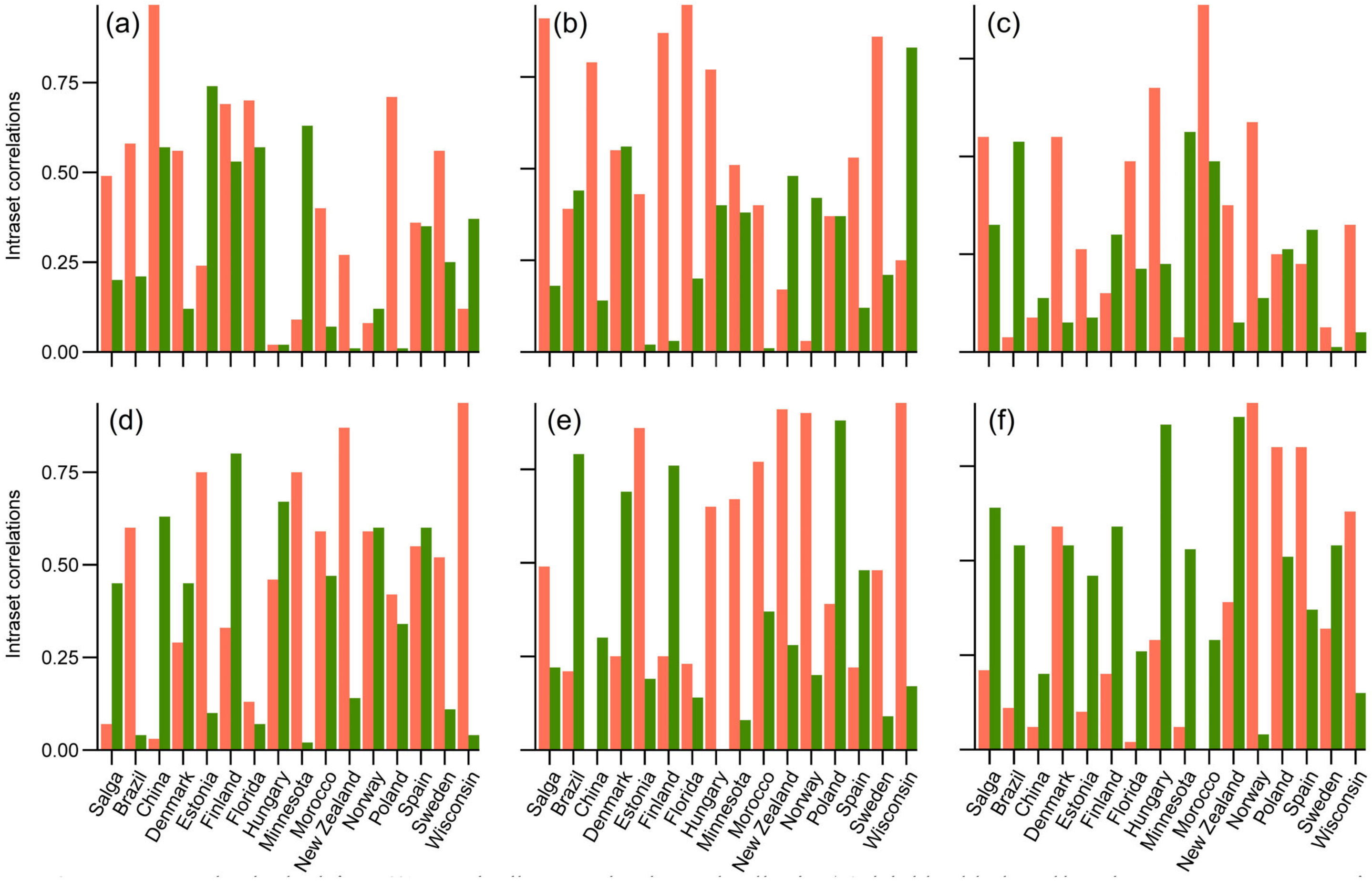

Fig 3. Community-environment relationships along the first two CCA axes as evidenced by intraset correlations between each variable predictor (**a**, Secchi depth; **b**, total phosphorus; **c**, lake area; **d**, mean temperature; **e**, temperature range; **f**, precipitation) and the ordination axes (CCA1, orange; CCA2, green). See Fig. 1a for abbreviations.

related to community composition in Wisconsin (CCA1) and New Zealand (CCA2), respectively. Similarly, total phosphorus, lake area and mean temperature were particularly important in Florida (CCA1), Morocco (CCA1), and Finland (CCA2), respectively.

Simple linear regressions showed that no ecological feature of metacommunities was significantly associated with variation in the Z-scores of coherence, the Z-scores of species range turnover or the index of range boundary clumping (Table 3). This indicated that the single components of the EMS analysis were not necessarily strongly related to ecological correlates describing metacommunity characteristics.

Discussion

While a relatively large number of studies have examined geographical variation in species richness across large spatial resolutions and extents (e.g., Raes et al. 2018; Murphy et al. 2019), fewer studies have examined species compositional variation worldwide based on local resolution (e.g., a lake) in the freshwater realm. In this regard, our study is unique in bringing together the three elements of metacommunity structure (i.e., coherence, species range turnover and range boundary clumping) and the varying ecological settings of multiple study regions to infer large-scale patterns and community-environment relationships of lake macrophytes across the world. Such a combination of techniques allowed us to better understand patterns in lake macrophyte metacommunities and the factors governing these patterns worldwide. We found mostly Clementsian (n = 8) and quasi-Clementsian (n = 7) metacommunity structures in the regions of our empirical data set, a finding which did not support our hypothesis of geographical variation in metacommunity types (H1). We also revealed highly context-dependent patterns in the community-environment relationships between different study regions, confirming our second hypothesis (H2). Unexpectedly (H3), our results also indicated that the three elements of metacommunity structure were weakly related to the predictor variables describing ecological features of metacommunities.

Table 3. Results of simple linear regression models for the Z-scores of coherence, the Z-scores of species turnover and the index of range boundary clumping. Simple linear regressions showed no significant relationships (*p*>0.05 in all cases).

	Coherence	Turnover	Boundary clumpling
Elevation range of convex hull	−0.23	0.12	−0.13
Area of convex hull	−0.06	0.39	−0.19
Latitude of convex hull	−0.25	0.00	−0.51
Longitude of convex hull	0.15	−0.15	−0.27
Estimated maximum lake age within convex hull	−0.39	0.05	0.22
Matrix fill	0.21	−0.26	−0.22
Species richness	−0.44	0.35	−0.38
PCO1	0.12	−0.09	0.43
PCO2	−0.01	0.00	0.36
PCPS1	−0.06	−0.22	0.23
PCPS2	−0.38	0.08	−0.16

PCO1 and *PCO2*, axes describing the principal coordinates of the functional distance matrix; *PCPS1* and *PCPS2*, axes describing the principal coordinates of phylogenetic structure.

Local communities show clumped boundaries but respond differently to environmental gradients

Species may experience environmental gradients as gradual or more-or-less discrete boundaries depending on species-specific characteristics (e.g., tolerance to abiotic factors and habitat specialization; Valanko et al. 2015). In our present study, Clementsian and quasi-Clementsian gradients were the most commonly found metacommunity types within regions along the ≈ 10,000 km latitudinal gradient. The idea of Clementsian gradients suggests that there are two or more groups of species (i.e., species associations) showing similar responses to the environment (i.e., species distributions are generally coherent), and that the responses differ among groups (Clements 1916). Consequently, the quasi-Clementsian structures observed here were probably the result of an artifact because species niche breadth extended beyond the range in which species turnover is significant (Presley et al. 2010), affecting the identification of boundaries in some study regions (Gascón et al. 2016). The Clementsian (or sometimes the quasi-Clementsian) pattern is commonly found in metacommunity studies conducted in aquatic systems, and both have already been reported in comparative analyses of lake biotas (Heino et al. 2015*a*,*b*), as well as for stream invertebrate metacommunities in Central Germany (Tonkin et al. 2016), Amazonian stream damselflies (Schlemmer-Brasil et al. 2017), soft-sediment benthic invertebrates from the Baltic Sea (Valanko et al. 2015), Hungarian stream fishes (Erős et al. 2014), and Mediterranean wetland microcrustaceans (Gascón et al. 2016). However, it is still particularly striking that environmental variation has such an important role in structuring lake macrophyte metacommunities in different biogeographical realms of the Earth (here, Palaearctic, Nearctic, Neotropical, Indomalayan, and Australasian). This finding may be related to the fact that lake systems and their drainage basin characteristics are inherently highly heterogeneous (Downing et al. 2006) and, hence, responses of macrophyte species groups to environmental variation are typically more complex than a simple gain or loss of species along major biologically-important thresholds (sensu Heino et al. 2015*a*).

Behind such general convergence, the disagreement among important community-environment relationships also highlights that no single mechanism (i.e., a single constraining environmental factor) is enough to account for the complex nature of compositional variation and metacommunity organization. Instead, it appears that metacommunity (i.e., regional) structuring of lake macrophytes is highly difficult to predict. This has been demonstrated in two recent global-scale studies that showed variable patterns in the factors shaping species-based beta diversity (Alahuhta et al. 2017) and community composition (Alahuhta et al. 2018*a*). Whatever the case, our study results agree with previous works in which climate and water quality were found to be primarily related to variation in macrophyte community composition at regional scales (Capers et al. 2010; García-Girón et al. 2019*a*,*b*; García-Girón et al. 2020). However, these findings should be interpreted with caution due to differences in sample timing between macrophytes and lake-level environmental variables in our study. Similarly, factors other than environmental filtering may also affect metacommunity structure. For example, connectivity among lakes and associated dispersal events may interfere with the environment in determining community composition by hindering species' tracking of local and climatic conditions (see García-Girón et al. 2019*b*). Nevertheless, associating the effects of dispersal with the idealized metacommunity types may be difficult, even if they existed (Meynard et al. 2013). Meanwhile, previous works using the same test data set showed that environmental filtering overcame the effects of potential connectivity in explaining local communities across the globe (Alahuhta et al. 2018*a*; García-Girón et al. 2020). We thus suggest that environmental differences between sites remain the main structuring force within lake macrophyte metacommunities worldwide, although individual metacommunities may respond differently to major limiting or constraining environmental gradients.

Metacommunity characteristics are poorly related to variation in coherence, species range turnover, and range boundary clumping

We found that the three elements of metacommunity structure were weakly correlated to the ecological variables describing individual metacommunity characteristics. In a recent study, Heino et al. (2015*b*) suggested that the ecological factors underlying variation in coherence, species range turnover, and range boundary clumping should not be inferred too strongly in isolation, because it is their combined influence which distinguishes different metacommunity structures. Previous studies suggested that accounting for trait and phylogenetic composition may provide more accurate predictions of metacommunity organization by approximating species niches similarities and evolution (Gianuca et al. 2018; García-Girón et al. 2019*a*). This is because functional traits and evolutionary legacy are key in determining diversity patterns within and among communities and species replacement along environmental gradients (de Bello et al. 2017). Interestingly, however, we found no general relationships between functional or phylogenetic composition and metacommunity structures. A reason for this lack of relationship may be that two or more groups of species sharing a common response to underlying environmental thresholds comprised either functionally dissimilar or distantly related macrophyte taxa. This finding contradicts our initial expectations and suggests that linking multi-trait and evolutionary information to the elements of metacommunity structure is not necessarily straightforward (but see Meynard et al. 2013). Nonetheless, we cannot exclude the possibility that future macrophyte studies decoupling trait and phylogenetic information at the metacommunity level will uncover hidden signals underlying species coexistence and replacements along major environmental gradients (see de Bello et al. 2017).

Conclusions

From a methodological perspective, our study shows that the simultaneous evaluation of the elements of metacommunity structure (i.e., coherence, species range turnover, and range boundary clumping) and the ecological settings of metacommunities can enhance our ability to understand large-scale patterns and community-environment relationships across the globe. More specifically, we found that our empirical data set fitted best Clementsian and quasi-Clementsian metacommunity types within regions, suggesting that lake macrophyte communities follow clumped species replacement structures. This information is relevant to the current debate about conservation of freshwater biodiversity, and we advance the notion that it needs to capture environmental variation at the metacommunity level (Socolar et al. 2016). Behind such general convergence of metacommunity types, our results also provide evidence that community-environment relationships are shaped by multiple environmental factors within regions. This finding suggests that individual metacommunities may respond differently to major limiting or constraining environmental thresholds, emphasizing the need to embrace the potential complexity of ecological inferences in metacommunity organization worldwide. We propose that future studies should examine the effects of climatic conditions, historical events and vicariance biogeography on species associations consistently occurring and disappearing at similar locations along the latitudinal gradient. Such an approach may not only provide insightful information about the evolutionary or physiological trade-offs associated with important ecogeographical thresholds (see Heino and Alahuhta 2015), but also offer a means of testing the very foundations of biogeographical regionalization and inferring major breakpoints in lake macrophyte community composition at global scale.

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Conflict of Interest

None declared.

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