

1 **Elements of lake macrophyte metacommunity structure:**
2 **global variation and community-environment relationships**

3 **Running head:** Exploring macrophyte metacommunities

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60 Macroecology; Metacommunity ecology; Spatial variation

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64 **Abstract**

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

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88 **Introduction**

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

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

131 Although the EMS approach was originally aimed at testing for multiple patterns across a set
132 of local communities (Leibold and Mikkelsen 2002), the same analytical routine can be adopted to
133 examine distributional patterns across regions at large biogeographical scales (Heino and Alahuhta
134 2015; Schlemmer-Brasil et al. 2017). Nonetheless, this approach is not without its problems, as
135 outlined recently by Ulrich and Gotelli (2013) and Schmera et al. (2018). Their criticism mainly
136 concentrated on the likely unreliable mathematical mechanisms that give rise to some idealised
137 structures (Schmera et al. 2018). While we agree that the EMS framework may be burdened by

138 anomalies in detecting some empirical patterns (e.g. checkerboard distributions, Presley et al. 2019),
139 we argue that its careful non-mechanistic interpretation and subsequent combination with alternative
140 analytical approaches should lead to a better understanding of main macroecological patterns and
141 community-environment relationships (Meynard et al. 2013; Heino and Alahuhta 2015). For
142 example, a simultaneous comparison of multiple study regions may help to elucidate whether
143 compositional variation is moulded predictably by a set of ecological settings or if that
144 compositional variation is context-dependent (Tonkin et al. 2016). Those settings could be revealed
145 using ecological correlates of metacommunity structure similar to functional traits and phylogenetic
146 distances of species in other contexts (Heino et al. 2015b; García-Girón et al. 2019a). Surprisingly,
147 to our knowledge, no single study has assessed both the best fit patterns of community variation and
148 the ecological features of regional metacommunities simultaneously at global scale.

149 Here, we present an analysis of geographical variation, context dependency and community-
150 environment relationships of macrophytes using data from 16 regions worldwide (Fig. 1a). We
151 specifically examined the following questions: **(i)** Which idealised metacommunity model best fits
152 the empirical data of lake macrophyte metacommunities within study regions? **(ii)** Are community-
153 environment relationships consistent or variable among different regions? **(iii)** What ecological
154 correlates describing metacommunity characteristics (i.e. elevation range, spatial extent, latitude,
155 longitude, age of the oldest lake within each region, matrix fill, species richness, functional
156 composition and phylogenetic composition) best determine variation in coherence, species range
157 turnover and range boundary clumping? Based on evidence from previous studies (Henrique-Silva et
158 al. 2013; Heino et al. 2015b), we expected to find clear geographical variation in metacommunity
159 structuring, with a change from Gleasonian to Clementsian gradients from the equator to the poles
160 **(H1)**. This is because we expected that two or more groups of species would respond similarly to the
161 typically harsher environmental conditions in boreal regions, leading to clumped range boundaries
162 in their geographical distributions (Heino et al. 2015b). We also hypothesised **(H2)** that a strong

163 context dependency would be observed in the community-environment relationships, not least
164 because the structuring of lake metacommunities can be highly variable among different regions
165 (Heino and Tolonen 2017; Alahuhta et al. 2017, 2018a). In addition, we predicted (**H3**) that
166 variables describing the ecological features of metacommunities would be good predictors of the
167 three elements of metacommunity structure, because multi-trait and evolutionary information should
168 be related to the predictability of the underlying distributional patterns (Meynard et al. 2013; García-
169 Girón et al. 2019a).

170 **Methods**

171 *Macrophyte data sets and regional characteristics*

172 We analysed a data set of 16 different study regions covering six continents across the Earth
173 (Fig. 1a, Supporting Information Appendix S1 and Fig. S1). The study regions and field methods
174 have been described previously (Alahuhta et al. 2018a) and are here outlined briefly to aid
175 understanding of the ecological context of individual regions. We had strict quality control for
176 selecting each data set: **(i)** each study region had to include ca. 30 lakes with similar geographical
177 distribution from the pool of candidate lakes; **(ii)** all lakes had to be mostly natural lentic systems
178 (i.e. reservoirs were excluded); and **(iii)** all macrophyte communities within each data set had to
179 have been empirically surveyed using similar methods to maintain data comparability. The selected
180 lakes ranged from glacial-origin and relatively stable lakes situated in temperate and boreal zones
181 (e.g. Finland, Sweden, Norway, Estonia, Denmark, Poland, New Zealand and US states of
182 Minnesota and Wisconsin) to semi-arid shallow Mediterranean lakes (e.g. Morocco and Spain).
183 Most of the study lakes suffered from various anthropogenic pressures such as water extraction,
184 invasive species, nutrient enrichment, and decreased connectivity, which cannot be avoided in an
185 increasingly human-dominated world.

186 Our data set consisted of presence-absence observations of aquatic macrophyte species (i.e.
187 species that are strongly bound to aquatic environments; see Kosten et al. 2009). These species

188 included submerged (elodeids and isoetids), floating-leaved, free-floating (ceratophyllids and
189 lemniids) and emergent forms (Cook 1999). The species list from each region was carefully checked
190 to guarantee that inconsistencies were minimal. To do this, non-aquatic helophytes, shore species,
191 aquatic bryophytes and charophytes were removed from the final data sets. Similarly, we excluded
192 hybrids, subspecies, and genus level identifications when species from the same genus were
193 recorded from the data.

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

195 Following the metacommunity framework originally proposed by Leibold and Mikkelsen
196 (2002), and thereafter expanded by Presley et al. (2010) and Henriques-Silva et al. (2013), we
197 analysed which metacommunity structure best fitted lake macrophyte data in each study region
198 across the globe. To do this, we adopted the “range perspective” in our analyses (Presley et al.
199 2010). The metacommunity types were assessed by analysing aspects of coherence, species range
200 turnover and range boundary clumping of site-by-species presence-absence matrices. Incidence
201 matrices were first ordinated via reciprocal averaging (CA). This procedure allowed us to obtain a
202 latent gradient in which sites were ordered according to species composition and species were
203 ordered according to site occurrences. After rearranging the data matrix, we tested the different
204 metacommunity elements in a hierarchical way, that is, (i) coherence, (ii) species range turnover,
205 and (iii) range boundary clumping (Fig. 1b; Table 1).

206 *Coherence* is based on calculating the number of embedded absences (i.e. gap in a species
207 range) in the ordinated empirical incidence matrix and then comparing the observed value to a null
208 distribution of embedded absences from 1,000 simulated matrices. A metacommunity is considered
209 to be coherent when the number of observed embedded absences is lower than expected by chance.
210 Significantly positive coherence thus suggests that species distributions are responding similarly to a
211 common environmental gradient represented by the ordinated site-by-species presence-absence
212 matrix. Non-significant coherence means that species are distributed at random, suggesting that

213 species are not responding to a common environmental gradient (Leibold and Mikkelsen 2002). For
214 metacommunities with positive and significant coherence, the range turnover component was tested
215 (Fig. 1b). *Species range turnover* was measured as the number of empirical replacements for each
216 possible pair of species and for each possible pair of sites in the ordinated matrix. Then, the number
217 of observed replacements was compared to a null distribution that randomly shifts the entire ranges
218 of species (Leibold and Mikkelsen 2002). Significantly negative turnover (i.e. the observed
219 replacement is lower than expected by chance) is consistent with a nested structure (i.e.
220 hyperdispersed species loss, random species loss and clumped species loss), whereas significantly
221 positive turnover (i.e. the number of observed replacements are higher than expected by chance)
222 indicates evenly spaced, Gleasonian or Clementsian metacommunity types. The cases of significant
223 positive coherence and non-significant turnover can be interpreted as quasi-structures (Presley et al.
224 2010). We further analysed *range boundary clumping* using Morisita's index of dispersion and a
225 subsequent χ^2 test that compares the empirical distribution of range boundaries to an expected
226 uniform distribution. Index values significantly larger than '1' indicate clumped range boundaries
227 (i.e. Clementsian and clumped species loss structures) and values significantly less than '1' suggest
228 hyperdispersed range boundaries (i.e. evenly spaced distribution and hyperdispersed species loss
229 structures). Species distributions that occur independently and idiosyncratically with respect to each
230 other (i.e. Gleasonian and random species loss structures) are indicated by a non-significant χ^2 test.
231 Correspondingly, quasi-evenly spaced, quasi-Gleasonian, quasi-Clementsian structures, quasi-
232 hyperdispersed species loss, quasi-random species loss and quasi-clumped species loss can be
233 separated by boundary clumping (Presley et al. 2010; see Fig. 1b).

234 The significance of the index values for coherence and range turnover was tested using the
235 fixed-proportional null model (Gotelli 2000), where the species richness of each site is maintained
236 (i.e. row sums are fixed) but species ranges (i.e. columns) are filled based on their marginal
237 probabilities. Random matrices for the fixed-proportional null model were produced by the 'r1'

238 method as implemented in the `vegan` package (Oksanen et al. 2016). Although the fixed-
239 proportional null model makes sense ecologically and is not highly sensitive to type I or type II
240 errors (Presley et al. 2009), this modelling approach does not involve shifting of ranges and
241 therefore our findings need to be treated with caution. We also used a strict and conservative fixed-
242 fixed null model based on the `'quasi-swap'` method in the R package `vegan` to find out if the null
243 model used affected the results. In the fixed-fixed null model, both species richness of each site and
244 species frequencies are maintained. We used 1,000 simulations to provide random matrices for
245 testing coherence and species range turnover. Elements of metacommunity structure were evaluated
246 for each study region along the first reciprocal averaging (i.e. correspondence analysis) axis because
247 we were interested in the most important species compositional gradient. Analyses of coherence,
248 species range turnover and range boundary clumping were performed using the `metacom` package
249 (Dallas 2013) in the R environment (R Core Team 2018).

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

$$252 \quad SES = \frac{obs - rnd.mean}{rnd.sd}$$

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

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

261 ***Community-environment relationships***

262 Community-environment relationships within the study regions were compared based on a set
263 of a priori determined lake-level variables. Physico-chemical variables consisted of lake area (km²),
264 Secchi depth (m) and water total phosphorus concentration (mg l⁻¹). These three physico-chemical
265 variables were chosen because they often account for significant variation in community structure of
266 lake macrophytes (see Alahuhta et al. 2018b), and correlate with other hydromorphological and
267 water chemistry variables that were not available for all study regions (e.g. Kosten et al. 2009).
268 Physico-chemical variables were surveyed and determined following similar procedures within each
269 study region (Supporting Information Appendix S1). Climate variables included atmospheric annual
270 mean temperature (°C), annual temperature range (°C), and annual precipitation (mm) defined for
271 each study lake based on 30 years average values (1 km resolution data) obtained from the
272 WorldClim (Hijmans et al. 2005). Climate variables were not only a surrogate for thermal energy
273 availability (Alahuhta et al. 2017) and water-level fluctuation (Carpenter et al. 2011), but also for
274 nutrient and material loading from the catchment (Sahoo et al. 2015).

275 Our main statistical method to explore community-environment relationships within regions
276 was canonical correspondence analysis (CCA), which is a constrained extension of reciprocal
277 averaging (Legendre and Legendre 2012), thus providing a link to the EMS analysis. We used the
278 intraset correlations between environmental variables and site scores along the first two ordination
279 axes to infer which factors were best related to variation in community composition and compare
280 whether the same environmental drivers were important in each study region (see Heino et al.
281 2015b). Note, however, that we cannot associate a given metacommunity type specifically to
282 environmental drivers, not least because there is no evidence that a particular mechanism can map
283 onto a particular structure. CCAs were run with the `cca` function using the R package vegan.

284 *Comparative analyses*

285 We used simple linear regression to analyse variation in the Z-scores of coherence, the Z-
286 scores of species range turnover or the index of range boundary clumping with a set of ecological

287 correlates (i.e. predictor variables) describing metacommunity characteristics (see below).
288 Standardised effect sizes of each metacommunity element (Y_i) were log-transformed
289 [$\min(Y_{max} + a = 1) \rightarrow \log(Y_i + a)$] before analyses to improve normality and reduce skewness.
290 We first summarised regional environmental information within convex hulls encompassing
291 the minimum area containing all surveyed lakes within each region. For each study region, we
292 defined *elevation range within the convex hull* (m), *area of the convex hull* (km²), *latitude of the*
293 *convex hull* (from centroid), *longitude of the convex hull* (from centroid), and estimated the
294 *maximum lake age within a particular region* (see Supporting Information Appendix 1 and Table S1
295 for variable information). These variables can indirectly affect lake macrophytes by indicating
296 variation in habitat suitability (Alahuhta et al. 2017), dispersal limitation (García-Girón et al.
297 2019b), environmental heterogeneity (Downing and Rath 1988), and temporal availability for
298 colonisation sources (Alahuhta et al. 2018a). Second, we used *matrix fill* (i.e. the proportion of '1s'
299 in the site-by-species incidence matrix) and *species richness* because data set characteristics may
300 have strong effects in comparative analyses of metacommunities (Heino et al. 2015b). Third, we
301 considered several key functional traits (Supporting Information Appendix S2, Table S2 and Fig.
302 S2) to provide information on multiple ecological aspects of each metacommunity (Heino et al.
303 2015b) and to give a broad characterisation of the realised niche of the species. We then used the
304 mixed-variables coefficient of distance (i.e. a generalization of Gower's distance; Borcard et al.
305 2011) to extract a functional distance matrix across the 16 data sets using the 'daisy' function in the
306 R library cluster (Maechler et al. 2014). The phylogenetic composition of each study region was
307 addressed using the phylogenetic fuzzy-weighting method implemented in the PCPS package
308 (Debastiani 2018). To do this, we used a molecular-based phylogeny for aquatic macrophytes
309 recently developed by García-Girón et al. (2020) (for details on phylogenetic reconstruction, see
310 Supporting Information Appendix S3 and Fig. S3). Thereafter, the pairwise output values for the
311 functional distance matrix were synthesised into principal coordinate analysis (PCO) following

312 Duarte et al. (2012). The scores of each single metacommunity along *PCO1*, *PCO2*, *PCPS1*, and
313 *PCPS2* components were then used to indicate the combined *functional* (i.e. PCO) and *phylogenetic*
314 (i.e. PCPS) *features of each metacommunity* (Supporting Information Appendix S4 and Fig. S4).

315 **Results**

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

330 Community-environment relationships varied among individual metacommunities and did not
331 allow us to single out a few environmental drivers among the set of available predictor variables
332 (Fig. 3), suggesting that specific details of community-environment relationships were largely
333 context dependent. For instance, Secchi depth had the highest effect on variation in community
334 composition in China (CCA1), whereas temperature range and precipitation were strongly related to
335 community composition in Wisconsin (CCA1) and New Zealand (CCA2), respectively. Similarly,

336 total phosphorus, lake area and mean temperature were particularly important in Florida (CCA1),
337 Morocco (CCA1) and Finland (CCA2), respectively.

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

343 **Discussion**

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

359 *Local communities show clumped range boundaries but respond differently to environmental*
360 *gradients*

361 Species may experience environmental gradients as gradual or more-or-less discrete
362 boundaries depending on species-specific characteristics (e.g. tolerance to abiotic factors and habitat
363 specialisation; Valanko et al. 2015). In our present study, Clementsian and quasi-Clementsian
364 gradients were the most commonly found metacommunity types within regions along the $\approx 10,000$
365 km latitudinal gradient. The idea of Clementsian gradients suggests that there are two or more
366 groups of species (i.e. species associations) showing similar responses to the environment (i.e.
367 species distributions are generally coherent), and that the responses differ among groups (Clements
368 1916). Consequently, the quasi-Clementsian structures observed here were probably the result of an
369 artefact because species niche breadth extended beyond the range in which species turnover is
370 significant (Presley et al. 2010), affecting the identification of boundaries in some study regions
371 (Gascón et al. 2016). The Clementsian (or sometimes the quasi-Clementsian) pattern is commonly
372 found in metacommunity studies conducted in aquatic systems, and both have already been reported
373 in comparative analyses of lake biotas (Heino et al. 2015a, 2015b), as well as for stream invertebrate
374 metacommunities in Central Germany (Tonkin et al. 2016), Amazonian stream damselflies
375 (Schlemmer-Brasil et al. 2017), soft-sediment benthic invertebrates from the Baltic Sea (Valanko et
376 al. 2015), Hungarian stream fishes (Erős et al. 2014), and Mediterranean wetland microcrustaceans
377 (Gascón et al. 2016). However, it is still particularly striking that environmental variation has such
378 an important role in structuring lake macrophyte metacommunities in different biogeographical
379 realms of the Earth (here, Palearctic, Nearctic, Neotropical, Indomalayan and Australasian). This
380 finding may be related to the fact that lake systems and their drainage basin characteristics are
381 inherently highly heterogeneous (Downing et al. 2006) and, hence, responses of macrophyte species
382 groups to environmental variation are typically more complex than a simple gain or loss of species
383 along major biologically-important thresholds (sensu Heino et al. 2015a).

384 Behind such general convergence, the disagreement among important community-
385 environment relationships also highlights that no single mechanism (i.e. a single constraining

386 environmental factor) is enough to account for the complex nature of compositional variation and
387 metacommunity organisation. Instead, it appears that metacommunity (i.e. regional) structuring of
388 lake macrophytes is highly difficult to predict. This has been demonstrated in two recent global-
389 scale studies that showed variable patterns in the factors shaping species-based beta diversity
390 (Alahuhta et al. 2017) and community composition (Alahuhta et al. 2018a). Whatever the case, our
391 study results agree with previous works in which climate and water quality were found to be
392 primarily related to variation in macrophyte community composition at regional scales (Capers et al.
393 2010; García-Girón et al. 2019a, 2019b, 2020). However, these findings should be interpreted with
394 caution due to differences in sample timing between macrophytes and lake-level environmental
395 variables in our study. Similarly, factors other than environmental filtering may also affect
396 metacommunity structure. For example, connectivity among lakes and associated dispersal events
397 may interfere with the environment in determining community composition by hindering species'
398 tracking of local and climatic conditions (see García-Girón et al. 2019b). Nevertheless, associating
399 the effects of dispersal with the idealised metacommunity types may be difficult, even if they existed
400 (Meynard et al. 2013). Meanwhile, previous works using the same test data set showed that
401 environmental filtering overcame the effects of potential connectivity in explaining local
402 communities across the globe (Alahuhta et al. 2018a; García-Girón et al. 2020). We thus suggest
403 that environmental differences between sites remain the main structuring force within lake
404 macrophyte metacommunities worldwide, although individual metacommunities may respond
405 differently to major limiting or constraining environmental gradients.

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

408 We found that the three elements of metacommunity structure were weakly correlated to the
409 ecological variables describing individual metacommunity characteristics. In a recent study, Heino
410 et al. (2015b) suggested that the ecological factors underlying variation in coherence, species range

411 turnover and range boundary clumping should not be inferred too strongly in isolation, because it is
412 their combined influence which distinguishes different metacommunity structures. Previous studies
413 suggested that accounting for trait and phylogenetic composition may provide more accurate
414 predictions of metacommunity organisation by approximating species niches similarities and
415 evolution (Gianuca et al. 2018; García-Girón et al. 2019a). This is because functional traits and
416 evolutionary legacy are key in determining diversity patterns within and among communities and
417 species replacement along environmental gradients (de Bello et al. 2017). Interestingly, however, we
418 found no general relationships between functional or phylogenetic composition and metacommunity
419 structures. A reason for this lack of relationship may be that two or more groups of species sharing a
420 common response to underlying environmental thresholds comprised either functionally dissimilar
421 or distantly related macrophyte taxa. This finding contradicts our initial expectations and suggests
422 that linking multi-trait and evolutionary information to the elements of metacommunity structure is
423 not necessarily straightforward (but see Meynard et al. 2013). Nonetheless, we cannot exclude the
424 possibility that future macrophyte studies decoupling trait and phylogenetic information at the
425 metacommunity level will uncover hidden signals underlying species coexistence and replacements
426 along major environmental gradients (see de Bello et al. 2017).

427 **Conclusions**

428 From a methodological perspective, our study shows that the simultaneous evaluation of the
429 elements of metacommunity structure (i.e. coherence, species range turnover and range boundary
430 clumping) and the ecological settings of metacommunities can enhance our ability to understand
431 large-scale patterns and community-environment relationships across the globe. More specifically,
432 we found that our empirical data set fitted best Clementsian and quasi-Clementsian metacommunity
433 types within regions, suggesting that lake macrophyte communities follow clumped species
434 replacement structures. This information is relevant to the current debate about conservation of
435 freshwater biodiversity, and we advance the notion that it needs to capture environmental variation

436 at the metacommunity level (Socolar et al. 2016). Behind such general convergence of
437 metacommunity types, our results also provide evidence that community-environment relationships
438 are shaped by multiple environmental factors within regions. This finding suggests that individual
439 metacommunities may respond differently to major limiting or constraining environmental
440 thresholds, emphasising the need to embrace the potential complexity of ecological inferences in
441 metacommunity organisation worldwide. We propose that future studies should examine the effects
442 of climatic conditions, historical events and vicariance biogeography on species associations
443 consistently occurring and disappearing at similar locations along the latitudinal gradient. Such an
444 approach may not only provide insightful information about the evolutionary or physiological trade-
445 offs associated with important ecogeographical thresholds (see Heino and Alahuhta 2015), but also
446 offer a means of testing the very foundations of biogeographical regionalisation and inferring major
447 breakpoints in lake macrophyte community composition at global scale.

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649 **Competing financial interests**

650 The authors declare no competing financial interests.

651

652 **Figure Legends**

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

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

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