

1 **MACROECOLOGY OF MACROPHYTES IN THE FRESHWATER REALM: PATTERNS,**
2 **MECHANISMS AND IMPLICATIONS**

3

4 Running title: Macroecology of aquatic macrophytes

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34 **ABSTRACT**

35 Broad-scale studies of species distributions and diversity have contributed to the emergence
36 of general macroecological rules. These rules are typically founded on research using well-
37 known terrestrial taxa as models and it is thus uncertain whether aquatic macrophytes follow
38 these macroecological rules. Our purpose is to draw together available information from
39 broad-scale research on aquatic macrophytes growing in lakes, ponds, wetlands, rivers and
40 streams. We summarize how different macroecological rules fit the patterns shown by
41 freshwater plants at various spatial scales. Finally, we outline future actions which should be
42 taken to advance macroecological research on freshwater plants. Our review suggested that
43 some macroecological patterns are relatively well-evidenced for aquatic macrophytes,
44 whereas little information exists for others. We found, for example, that the species richness-
45 latitude relationship follows a unimodal pattern, and species turnover prevails over species
46 nestedness, whereas higher nestedness-related richness differences are found in low beta
47 diversity regions. Contrary to terrestrial plants, climate or history seem not to be dominant
48 determinants explaining these broad-scale patterns; instead local explanatory variables (e.g.,
49 water quality, such as alkalinity and nutrients, and hydromorphology) are often important for
50 freshwater plants. We identified several knowledge gaps related, for example, to a smaller
51 number of studies in lotic habitats, compared with lentic habitats, lack of spatially-adequate
52 aquatic plant studies, deficiency of comprehensive species traits databases for aquatic
53 macrophytes, and absence of a true phylogeny comprising most freshwater plant lineages. We
54 hope this review will encourage the undertaking of additional macroecological investigations
55 on freshwater plants across broad spatial and temporal scales.

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59 **KEYWORDS:** Aquatic plants, Biogeography, Freshwaters, Hydrophytes, Helophytes, Lakes,
60 Ponds, Streams, Rivers

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69 **1 INTRODUCTION**

70

71 Macroecology focuses on the relationship between organisms and their environment at broad
72 spatial and temporal scales. It emphasizes the description and explanation of patterns in
73 abundance, distribution and diversity (Brown, 1995). In recent decades, there has been an
74 increasing number of studies using the macroecological approach (Smith *et al.*, 2008). One of
75 the reasons for the growth in popularity is that this approach has shown its potential in
76 combining distinct disciplines like ecology, biogeography, palaeontology and evolutionary
77 biology in characterizing broad-scale patterns in nature (Brown, 1995; Smith *et al.*, 2008).
78 Additionally, the regional, continental and global environmental problems, such as climate
79 change, have created a need for broad-scale studies on biodiversity (Kerr *et al.*, 2007).

80

81 Macroecology has several predictive approaches, and their validity has been evaluated in
82 various ecosystems using different biotas. They range, for example, from geographical
83 diversity patterns (e.g., relationships of species diversity with latitude, altitude, and depth) to
84 species-area relationships and species turnover patterns (e.g., assemblage compositional
85 changes along environmental and spatial gradients). In addition to studies using solely
86 taxonomic approaches, an increase in macroecological studies using trait-based and
87 phylogeny-based approaches has occurred in recent years (Heino *et al.*, 2013; Pacifici *et al.*,
88 2017). However, many of these investigations have been conducted in terrestrial ecosystems,
89 and much less is known about macroecological patterns in freshwater systems (Heino, 2011;
90 Heino *et al.*, 2013). Broad-scale studies in inland waters have so far mainly focused on well-
91 known and economically valued taxa, such as fish (e.g. Leroy *et al.*, 2019) and
92 macroinvertebrates (e.g. Heino *et al.*, 2018). As a result, our understanding of
93 macroecological patterns in many freshwater taxa that have high ecological importance is
94 largely missing. One such group is aquatic macrophytes, which play a structurally and
95 functionally fundamental role in aquatic ecosystems (O'Hare *et al.*, 2018).

96

97 Within the freshwater realm (e.g., Beger *et al.*, 2009), aquatic macrophytes are usually
98 defined as “aquatic photosynthetic organisms, large enough to see with the naked eye, that
99 actively grow permanently or periodically submerged below, floating on, or up through the
100 water surface” of inland freshwater or brackish waterbodies, including a diverse set of both
101 vascular (clubmosses, ferns and angiosperms) and non-vascular plants (bryophytes and some

102 macroalgae) (Chambers et al., 2008; Murphy et al., 2019). In this paper, we focus on the
103 vascular plants of freshwater environments, and hereafter use the term “aquatic
104 macrophyte(s)” solely in that context. Aquatic macrophytes have important functional and
105 structural roles in inland waters: they provide habitats and shelter to other organisms, increase
106 variation in the habitat structure of aquatic environments (Jeppesen *et al.*, 1998), and are an
107 important food source for a wide variety of other organisms (Jupp and Spence, 1977;
108 Franceschini *et al.*, 2020a,b). They also play an important role in the carbon and nutrient
109 cycles (Carpenter and Lodge, 1986), and influence a range of hydrological and sedimentation
110 processes in aquatic environments (Sand-Jensen, 1998).

111
112 The main aim of this review is to bring together current advances made in macroecological
113 research on freshwater macrophytes. Although individual overviews have been undertaken for
114 aquatic macrophytes (e.g., in relation to local environment and climate gradients: Lacoul and
115 Freedman, 2006a; Bornette and Puijalon, 2011), no previous review has explicitly
116 summarized how general macroecological rules fit the patterns shown by aquatic macrophytes
117 at various spatial and temporal scales. Here, we focus on broad-scale patterns related to
118 species taxonomy, functional traits and phylogenetic relationships, seen for aquatic
119 macrophytes in freshwater systems ranging from lakes, reservoirs, ponds and wetlands to
120 rivers, streams, and artificially-constructed channels such as canals. Finally, we summarize
121 where we are now in freshwater plant macroecology and address potentially fruitful future
122 avenues of research.

123
124 Owing to the scarcity of studies for aquatic macrophytes with regard to a number of different
125 macroecological phenomena, it is impractical at this point in time to attempt a formal meta-
126 analysis of previous work on macroecological patterns in these plants. However, our review
127 presents a first synthesis of the results to date of work on aquatic macrophytes in a broad-
128 scale context. Moreover, we are aware that different anthropogenic pressures modify aquatic
129 macrophyte distributions at local scales (e.g., introduction of alien plant species,
130 hydromorphological alterations of rivers, eutrophication and construction of dams) but they
131 are not *per se* drivers of (classical) general macroecological patterns of species distributions
132 and including their effects on broad-scale patterns of aquatic macrophytes is thus beyond the
133 scope of this review.

134
135 **2 GENERAL MACROECOLOGICAL PATTERNS AND AQUATIC MACROPHYTES**

136 In this part of the review, we focus on three main general macroecological patterns as shown
137 by aquatic macrophytes (Fig. 1): geographical gradients in species diversity (2.1), species-
138 area relationship, (2.2) and community changes along environmental and spatial gradients
139 (2.3). These main broad-scale patterns are examined with regard to more detailed organism-
140 environment relationships following commonly used classifications (e.g. Gaston, 2000;
141 Heino, 2011).

142

143 **2.1 Geographical gradients in freshwater plant diversity**

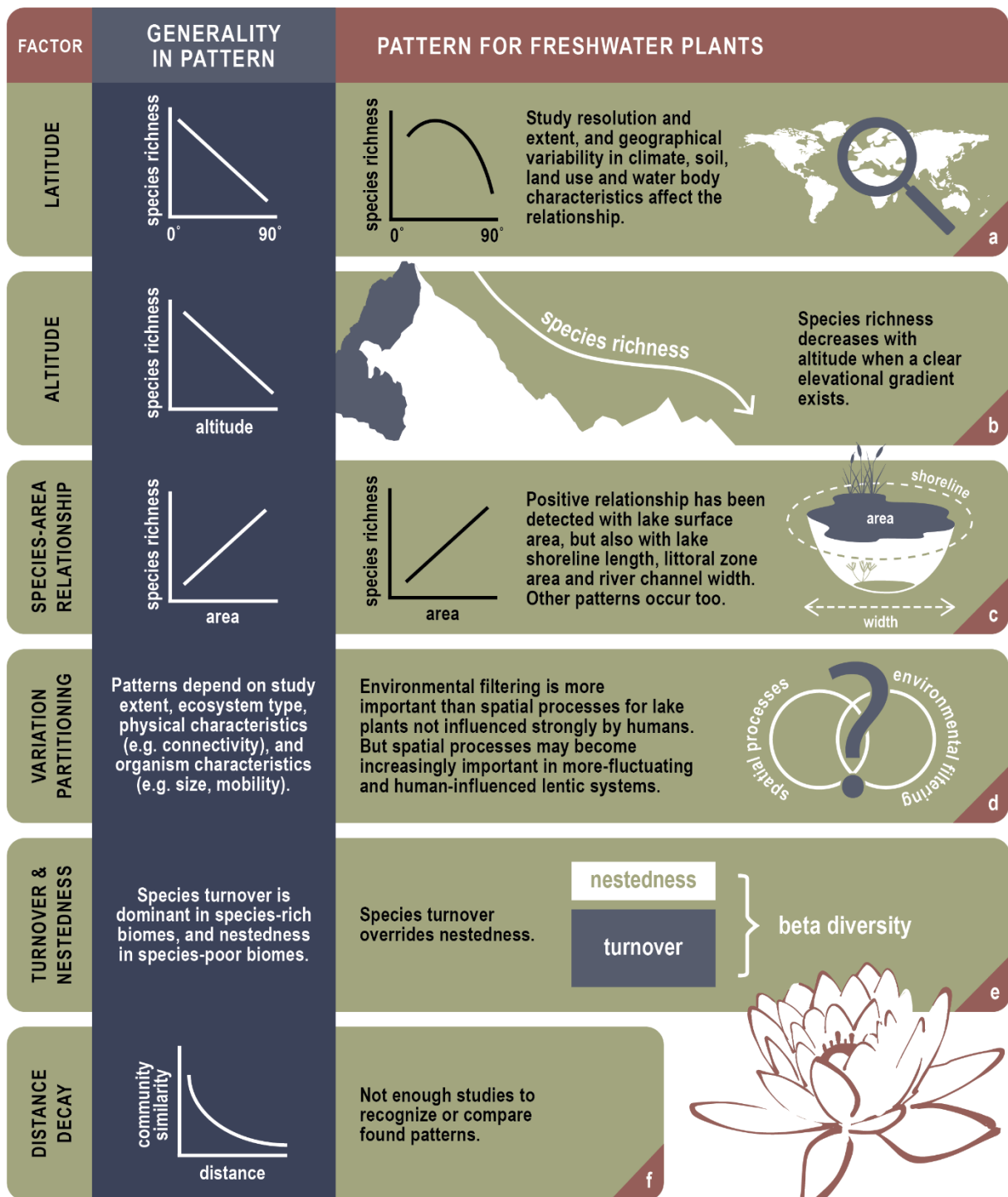
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145 2.1.1 Latitudinal gradient in species diversity

146

147 The latitudinal gradient in species diversity is typically considered to decrease relatively
148 linearly from the Equator towards the Poles (Gaston, 2000; Fig. 1a). Various contemporary
149 explanations for this trend have been offered (e.g., less solar energy is available for high
150 latitude areas compared to the tropics), but the observed trend may also stem from historical
151 factors (e.g., variation in glacial coverage during the late Quaternary) and climate variations
152 (Field *et al.*, 2009). This pattern has primarily been evidenced using well-studied terrestrial
153 taxa. However, considerable variation in the species diversity-latitude pattern has been found
154 for various aquatic and terrestrial taxa at scales ranging from regional to global (Heino, 2002;
155 Kerswell, 2006; Kindlemann *et al.*, 2007).

156



157

158 Fig. 1. Examples of different macroecological patterns based on species richness and
 159 community changes for freshwater macrophytes.

160

161

162 To some extent, there have been conflicting results for the diversity-latitude relationship of
 163 aquatic macrophytes at regional, continental and global scales. In a review focused explicitly
 164 on shallow lakes, the authors concluded that no clear pattern exists for plant species richness
 165 and latitude at regional or global scales (Meerhoff *et al.*, 2012). Similarly, Kosten *et al.*

166 (2011) found a lack of latitudinal gradient in the species richness of submerged plants in
167 shallow lakes across South America. On the other hand, Chambers et al. (2008) concluded in
168 their global descriptive exercise that the highest number of vascular aquatic macrophytes is
169 found in the Neotropics (see also Murphy *et al.*, 2019). Chappuis et al. (2012) found evidence
170 that aquatic vascular macrophyte richness peaked between 40°N and 50°N across Europe and
171 North Africa. There was a unimodal pattern, as species richness was lower at higher and
172 lower latitudes. Interestingly, the proportion of hydrophytes increased linearly from North
173 Africa towards the North Pole (Chappuis *et al.*, 2012). A recent study, also indicating a
174 unimodal pattern in species richness-latitude relationship, suggested that the highest number
175 of aquatic macrophyte species is found around 50-55°N in Europe and ~40°N in North
176 America (Alahuhta *et al.*, 2020a). Crow (1993) found limited evidence to suggest that aquatic
177 macrophyte species richness was higher in temperate than in tropical regions. Perhaps most
178 importantly, Murphy et al. (2019) showed in their global analysis that freshwater macrophyte
179 species richness is highest in sub-tropical to low tropical latitudes (20-30°). Despite different
180 study scales, the evidence clearly suggests that species richness of aquatic macrophytes does
181 not linearly decrease from the Equator towards the Poles, but follows a unimodal latitudinal
182 pattern.

183
184 For other biodiversity measures, the diversity-latitude relationship is more complicated. In a
185 global analysis Alahuhta *et al.* (2017a) found a weak positive linear pattern between
186 lacustrine plant beta diversity (i.e., the spatial variation of species composition among sites
187 across space, Anderson *et al.*, 2011) and latitude. This finding suggested that freshwater plant
188 beta diversity increases towards the high latitudes. Latitudinal climatic effects had some effect
189 on beta diversity of lake plants across 16 regions worldwide, but their contributions were
190 overshadowed by altitude (Alahuhta *et al.*, 2018). Using the same set of lake plants in 16
191 regions, Garcia-Giron et al. (2020a) discovered that multiple beta diversity facets clearly
192 decreased with increasing latitude. Unfortunately, no similar studies exist for plants in lotic
193 habitats.

194
195 The correlates which have been found to explain the species diversity-latitude relationship
196 stem not only from different spatial scales, but also from geographical variations in climate,
197 geology and soil, water body and drainage characteristics, and land use. It is challenging to
198 compare studies focused at different spatial scales (i.e., both resolution and extent), but the
199 species richness-latitude pattern is relatively similar regardless of spatial resolution. In

200 general, important drivers (such as climate, land use and area of inland water) of plant
201 biodiversity are not equally distributed across the earth (Murphy *et al.*, 2019; Alahuhta *et al.*,
202 2020a).

203

204 2.1.2 Altitude influences freshwater plant diversity

205

206 Species richness often decreases with increasing altitude (Gaston, 2000; Fig. 1b). Similar to
207 latitude, altitude mirrors different current and historical environmental factors, as well as
208 geographical, biotic and stochastic forces (Rahbek, 1995). At broad scales, the general trend
209 is that freshwater macrophyte species richness decreases with altitude when a strong
210 elevational gradient exists (e.g. Lacoul and Freedman, 2006a; 2006b). Studies focusing purely
211 on altitudinal gradient effects on aquatic macrophytes are sparse and mainly done in
212 mountainous areas, such as the Pyrenees (Chappuis *et al.*, 2011; Pulido *et al.*, 2014) or
213 Himalaya (Lacoul and Freedman, 2006b). Yet, altitude has been shown to be a strong
214 predictor of aquatic macrophyte diversity irrespective of geographical location (Tapia
215 Grimaldo *et al.*, 2016; Alahuhta *et al.*, 2018). However, due to altitude's potential as a
216 surrogate for many abiotic characteristics (e.g. climate or physico-chemistry), it is unlikely to
217 be the only important driver of aquatic macrophyte richness unless the study area has a wide
218 elevational range (Jones *et al.*, 2003; Chappuis *et al.*, 2012; Fernández-Aláez *et al.*, 2018).
219 From a conservation viewpoint, studying altitudinal gradients is interesting especially in
220 terms of climate change, because there are large climatic differences over short geographical
221 distances. For example, endemic high-altitude species are particularly vulnerable to climate
222 change (Chambers *et al.*, 2008). In a wider context, altitude can be included in overall abiotic
223 diversity measures, such as geodiversity indices (Toivanen *et al.*, 2019).

224

225 Altitude has also been used to divide a given study area into spatial and ecological units with
226 similar natural characteristics (Baláži and Hrivnák, 2015) or to classify study sites into
227 lowland and upland groups (Sun *et al.*, 2019). The importance of different factors (e.g., land
228 use) in promoting the establishment or hindering the maintenance of freshwater plant species
229 and communities is likely to vary across elevational gradients (Sun *et al.*, 2019). For example,
230 land use can be a more important predictor at lower altitudes, whereas natural variation in
231 nutrient concentrations or soil properties becomes more important at higher elevations
232 (Fernández-Aláez *et al.*, 2018).

233

234 Aquatic macrophytes have varying altitudinal ranges, with some covering a wide altitudinal
235 gradient (e.g., *Callitriche palustris*) and others being extremely restricted (e.g., *Isoetes*
236 *bolanderi*) (Chambers *et al.*, 2008; Fernández-Aláez *et al.*, 2018). This makes determining
237 aquatic macrophyte diversity across altitudinal gradients a complex endeavour, and it could
238 be complemented by studies utilising information on species traits. For example, altitude has
239 been observed to affect leaf trait variation in terrestrial plants, whereas biotic drivers were
240 more important at low altitude and abiotic drivers at high altitude (Hulshof *et al.*, 2013). At
241 broad spatial scales, it has been suggested that the general trend in the freshwater realm is that
242 abiotic geo-climatic factors (such as altitude and temperature) dominate over human impact
243 factors (Feld *et al.*, 2009). However, at coarse spatial resolution ($10 \times 10^\circ$ latitude x
244 longitude), in a global analysis of plant diversity (Murphy *et al.*, 2019), altitude was
245 overridden by the effect of latitude, land use and area of waterbodies, all of which are directly
246 or indirectly related to climate (Dodds *et al.*, 2019). Thus, even though altitude is widely used
247 as a surrogate for many abiotic characteristics, it is also important to be able to separate the
248 effects of different abiotic factors driving freshwater plant diversity.

249

250 **2.2 Species-area relationship**

251

252 Species richness-area relationship (SAR) have deep roots in classical ecological theories
253 (Arrhenius, 1921), predicting that species richness should increase with increasing island area
254 (Lawton, 1999; Fig. 1c). In the freshwater realm, evaluation of SAR is especially suitable in
255 lentic systems, which can be viewed as aquatic islands in an uninhabitable matrix of terrestrial
256 landscapes (Hortal *et al.*, 2014). Similar to lakes and ponds, rivers and streams can also be
257 viewed as “islands”. Aquatic ecologists early on grasped this topic, making SAR one of the
258 most investigated ecological rules in macroecological studies of aquatic macrophytes.

259

260 An increasing number of freshwater plant species with increasing ecosystem size has been
261 demonstrated in several studies (Møller and Rørdam, 1985; Rørslett, 1991; Vestergaard and
262 Sand-Jensen, 2000; Jones, Li and Maberly, 2003; Søndergaard, Jeppesen and Jensen, 2005;
263 Alahuhta *et al.*, 2017b). The positive effect of patch size on species richness can be attributed
264 to the separate, but not mutually exclusive, effects of increased area per se and habitat
265 diversity (Kohn and Walsh, 1994; Ricklefs and Lovette, 1999). Commonly, habitat diversity
266 and area are strongly correlated because more habitats and microhabitats appear when area
267 size increases. These two variables can thus be hard to tease apart. So far, direct attempts to

268 quantify the relative roles of habitat diversity and area for the species richness of aquatic
269 macrophytes have been scarce. Vestergaard and Sand-Jensen (2000) suggested that increased
270 water transparency, allowing for more vertical habitat variation with increasing depth, had
271 larger effects on species richness than lake area. Fernández-Aláez *et al.* (2020) also suggested
272 that species richness is higher in more heterogeneous ponds, caused by longer hydroperiod,
273 but a similar pattern may not hold in lakes. These findings thus suggest that habitat diversity
274 likely plays an important role for aquatic macrophyte species richness. The pure area effect
275 has been attributed to the lowered extinction rates caused by large local population sizes
276 (MacArthur and Wilson, 1967), but also to a positive effect of area on the immigration rate
277 known as ‘the target area effect’ (Lomolino, 1990). For lakes, this latter effect is supported by
278 a larger initial colonization rate into large re-established lakes (Baastrup-Spohr *et al.*, 2016)
279 compared to smaller ones (Søndergaard *et al.*, 2018; Søb *et al.*, 2020).

280

281 The species richness of aquatic macrophytes does not always correlate strongly or at all with
282 water body size (Vestergaard and Sand-Jensen, 2000; Chappuis, Gacia and Ballesteros, 2014;
283 Nolby *et al.*, 2015). Such deviations from the expected relationship have generally been
284 attributed to overriding local environmental effects, variable degree of disturbance on water
285 bodies and the difference between water body size and vegetated area within it. In lakes, the
286 entire bottom is rarely covered with vegetation, because light limits the distribution of plants
287 in deeper sites and wave action limits plant growth in exposed sites (Jupp and Spence, 1977).
288 For instance, Vestergaard and Sand-Jensen (2000) found no significant effect of lake surface
289 area on species richness, but when using estimates of vegetated area, they found a strong
290 relationship between area and species richness. This idea is supported by the findings of
291 Møller and Rørdam (1985), showing that species richness was more closely related to area of
292 the littoral zone than the entire surface area of ponds.

293

294 Theoretically, larger lakes, irrespective of vegetated area, should receive more propagules
295 compared to smaller ones due to the target area effect. This effect is not only caused by a
296 higher passive immigration rate to larger sites, but also by a more directed dispersal in the
297 form of zoochorous dispersal due to larger populations of dispersal vectors, such as waterfowl
298 (Brochet *et al.*, 2009; Lovas-Kiss *et al.*, 2019). Larger lakes also tend to have more inflows,
299 therefore increasing probability of immigrations via hydrochory (Jones *et al.*, 2003). These
300 effects of area on immigration rate, and subsequently on species richness, have not been
301 investigated to date for aquatic macrophytes.

302

303 The species richness-area relationship can also be modified or interfered with by natural
304 environmental conditions, such as bicarbonate concentration, shaping the pool of species
305 potentially able to inhabit individual locations (Vestergaard and Sand-Jensen, 2000; Iversen *et al.*,
306 2019). In areas of northwestern Europe, for example, where the species pool is larger in
307 bicarbonate-rich waters, a steeper relationship between species richness and area should be
308 expected for bicarbonate rich lakes compared with areas having more species-poor low-
309 bicarbonate systems. Likewise, an increase in the slope of the species area relationship should
310 be expected with increasing regional species richness (Qian *et al.*, 2007). For aquatic
311 macrophytes, this implies steeper SARs at lower latitudes, particularly in the Neotropics,
312 where regional species richness is highest (Murphy *et al.*, 2019). In sum, there is evidence for
313 positive SARs for plants in lentic systems but details about their shape, causes and underlying
314 mechanisms are still relatively unknown.

315

316 For river plants, much less is known about SARs, although patterns similar to those seen in
317 lentic systems could be expected in lotic ecosystems. For other aquatic organisms, an effect of
318 stream area on species richness has been observed (e.g., Brönmark *et al.*, 1984), but this
319 pattern has been little-explored for river plants. However, when looking at single river
320 stretches, Szoszkiewicz *et al.* (2014) found a significant effect of river width and water depth
321 on species richness of aquatic macrophytes. In temperate small and intermediate-sized
322 lowland streams, channel width also strongly affected plant species richness (Hachol *et al.*,
323 2019). Modelling river plants, Gillard *et al.* (2020) also found that river width was one of the
324 main drivers of the distributions of different species. Yet, river plant diversity and
325 distributions are often related less to stream width and water depth than to current velocity
326 and flood-pulse factors, which further stem, for example, from a variable degree of
327 precipitation (e.g., Chambers *et al.*, 1991; Davidson *et al.*, 2012; Varandas Martins *et al.*,
328 2013). However, all of these variables are usually both closely interrelated and associated
329 strongly with stream order, which indicates the level of branching in a river system (e.g.,
330 Neiff *et al.*, 2014; Morandeira and Kandus, 2015). For example, in a study of tropical rivers in
331 Zambia, Kennedy *et al.* (2015) found that stream order was a major correlate of macrophyte
332 richness and community composition. The general paucity of studies clearly illustrates that
333 the SAR remains relatively unexplored for river plants and even basic patterns need to be
334 better described, not to mention the underlying mechanisms.

335

336 **2.3 Community changes along environmental and spatial gradients**

337

338 2.3.1 The effects of environmental and spatial gradients on species composition

339

340 A highly popular approach for examination of whether environmental factors and biotic
341 interactions or spatial processes (e.g., dispersal limitation and historical factors) structure
342 biological communities is to partition the variation in community composition into
343 environmental, spatial, and their joint effects (Fig. 1d). Spatial variables have often been
344 derived from spatial eigenfunction analysis (e.g., Moran's eigenvector maps) or from simple
345 polynomials of geographical coordinates (Dray *et al.*, 2012). Here, we discuss whether niche-
346 based or spatial processes are the dominant forces driving freshwater plant assemblages at
347 different spatial scales.

348

349 The variation partitioning approach to investigate the effects of environmental and spatial
350 factors on plant communities has been more popular for lakes than rivers. In lakes,
351 environmental filtering is typically more important than spatial processes in explaining plant
352 community variation, especially in glacial-originated lakes. This has been shown, for
353 example, for aquatic macrophyte communities in hundreds of US lakes (Capers *et al.*, 2010;
354 Mikulyuk *et al.*, 2011; Alahuhta and Heino, 2013), for Fennoscandian and Siberian lakes
355 (Alahuhta *et al.*, 2013; Alahuhta *et al.*, 2020b), and for plant species richness variation in
356 European lakes (Alahuhta *et al.*, 2013; Viana *et al.*, 2014). However, joint effects of
357 environment and space often override pure environmental effects due to strong geographical
358 structuring of key water quality and hydromorphology variables, or because spatially-explicit
359 environmental variables were missing from the studies (Mikulyuk *et al.*, 2011; O'Hare *et al.*,
360 2012; Alahuhta *et al.*, 2020b). In addition, spatial factors have often explained significant
361 variation in lake macrophyte communities (Capers *et al.*, 2010; Mikulyuk *et al.*, 2011). For
362 example, De Bie *et al.* (2012) found that spatial factors dominated over environmental factors
363 across Belgium farmland ponds.

364

365 So far, the most comprehensive assessments of environment vs. space were undertaken by
366 Alahuhta *et al.* (2018) and García-Girón *et al.* (2020a) using the same set of lake plants in 16
367 regions across the world. They reported that environmental factors were typically more
368 important than spatial effects in structuring plant community composition, but spatial
369 variables were also associated with lake plant community variation in some regions, and joint

370 effects were often high. It seems that spatial processes play an essential role in structuring
371 freshwater plant communities especially in highly human-affected environments.
372 Furthermore, spatial processes have been a dominant force explaining variation in plant
373 communities in environmentally more unstable floodplain lakes (Padial *et al.*, 2014; Alahuhta
374 *et al.*, 2018), Mediterranean lakes (García-Girón *et al.*, 2020a), and semi-lentic environments
375 (Hajek *et al.*, 2011). These results suggest that environmental filtering is more important than
376 spatial processes for lake plants not influenced strongly by human activities, but spatial
377 processes may become increasingly important in more-fluctuating and human-influenced
378 lentic systems.

379

380 For river plants, the importance of environmental filtering and spatial processes seems to be
381 more dependent on the studied region, making it challenging to draw uniform conclusions
382 about these gradients. Tapia Grimaldo *et al.* (2016) found that spatial variables and spatially-
383 structured environmental variables contributed more than pure environment in explaining
384 plant species richness and community composition in calcareous rivers of the UK and
385 Zambia. On the other hand, environmental variables solely or mainly structured community
386 composition of river plants in Finland (Alahuhta *et al.*, 2015) and in Canada (Bourgeois *et al.*,
387 2016). Variation in lowland river plant communities was similarly explained by only local
388 environment, whereas both the environment and space contributed to variation in headwater
389 river plant communities in Denmark (Göthe *et al.*, 2017). These few and rather contradictory
390 findings highlight the need for further research to examine the relative roles of environmental
391 filtering and spatial processes on river plant communities.

392

393 Understanding of the influence of spatial scale in structuring freshwater plant communities is
394 also poor. The importance of spatial processes should increase with increasing scale (Leibold
395 *et al.*, 2004). There has been some indication that the importance of spatial processes
396 increases with increasing spatial scale for both lake (Alahuhta and Heino, 2013) and river
397 (Tapia Grimaldo *et al.*, 2016) plants. However, no other investigations exist in which multiple
398 spatial scales were studied simultaneously for freshwater plant communities in this context.

399

400 2.3.2 Distance decay

401

402 How community similarity decreases with spatial or environmental distance has been a
403 popular research question since the turn of the millennium (Nekola and White, 1999; Fig. 1e).

404 The correlation of similarity against distance incorporates several ecological mechanisms,
405 thus providing a suitable perspective for investigating the spatial turnover across regions
406 (Soininen *et al.*, 2007). In general, steeper slopes of distance decay suggest higher beta
407 diversity. When it comes to underlying mechanisms, this pattern suggests more restricted
408 dispersal and/or stronger relation to local environmental conditions. Thus, distance-decay
409 relationships may indicate how communities are structured by niche-based and neutral
410 processes because community similarity often decreases with increasing environmental and
411 spatial distance, respectively (Nekola and White, 1999; Soininen *et al.*, 2007).

412
413 Only a few studies of distance decay of freshwater plant communities exist. For example, in
414 tropical Australia, Warfe *et al.* (2012) discovered no evidence for dispersal limitation (i.e.,
415 spatial distance-decay as a proxy) in connected river sites, and little dispersal limitation was
416 reported in disconnected sites along a 480 km length of river. Community similarity
417 decreased significantly with both geographical and environmental distance in four isolated
418 Chinese wetlands with different agricultural drainage ditch densities (Lu *et al.*, 2009). This
419 finding suggests that distance decay rate decreases with increasing disturbance intensity.
420 However, the lack of studies on distance decay of freshwater plant communities hinders the
421 possibilities of further discussing the topic, let alone comparing any patterns found for aquatic
422 macrophytes with other freshwater taxa. Moreover, future studies should consider whether
423 observed patterns of distance decay are not only a result of drier areas having greater
424 distances between aquatic habitats. These water bodies of drier areas are also often more
425 turbid and have greater salinity, further affecting aquatic macrophyte distributions.

426

427 2.3.3 Partitioning of beta diversity into distinct components

428

429 Beta diversity refers to the variation in species composition among communities across space
430 or time (Anderson *et al.*, 2011), and it is fundamentally related to two processes (Legendre,
431 2014): species turnover or replacement (i.e. one species replaces another with no change in
432 richness), and species richness difference (i.e. one community may include a larger number of
433 species than another) or nestedness (a special case of species richness difference: nestedness-
434 related species richness differences being due to species gain or loss). Mechanisms
435 responsible for species turnover/replacement may originate from environmental filtering,
436 competition and historical events (Anderson *et al.*, 2011). In contrast, species richness
437 differences originate from species thinning or from other ecological processes (Baselga, 2010;

438 Legendre, 2014), such as physical barriers or human disturbance. Beta diversity has been
439 reported to decrease with latitude and increase with elevation and biome area (Anderson *et*
440 *al.*, 2011; Soininen *et al.*, 2018). However, increasing evidence suggests that patterns in beta
441 diversity depend on the studied ecosystem, organisms, geographical location and spatial
442 extent (Legendre, 2014; Soininen *et al.*, 2018).

443

444 For freshwater plants, new insights into their beta diversity patterns have accumulated from
445 various regions and scales. Based on these studies, it is evident that freshwater plant
446 communities are primarily structured by species turnover (Alahuhta *et al.*, 2017a; Murphy *et*
447 *al.*, 2020; Fig. 1e). Regarding temporal beta diversity patterns, Boschilia *et al.* (2016) studied
448 changes in plant communities in a Brazilian reservoir and found high values of beta diversity
449 with the prevalence of species turnover over the course of a decade. For the spatial beta
450 diversity patterns, species turnover prevailed for lake plants across five regions in Europe
451 (Viana *et al.*, 2016) and between permanent and temporal agricultural ponds (Fernández-
452 Aláez *et al.*, 2020). Murphy *et al.* (2020) found evidence for the existence of a latitudinal beta
453 diversity gradient, which was only poorly explained by nestedness for the global distribution
454 of range-sizes of 1083 freshwater plant species, suggesting that species turnover made a
455 higher contribution to beta diversity. In a global analysis of freshwater plant beta diversity
456 across 21 regions, Alahuhta *et al.* (2017a) showed that species turnover overrode nestedness
457 in shaping aquatic macrophyte communities. This was most evident in regions with high
458 overall beta diversity, whereas nestedness was highest, but still lower than species turnover,
459 in regions with low beta diversity.

460

461

462 **3 FUNCTIONAL AND PHYLOGENETIC PERSPECTIVES**

463

464 The widespread appreciation that the interaction between an organism and its environment is
465 primarily determined by biological traits, rather than taxonomic position (McGill *et al.*,
466 2006), has led to a rapid growth of the applications of the functional dimension in
467 macroecology. Consequently, macroecological research has recently started to improve
468 understanding of the mechanistic basis behind broad-scale patterns in biodiversity through
469 focusing on the relationships between species traits and their distributions (Heino *et al.*,
470 2013). In this regard, species traits have shown their advantages in studies of several
471 biological groups and different environments, for example, in climate change (e.g., Pacifici *et*

472 *al.*, 2017), ecosystem functioning (Petchey and Gaston, 2006), and range shift contexts
473 (Estrada *et al.*, 2016).

474

475 Whereas the traditional taxonomic approach requires only information on the geographical
476 distributions of species, functional analyses require an additional suite of trait measurements
477 for each species. Traditionally, studies with aquatic macrophytes have dealt with this
478 functional dimension of biodiversity using different types of categorical divisions derived
479 mainly from the growth form and the life form concepts (Vermaat *et al.*, 2000; Willby *et al.*,
480 2000). However, some studies have utilized a broader range of morphological and
481 physiological traits to characterize aquatic macrophyte species and communities in functional
482 terms (Hills *et al.*, 1994; Hills and Murphy, 1996; Garbey *et al.*, 2004). Of the categorical
483 divisions, the functional groups based on life form have probably been the most used (e.g.,
484 Chappuis *et al.*, 2012; Mormul *et al.*, 2015; García-Girón *et al.*, 2018). More recently, species
485 traits have been utilized in broad-scale studies without categorical divisions of trait
486 composition, but instead using continuous or experimentally quantified values (e.g., Göthe *et*
487 *al.*, 2017; Iversen *et al.*, 2019). Over the last few decades, research has focused on several
488 morphological, physiological and life-history traits that are related to plant morphology and
489 hydrology, perennation (i.e., a species growing for a single or several years), use of carbon,
490 photosynthetic efficiency, and dispersal vectors (e.g., De Wilde *et al.*, 2014; Fu *et al.*, 2014;
491 García-Girón *et al.*, 2019a,b, 2020a,b; Iversen *et al.*, 2019; Lindholm *et al.*, 2020a,b). This
492 shift of focus has given new insights into patterns and processes of species distributions and
493 community assembly that otherwise would be missed, or even misrepresented, from the
494 standard taxonomic viewpoint. For example, Lukács *et al.* (2017) showed the importance of
495 traits related to competitive ability (e.g., growth rate and leaf economics spectrum) during
496 aquatic macrophyte invasions in Europe, while García-Girón *et al.* (2019b) showed that a
497 trait-based approach could help explain the abundance structure of Mediterranean pond plant
498 metacommunities, using dispersal vectors (i.e., wind- vs water-dispersed species) and trait-
499 environment relationships at different spatial scales. At global scale, Iversen *et al.* (2019)
500 showed that functional composition (bicarbonate users vs CO₂ users) of plant communities
501 was structured by environmental bicarbonate concentrations. Despite these rather few new
502 studies, the general shortage of studies at broad scales still hinders our ability to test and
503 validate macroecological hypotheses, and consequently also affects our ability to answer
504 questions about how the trait composition of aquatic macrophyte communities varies along
505 geographical gradients and environmental gradients (see also Dalla Vecchia *et al.*, 2020). For

506 the most part, this is due to the fact that very few studies (but see García-Girón *et al.*, 2020a)
507 have yet used the same analytical methods to examine community variation based on multiple
508 traits in various geographical regions at global scale.

509

510 Lack of comprehensive species trait information on aquatic macrophytes has also created
511 further challenges (see Supporting Information for more discussion). In the absence of
512 species-specific multi-trait data, plant researchers have tried to test the validity of predicting
513 traits from congeneric or confamilial species, as has been recently done at regional (García-
514 Girón *et al.*, 2019a) and continental scales (Alahuhta *et al.*, 2017a; García-Girón *et al.*,
515 2020a). These evaluations are based on assessing the ‘phylogenetic niche conservatism’ (e.g.,
516 Blomberg *et al.*, 2003) of the traits under study. This approach aims to determine whether
517 similarity in the biological or ecological characteristics of the species is influenced by the
518 effect of ancestor-descendant relationships (Roquet *et al.*, 2013). For the moment, their
519 outcomes have been somewhat contradictory, finding evidence of either some level of species
520 niche conservatism (Alahuhta *et al.*, 2017b) but also often low phylogenetic signal in traits
521 (García-Girón *et al.*, 2019a; García-Girón *et al.*, 2020a). This hinders our ability to establish a
522 general picture of whether traits are conserved or not in aquatic macrophytes, and to compare
523 patterns found with other organisms. A likely reason is that the rather phylogenetically-distant
524 nature of aquatic macrophytes causes difficulties for phylogenetic studies (Hu *et al.*, 2017), as
525 these plants are evolutionarily highly dispersed across the Tree of Life (Du *et al.*, 2016), with
526 at least 50 independent origins from their closest terrestrial relatives (Cook, 1990).

527

528 To further understand how evolutionary history shapes the geographical distribution of
529 aquatic macrophytes, we need accurate information on the phylogenetic relationships between
530 plant species. To date, this has been performed using several methods of varying complexity
531 and reliability, but the implementation of this new era of ‘ecophylogenetics’ (Mouquet *et al.*,
532 2012) to the macroecology of aquatic macrophytes is still facing a number of methodological
533 challenges (Hu *et al.*, 2017). As a first step, some studies have used taxonomic classification
534 as a surrogate for evolutionary relatedness, as implemented recently by Alahuhta *et al.*
535 (2017c) and García-Girón *et al.* (2019c), in order to develop proxies for aquatic macrophyte
536 phylogenetic diversity. However, such an approach is rather unrealistic since it assumes that
537 topological relationships (i.e., intrageneric relatedness) are equal for all genera (Roquet *et al.*,
538 2013). In other published works, phylogenetic inferences have been done by incorporating the
539 topological information from published phylogenies. For example, De Wilde *et al.* (2014)

540 used the released compilation of angiosperm phylogeny based on Angiosperm Phylogeny
541 Group III (2009) to determine whether phylogenetic position at family level controls the
542 effects of dewatering on aquatic macrophyte performance. Although appealing, such an
543 approach provides no estimates of branch lengths, i.e., quantitative evolutionary relationships
544 of species.

545

546 The super matrix approach (Roquet *et al.*, 2013) has been recently proposed as an alternative
547 method to simultaneously analyze large DNA sequence datasets from either nuclear,
548 ribosomal or plastid regions, and thus estimate meaningful branch length values (see Hu *et*
549 *al.*, 2017 for instructions). However, when it comes to aquatic macrophytes, this super matrix
550 approach has only been used in systematic studies (e.g., Cai *et al.*, 2010 for Ranunculaceae;
551 Chen *et al.*, 2012 for Alismataceae; and Bernardini and Lucchese 2018 for Hydrocharitaceae),
552 meaning that no accurate species-level phylogenetic tree exists for the diverse group of
553 freshwater plants, thus imposing significant constraints upon current macroecological
554 research. This is unfortunate considering the constant increase of available molecular data in
555 GenBank, the growing number of algorithms for alignment, optimization and depuration (e.g.,
556 Tamura *et al.*, 2011), and the recent improvements in freely available software (e.g., MEGA;
557 GARLI; RAxML) able to handle extremely large data sets within a moderate amount of time.
558 Recently, García-Girón *et al.* (2020a) advanced our understanding of the phylogenetic
559 relatedness of freshwater plants by building the very first genus-level DNA-based phylogeny
560 (i.e. the maximum likelihood on sequences from two chloroplast DNA regions) comprising
561 most plant lineages (from *Lycopodiopsida* to *Eudicotyledoneae*). However, more accurate,
562 fully resolved phylogenies are still needed to reduce possible artefacts due to data patchiness
563 and improve historical inferences from current macroecological patterns of aquatic
564 macrophytes.

565

566 Globally, our review reveals that the basic functional and evolutionary biology of freshwater
567 plants has been mostly ignored, highlighting the need for greater efforts to collect multi-trait
568 and phylogenetic data and to make them available in a standard format using existing portals
569 (e.g., TRY and GenBank) and digital repositories (e.g., Dryad and Figshare).

570

571 **4 WHERE TO GO FROM HERE?**

572

573 Freshwater macrophyte research has lagged behind that for many other terrestrial, marine and
574 freshwater groups with regard to investigation of different macroecological patterns. This
575 derives from several reasons related to research community size, field surveys and research
576 perspectives (Table 1). (i) The number of scientists working with aquatic macrophytes is
577 small compared with terrestrial plants and most other freshwater groups, such as fish and
578 macroinvertebrates. This means that fewer aquatic macrophyte ecologists are interested in
579 macroecological research questions. (ii) Previous freshwater plant studies have often been
580 conducted by botanists with completely different study aims compared to those of ecologists
581 and biogeographers. The focus in many of these previous botany-related plant studies has
582 been on local patterns and processes using data at fine scales and with a limited number of
583 surveyed water bodies. (iii) A notable proportion of freshwater plant studies has focused on
584 specific genera and/or invasive species. As a result, community composition of aquatic
585 macrophytes has not always been surveyed, hindering our possibilities to investigate aquatic
586 vegetation in a macroecological context. Fortunately, there has been an awakening in
587 macroecological freshwater plant studies during recent years due to the improved quality and
588 quantity of available data (both field and atlas data), GIS-programs and computer efficiency.
589 However, we still need more aquatic macrophyte surveys to be carried out in geographically
590 less-studied regions (e.g., Africa, Asia, Russia, North America [for river plants], South
591 America and Oceania, in addition to the highest or lowest latitudes) in order to advance
592 macroecological research on freshwater plants.

593

594 In addition to these field survey and botanical research perspectives, our review revealed that
595 most macroecological studies on plants have been done in lentic ecosystems (e.g., Alahuhta *et*
596 *al.*, 2018). Nevertheless, there are a few examples of moderately broad-scale river plant
597 studies in this context, for both tropical (e.g., Kennedy *et al.*, 2015) and temperate areas (e.g.,
598 Janauer *et al.*, 2018). Recent studies suggest that lake and river plants may not respond
599 similarly to the same ecological gradients. For example, alkalinity was found to be a highly
600 important driver of plant distributions in lakes but less so in rivers (Iversen *et al.*, 2019), and
601 even the distributions of the same plant species can be explained by different environmental
602 gradients in lakes and rivers (Gillard *et al.*, 2020). Recent compilation of a global lake plant
603 dataset has permitted an increase in macroecological studies on lentic plants, and we clearly
604 need a similar worldwide database on river plants. This problem is more challenging to
605 overcome with atlas data, where lentic and lotic ecosystems are rarely distinguished. More
606 efforts to build a grid cell-based freshwater plant database, distinguishing also different water

607 body types, should be made. Current biodiversity databases (e.g., GBIF) can form the basis
608 for this work and further promote finer-scale global databases of freshwater plants.

609

610 Biases in studied macroecological questions were clear based on our overview. For example,
611 latitudinal, altitudinal and area-related patterns in species diversity were relatively well
612 studied, whereas only a few investigations had examined distance-decay relationships. The
613 better scientific coverage of these well-investigated patterns partly stems from a longer
614 tradition of studying such ecological phenomena. More research is required not only for less-
615 studied macroecological phenomena but also for better-recognized patterns in order to
616 improve our knowledge of the causal mechanisms underlying these patterns in freshwater
617 plants.

618

619 Temporal studies in macroecological context are also mostly lacking for aquatic macrophytes
620 (but see Sand-Jensen *et al.*, 2000; Baastrup-Spohr *et al.*, 2013). This shortage is mostly due to
621 unavailable historical data. So far most temporal exercises have focused on single water
622 bodies (e.g., Varandas Martins *et al.*, 2013; Ceschin *et al.*, 2009, 2010; Sand-Jensen *et al.*,
623 2017), or are based on palaeolimnological approaches (e.g., Dieffenbacher-Krall and
624 Jacobson, 2001; Sawada *et al.*, 2003) but spatially-explicit temporal data founded on
625 historical field surveys is needed for broad-scale studies (Lindholm *et al.*, 2020a,b and
626 references therein). Temporal macroecological investigations are especially important
627 nowadays because of threats posed by global change to highly vulnerable and biodiversity-
628 rich freshwater ecosystems (Heino *et al.*, 2020).

629

630 Biotic interactions in individual water bodies have been intensively investigated at small
631 spatial scales for decades. However, there is very little evidence about how biotic interactions
632 affect communities among freshwater systems. For example, a high proportion of unexplained
633 variation is often detected when variation partitioning analysis has been applied to freshwater
634 plant communities (e.g. Alahuhta & Heino, 2013; Sun *et al.*, 2019). This may be due to the
635 lack of inquiry for biotic interactions in the study designs. In fact, García-Girón *et al.* (2020c)
636 recently discovered that potential biotic interactions among pond plant species clearly
637 overrode the environmental effects in explaining variation in Mediterranean pond
638 communities. This finding may be very important considering not only the high ecological
639 relevance of plants in the freshwater realm (O'Hare *et al.*, 2018; Law *et al.*, 2019), but also
640 the degradative nature of certain invasive aquatic macrophyte species (Hussner, 2012;

641 Ceschin *et al.*, 2020). However, further evaluations in different regions and different types of
 642 inland ecosystems are certainly needed.

643
 644 Finally, future research should consider the integration of functional traits with phylogenetic
 645 analyses for the extraction of well-curated aquatic macrophyte data among different
 646 geographical entities, including drainage basins, ecoregions and biogeographical realms. To
 647 achieve this, freshwater plant researchers will need to combine large trait databases, species-
 648 level field and laboratory measurements, regional floras and botanical checklists with deep
 649 sequencing and comparative phylogenetics. By doing so, we should be able to build high-
 650 quality functional and phylogenetic datasets for hypothesis testing, thereby permitting the
 651 validation and extension of macroecological patterns and understanding of underlying
 652 processes. We hope that our review will stimulate more macroecological research on
 653 freshwater plant across different geographical areas, scales and ecosystems.

654
 655 Table 1. Summary of known research gaps and suggestions for possible future research
 656 directions for macroecology of freshwater plants.

Research gap	Suggestion for future study direction
Lack of spatially adequate freshwater plant surveys	First, combining and harmonization of existing surveys (e.g., collected for ecological quality assessments and/or existing in different databases). Second, more complementary surveys with macroecological study focus should be carried out.
Geographical biases in freshwater plant studies	Europe and North America (the latter continent only for lakes though) are intensively surveyed. More studies are needed from, for example, Africa, different parts of Asia, Central and South America as well as Oceania. Investigations from both highest and lowest latitudes are also required.
Scarcity of river plant studies	Lentic ecosystems are predominantly represented in macroecological plant studies and more information about how river plants respond to ecological gradients at broad scales is required. In addition, species growing in lentic and lotic systems may respond differently to macroecological gradients, highlighting the need for further river studies.
Bias in certain macroecological phenomena	Certain phenomena are relatively well-studied (e.g., species diversity-latitude, diversity-altitude and diversity-area relationships, and environmental vs. spatial effects on community composition), but our knowledge is deficient for many others (e.g., patterns of abundance, functional diversity and phylogenetic diversity). More research is needed for understanding these less well-studied macroecological phenomena.

Lack of temporal studies with macroecological perspectives	Majority of temporal investigations on aquatic macrophytes have focused on single (or few) water bodies but macroecological gradients cannot be studied with such a small number of lakes or rivers. More comprehensive temporal data is needed to better understand temporal macroecological patterns in aquatic macrophytes.
Omission of biotic interactions in a spatial context	Information on biotic interactions between pairs of freshwater plant species at among-water bodies scales is missing. A high amount of unexplained variation in community composition analyses can originate from species interactions, but this needs to be further addressed.
Suitable species traits for macroecological studies	Terrestrial plants dominate in many existing species trait databases, and the information therein is not often ecologically relevant for freshwater plants. Thus, new species trait measurements are needed from different regions. In addition, the high level of intraspecific variation in species traits should be accounted for in these measurements.
Shortage of true phylogeny	Efforts to construct true and comprehensive aquatic macrophyte phylogeny need to be undertaken.

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