



## Review

# Macroecology of macrophytes in the freshwater realm: Patterns, mechanisms and implications

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## ABSTRACT

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

## 1. Introduction

Macroecology focuses on the relationship between organisms and their environment at broad spatial and temporal scales. It emphasizes the description and explanation of patterns in abundance, distribution and diversity (Brown, 1995). In recent decades, there has been an increasing number of studies using the macroecological approach (Smith et al., 2008). One of the reasons for the growth in popularity is that this approach has shown its potential in combining distinct disciplines like ecology, biogeography, palaeontology and evolutionary biology in characterizing broad-scale patterns in nature (Brown, 1995;

Smith et al., 2008). Additionally, the regional, continental and global environmental problems, such as climate change, have created a need for broad-scale studies on biodiversity (Kerr et al., 2007).

Macroecology has several predictive approaches, and their validity has been evaluated in various ecosystems using different biotas. They range, for example, from geographical diversity patterns (e.g., relationships of species diversity with latitude, altitude, and depth) to species-area relationships and species turnover patterns (e.g., assemblage compositional changes along environmental and spatial gradients). In addition to studies using solely taxonomic approaches, an increase in macroecological studies using trait-based and phylogeny-

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based approaches has occurred in recent years (Heino et al., 2013; Pacifici et al., 2017). However, many of these investigations have been conducted in terrestrial ecosystems, and much less is known about macroecological patterns in freshwater systems (Heino, 2011; Heino et al., 2013). Broad-scale studies in inland waters have so far mainly focused on well-known and economically valued taxa, such as fish (e.g. Leroy et al., 2019) and macroinvertebrates (e.g. Heino et al., 2018). As a result, our understanding of macroecological patterns in many freshwater taxa that have high ecological importance is largely missing. One such group is aquatic macrophytes, which play a structurally and functionally fundamental role in aquatic ecosystems (O'Hare et al., 2018).

Within the freshwater realm (e.g., Beger et al., 2009), aquatic macrophytes are usually defined as “aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or up through the water surface” of inland freshwater or brackish waterbodies, including a diverse set of both vascular (clubmosses, ferns and angiosperms) and non-vascular plants (bryophytes and some macroalgae) (Chambers et al., 2008; Murphy et al., 2019). In this paper, we focus on the vascular plants of freshwater environments, and hereafter use the term “aquatic

macrophyte(s)” solely in that context. Aquatic macrophytes have important functional and structural roles in inland waters: they provide habitats and shelter to other organisms, increase variation in the habitat structure of aquatic environments (Jeppesen et al., 1998), and are an important food source for a wide variety of other organisms (Jupp and Spence, 1977; Franceschini et al., 2020a,b). They also play an important role in the carbon and nutrient cycles (Carpenter and Lodge, 1986), and influence a range of hydrological and sedimentation processes in aquatic environments (Sand-Jensen, 1998).

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

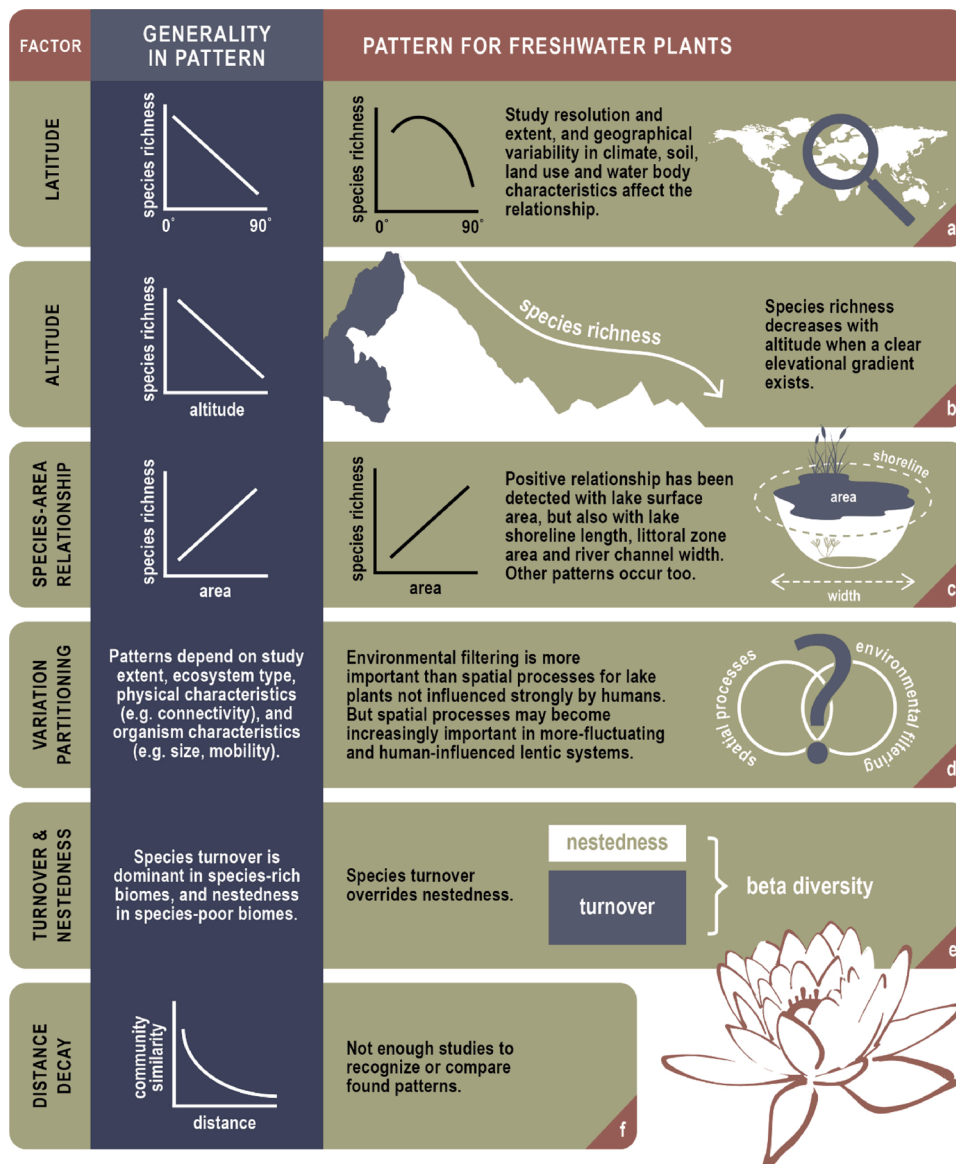


Fig. 1. Examples of different macroecological patterns based on species richness and community changes for freshwater macrophytes.

plant macroecology and address potentially fruitful future avenues of research.

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

## 2. General macroecological patterns and aquatic macrophytes

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

### 2.1. Geographical gradients in freshwater plant diversity

#### 2.1.1. Latitudinal gradient in species diversity

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

To some extent, there have been conflicting results for the diversity-latitude relationship of aquatic macrophytes at regional, continental and global scales. In a review focused explicitly on shallow lakes, the authors concluded that no clear pattern exists for plant species richness and latitude at regional or global scales (Meerhoff et al., 2012). Similarly, Kosten et al. (2011) found a lack of latitudinal gradient in the species richness of submerged plants in shallow lakes across South America. On the other hand, Chambers et al. (2008) concluded in their global descriptive exercise that the highest number of vascular aquatic macrophytes is found in the Neotropics (see also Murphy et al., 2019). Chappuis et al. (2012) found evidence that aquatic vascular macrophyte richness peaked between 40 °N and 50 °N across Europe and North Africa. There was a unimodal pattern, as species richness was lower at higher and lower latitudes. Interestingly, the proportion of hydrophytes increased linearly from North Africa towards the North Pole (Chappuis et al., 2012). A recent study, also indicating a unimodal pattern in species richness-latitude relationship, suggested that the highest number of aquatic macrophyte species is found around 50–55 °N in Europe and ~40 °N in North America (Alahuhta et al., 2020a). Crow (1993) found limited evidence to suggest that aquatic macrophyte species richness was higher in temperate than in tropical regions. Perhaps most importantly, Murphy et al. (2019) showed in their global analysis that freshwater macrophyte species richness is highest in sub-tropical to low tropical latitudes (20–30°). Despite different study scales, the evidence clearly suggests that species richness of aquatic macrophytes does not linearly decrease from the Equator towards the Poles, but follows a

unimodal latitudinal pattern.

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

The correlates which have been found to explain the species diversity-latitude relationship stem not only from different spatial scales, but also from geographical variations in climate, geology and soil, water body and drainage characteristics, and land use. It is challenging to compare studies focused at different spatial scales (i.e., both resolution and extent), but the species richness-latitude pattern is relatively similar regardless of spatial resolution. In general, important drivers (such as climate, land use and area of inland water) of plant biodiversity are not equally distributed across the earth (Murphy et al., 2019; Alahuhta et al., 2020a).

#### 2.1.2. Altitude influences freshwater plant diversity

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

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

Aquatic macrophytes have varying altitudinal ranges, with some covering a wide altitudinal gradient (e.g., *Callitriche palustris*) and others being extremely restricted (e.g., *Isoetes bolanderi*) (Chambers et al., 2008; Fernández-Aláez et al., 2018). This makes determining aquatic macrophyte diversity across altitudinal gradients a complex endeavour, and it could be complemented by studies utilising information on species traits. For example, altitude has been observed to affect leaf trait variation in terrestrial plants, whereas biotic drivers were more important at

low altitude and abiotic drivers at high altitude (Hulshof et al., 2013). At broad spatial scales, it has been suggested that the general trend in the freshwater realm is that abiotic geo-climatic factors (such as altitude and temperature) dominate over human impact factors (Feld et al., 2009). However, at coarse spatial resolution ( $10 \times 10^\circ$  latitude x longitude), in a global analysis of plant diversity (Murphy et al., 2019), altitude was overridden by the effect of latitude, land use and area of waterbodies, all of which are directly or indirectly related to climate (Dodds et al., 2019). Thus, even though altitude is widely used as a surrogate for many abiotic characteristics, it is also important to be able to separate the effects of different abiotic factors driving freshwater plant diversity.

## 2.2. Species-area relationship

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

An increasing number of freshwater plant species with increasing ecosystem size has been demonstrated in several studies (Møller and Rørdam, 1985; Rørslett, 1991; Vestergaard and Sand-Jensen, 2000; Jones et al., 2003; Søndergaard et al., 2005; Alahuhta et al., 2017b). The positive effect of patch size on species richness can be attributed to the separate, but not mutually exclusive, effects of increased area per se and habitat diversity (Kohn and Walsh, 1994; Ricklefs and Lovette, 1999). Commonly, habitat diversity and area are strongly correlated because more habitats and microhabitats appear when area size increases. These two variables can thus be hard to tease apart. So far, direct attempts to quantify the relative roles of habitat diversity and area for the species richness of aquatic macrophytes have been scarce. Vestergaard and Sand-Jensen (2000) suggested that increased water transparency, allowing for more vertical habitat variation with increasing depth, had larger effects on species richness than lake area. Fernández-Aláez et al. (2020) also suggested that species richness is higher in more heterogeneous ponds, caused by longer hydroperiod, but a similar pattern may not hold in lakes. These findings thus suggest that habitat diversity likely plays an important role for aquatic macrophyte species richness. The pure area effect has been attributed to the lowered extinction rates caused by large local population sizes (MacArthur and Wilson, 1967), but also to a positive effect of area on the immigration rate known as ‘the target area effect’ (Lomolino, 1990). For lakes, this latter effect is supported by a larger initial colonization rate into large re-established lakes (Baastrup-Spohr et al., 2016) compared to smaller ones (Søndergaard et al., 2018; Sø et al., 2020).

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

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

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

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

## 2.3. Community changes along environmental and spatial gradients

### 2.3.1. The effects of environmental and spatial gradients on species composition

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

The variation partitioning approach to investigate the effects of environmental and spatial factors on plant communities has been more



popular for lakes than rivers. In lakes, environmental filtering is typically more important than spatial processes in explaining plant community variation, especially in glacial-originated lakes. This has been shown, for example, for aquatic macrophyte communities in hundreds of US lakes (Capers et al., 2010; Mikulyuk et al., 2011; Alahuhta and Heino, 2013), for Fennoscandian and Siberian lakes (Alahuhta et al., 2013, 2020b), and for plant species richness variation in European lakes (Alahuhta et al., 2013; Viana et al., 2014). However, joint effects of environment and space often override pure environmental effects due to strong geographical structuring of key water quality and hydro-morphology variables, or because spatially-explicit environmental variables were missing from the studies (Mikulyuk et al., 2011; O'Hare et al., 2018; Alahuhta et al., 2020b). In addition, spatial factors have often explained significant variation in lake macrophyte communities (Capers et al., 2010; Mikulyuk et al., 2011). For example, De Bie et al. (2012) found that spatial factors dominated over environmental factors across Belgium farmland ponds.

So far, the most comprehensive assessments of environment vs. space were undertaken by Alahuhta et al. (2018) and García-Girón et al. (2020a) using the same set of lake plants in 16 regions across the world. They reported that environmental factors were typically more important than spatial effects in structuring plant community composition, but spatial variables were also associated with lake plant community variation in some regions, and joint effects were often high. It seems that spatial processes play an essential role in structuring freshwater plant communities especially in highly human-affected environments. Furthermore, spatial processes have been a dominant force explaining variation in plant communities in environmentally more unstable floodplain lakes (Padial et al., 2014; Alahuhta et al., 2018), Mediterranean lakes (García-Girón et al., 2020a), and semi-lentic environments (Hajek et al., 2011). These results suggest that environmental filtering is more important than spatial processes for lake plants not influenced strongly by human activities, but spatial processes may become increasingly important in more-fluctuating and human-influenced lentic systems.

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

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

### 2.3.2. Distance decay

How community similarity decreases with spatial or environmental distance has been a popular research question since the turn of the millennium (Nekola and White, 1999; Fig. 1e). The correlation of similarity against distance incorporates several ecological mechanisms, thus providing a suitable perspective for investigating the spatial turnover

across regions (Soininen et al., 2007). In general, steeper slopes of distance decay suggest higher beta diversity. When it comes to underlying mechanisms, this pattern suggests more restricted dispersal and/or stronger relation to local environmental conditions. Thus, distance-decay relationships may indicate how communities are structured by niche-based and neutral processes because community similarity often decreases with increasing environmental and spatial distance, respectively (Nekola and White, 1999; Soininen et al., 2007).

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

### 2.3.3. Partitioning of beta diversity into distinct components

Beta diversity refers to the variation in species composition among communities across space or time (Anderson et al., 2011), and it is fundamentally related to two processes (Legendre, 2014): species turnover or replacement (i.e. one species replaces another with no change in richness), and species richness difference (i.e. one community may include a larger number of species than another) or nestedness (a special case of species richness difference: nestedness-related species richness differences being due to species gain or loss). Mechanisms responsible for species turnover/replacement may originate from environmental filtering, competition and historical events (Anderson et al., 2011). In contrast, species richness differences originate from species thinning or from other ecological processes (Baselga, 2010; Legendre, 2014), such as physical barriers or human disturbance. Beta diversity has been reported to decrease with latitude and increase with elevation and biome area (Anderson et al., 2011; Soininen et al., 2018). However, increasing evidence suggests that patterns in beta diversity depend on the studied ecosystem, organisms, geographical location and spatial extent (Legendre, 2014; Soininen et al., 2018).

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

### 3. Functional and phylogenetic perspectives

The widespread appreciation that the interaction between an organism and its environment is primarily determined by biological traits, rather than taxonomic position (McGill et al., 2006), has led to a rapid growth of the applications of the functional dimension in macroecology. Consequently, macroecological research has recently started to improve understanding of the mechanistic basis behind broad-scale patterns in biodiversity through focusing on the relationships between species traits and their distributions (Heino et al., 2013). In this regard, species traits have shown their advantages in studies of several biological groups and different environments, for example, in climate change (e.g., Pacifici et al., 2017), ecosystem functioning (Petchey and Gaston, 2006), and range shift contexts (Estrada et al., 2016).

Whereas the traditional taxonomic approach requires only information on the geographical distributions of species, functional analyses require an additional suite of trait measurements for each species. Traditionally, studies with aquatic macrophytes have dealt with this functional dimension of biodiversity using different types of categorical divisions derived mainly from the growth form and the life form concepts (Vermaat et al., 2000; Willby et al., 2000). However, some studies have utilized a broader range of morphological and physiological traits to characterize aquatic macrophyte species and communities in functional terms (Hills et al., 1994; Hills and Murphy, 1996; Garbey et al., 2004). Of the categorical divisions, the functional groups based on life form have probably been the most used (e.g., Chappuis et al., 2012; Mormul et al., 2015; García-Girón et al., 2018). More recently, species traits have been utilized in broad-scale studies without categorical divisions of trait composition, but instead using continuous or experimentally quantified values (e.g., Göthe et al., 2017; Iversen et al., 2019). Over the last few decades, research has focused on several morphological, physiological and life-history traits that are related to plant morphology and hydrology, perennation (i.e., a species growing for a single or several years), use of carbon, photosynthetic efficiency, and dispersal vectors (e.g., De Wilde et al., 2014; Fu et al., 2014; García-Girón et al., 2019a, b, 2020a, 2020b; Iversen et al., 2019; Lindholm et al., 2020a, b). This shift of focus has given new insights into patterns and processes of species distributions and community assembly that otherwise would be missed, or even misrepresented, from the standard taxonomic viewpoint. For example, Lukács et al. (2017) showed the importance of traits related to competitive ability (e.g., growth rate and leaf economics spectrum) during aquatic macrophyte invasions in Europe, while García-Girón et al. (2019b) showed that a trait-based approach could help explain the abundance structure of Mediterranean pond plant metacommunities, using dispersal vectors (i.e., wind- vs water-dispersed species) and trait-environment relationships at different spatial scales. At global scale, Iversen et al. (2019) showed that functional composition (bicarbonate users vs CO<sub>2</sub> users) of plant communities was structured by environmental bicarbonate concentrations. Despite these rather few new studies, the general shortage of studies at broad scales still hinders our ability to test and validate macroecological hypotheses, and consequently also affects our ability to answer questions about how the trait composition of aquatic macrophyte communities varies along geographical gradients and environmental gradients (see also Dalla Vecchia et al., 2020). For the most part, this is due to the fact that very few studies (but see García-Girón et al., 2020a) have yet used the same analytical methods to examine community variation based on multiple traits in various geographical regions at global scale.

Lack of comprehensive species trait information on aquatic macrophytes has also created further challenges (see Supporting Information for more discussion). In the absence of species-specific multi-trait data, plant researchers have tried to test the validity of predicting traits from congeneric or confamilial species, as has been recently done at regional (García-Girón et al., 2019a) and continental scales (Alahuhta et al., 2017a; García-Girón et al., 2020a). These evaluations are based on

assessing the ‘phylogenetic niche conservatism’ (e.g., Blomberg et al., 2003) of the traits under study. This approach aims to determine whether similarity in the biological or ecological characteristics of the species is influenced by the effect of ancestor-descendant relationships (Roquet et al., 2013). For the moment, their outcomes have been somewhat contradictory, finding evidence of either some level of species niche conservatism (Alahuhta et al., 2017b) but also often low phylogenetic signal in traits (García-Girón et al., 2019a; 2020a). This hinders our ability to establish a general picture of whether traits are conserved or not in aquatic macrophytes, and to compare patterns found with other organisms. A likely reason is that the rather phylogenetically-distant nature of aquatic macrophytes causes difficulties for phylogenetic studies (Hu et al., 2017), as these plants are evolutionarily highly dispersed across the Tree of Life (Du et al., 2016), with at least 50 independent origins from their closest terrestrial relatives (Cook, 1990).

To further understand how evolutionary history shapes the geographical distribution of aquatic macrophytes, we need accurate information on the phylogenetic relationships between plant species. To date, this has been performed using several methods of varying complexity and reliability, but the implementation of this new era of ‘ecophylogenetics’ (Mouquet et al., 2012) to the macroecology of aquatic macrophytes is still facing a number of methodological challenges (Hu et al., 2017). As a first step, some studies have used taxonomic classification as a surrogate for evolutionary relatedness, as implemented recently by Alahuhta et al. (2017c) and García-Girón et al. (2019c), in order to develop proxies for aquatic macrophyte phylogenetic diversity. However, such an approach is rather unrealistic since it assumes that topological relationships (i.e., intrageneric relatedness) are equal for all genera (Roquet et al., 2013). In other published works, phylogenetic inferences have been done by incorporating the topological information from published phylogenies. For example, De Wilde et al. (2014) used the released compilation of angiosperm phylogeny based on *Angiosperm Phylogeny Group III (2009)* to determine whether phylogenetic position at family level controls the effects of dewatering on aquatic macrophyte performance. Although appealing, such an approach provides no estimates of branch lengths, i.e., quantitative evolutionary relationships of species.

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

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

(e.g., Dryad and Figshare).

#### 4. Where to go from here?

Freshwater macrophyte research has lagged behind that for many other terrestrial, marine and freshwater groups with regard to investigation of different macroecological patterns. This derives from several reasons related to research community size, field surveys and research perspectives (Table 1). (i) The number of scientists working with aquatic macrophytes is small compared with terrestrial plants and most other freshwater groups, such as fish and macroinvertebrates. This means that fewer aquatic macrophyte ecologists are interested in macroecological research questions. (ii) Previous freshwater plant studies have often

**Table 1**

Summary of known research gaps and suggestions for possible future research 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.

been conducted by botanists with completely different study aims compared to those of ecologists and biogeographers. The focus in many of these previous botany-related plant studies has been on local patterns and processes using data at fine scales and with a limited number of surveyed water bodies. (iii) A notable proportion of freshwater plant studies has focused on specific genera and/or invasive species. As a result, community composition of aquatic macrophytes has not always been surveyed, hindering our possibilities to investigate aquatic vegetation in a macroecological context. Fortunately, there has been an awakening in macroecological freshwater plant studies during recent years due to the improved quality and quantity of available data (both field and atlas data), GIS-programs and computer efficiency. However, we still need more aquatic macrophyte surveys to be carried out in geographically less-studied regions (e.g., Africa, Asia, Russia, North America [for river plants], South America and Oceania, in addition to the highest or lowest latitudes) in order to advance macroecological research on freshwater plants.

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

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

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

Biotic interactions in individual water bodies have been intensively investigated at small spatial scales for decades. However, there is very little evidence about how biotic interactions affect communities among freshwater systems. For example, a high proportion of unexplained variation is often detected when variation partitioning analysis has been applied to freshwater plant communities (e.g. Alahuhta and Heino,



2013; Sun et al., 2019). This may be due to the lack of inquiry for biotic interactions in the study designs. In fact, García-Girón et al. (2020c) recently discovered that potential biotic interactions among pond plant species clearly overrode the environmental effects in explaining variation in Mediterranean pond communities. This finding may be very important considering not only the high ecological relevance of plants in the freshwater realm (O'Hare et al., 2018; Law et al., 2019), but also the degradative nature of certain invasive aquatic macrophyte species (Hussner, 2012; Ceschin et al., 2020). However, further evaluations in different regions and different types of inland ecosystems are certainly needed.

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

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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