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Discussions and interventions

Freshwater plant macroecology needs to step forward from the shadows of the terrestrial domain

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Abstract

Freshwater plants, or macrophytes, make up only 1-2% of all plant species on Earth but play a crucial role in aquatic ecosystems. They are key to primary production, provide habitat and food for various organisms, and influence water quality. Despite their importance, freshwater plants face significant threats from global changes, which necessitates research at broader scales. Historically, freshwater plants have been less studied than terrestrial plants, partly due to a lack of global data and a focus on local scales by aquatic ecologists. Unlike terrestrial plants, freshwater plants do not always follow the same ecological patterns. In this text, we summarise current knowledge on three well-known macroecological patterns and how they differ between freshwater and terrestrial plants: latitude-species richness gradient, Rapoport's rule and species turnover vs. nestedness components of spatial beta diversity. For example, terrestrial plants follow the latitudinal diversity gradient hypothesis, whereas species richness peaks in the sub-tropics for freshwater plants. Although findings on Rapoport's rule are less clear, research on terrestrial plants in North America shows that turnover (i.e., species replacing each other from one site to another) is more significant in areas with high species richness and environmental stability, whereas nestedness (i.e., species

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composition at one site being a subset of a richer site) is more common in species-poor areas with high environmental variability. For freshwater plants, beta diversity patterns vary with latitude, but species turnover generally dominates over nestedness in a spatial context. Overall, freshwater plants exhibit unique macroecological patterns that differ from terrestrial plants, highlighting the need for more extensive research to understand their biodiversity and ecological roles. This can be achieved with more harmonized data sets and equal research efforts in both realms. Better knowledge of macroecological patterns and their drivers for freshwater plants is crucial for conservation efforts and policy-making aimed at preserving plant species diversity and sustaining ecosystem services in freshwater environments.

Keywords: *Aquatic macrophytes, Biogeography, Macroecology, Macrophytes*

Freshwater plants in a changing world

Freshwater plants (i.e. macrophytes) constitute only 1-2 % of all plant species growing on Earth (Cook 1999). Yet, their importance as foundation species and ecosystem engineers (O´Hare *et al.* 2018) exceeds their expected ecological value given their relatively low richness compared to plants in terrestrial ecosystems in those lakes, rivers and wetlands, where freshwater plants are primarily responsible for primary production, provide food, habitat, reproduction and prey areas for other aquatic and terrestrial organisms and influence water quality (Lacoul & Freedman 2006). Freshwater plants are also involved in producing and sustaining numerous vital ecosystem services of inland waters (Engelhardt & Ritchie 2001). At the same time, global change is threatening freshwaters more severely than other natural ecosystems in the Anthropocene, for example, by facilitating the spread of invasive species (Gillard *et al.* 2017; Reid *et al.* 2019; Albert *et al.* 2021; Bolpagni 2021; Hussner *et al.* 2021). Many of the global change pressures affect biodiversity beyond local ecosystems, requiring ecological research efforts to focus on regional and global spatial scales. Although these facts highlight the need to study freshwater plants more intensively at broad scales, until recently these species have been examined less rigorously than their terrestrial counterparts (e.g., Alahuhta *et al.* 2017; 2018; Murphy *et al.* 2019; García-Girón *et al.* 2020a, 2020b; Murphy *et al.* 2020; García-Girón *et al.* 2023a; Lobato-de Magalhães *et al.* 2023; Pan *et al.* 2023; Azzella *et al.* 2024; Lobato-de Magalhães *et al.* 2024; Luukkonen *et al.* 2024), due in part to the lack of comparable data from across the world. The shortage of studies on the macroecology of freshwater plants may also stem from the fact that many freshwater ecologists and limnologists are concerned with describing assemblage-environment relationships at local scales (for example, within a single drainage basin) or are ecosystem-oriented (Heino 2011), thereby hindering attempts to further examine the mechanistic basis of broad-scale biodiversity patterns on these plant species.

Ecological generalities evidenced using terrestrial plants may not be used to explain macroecological patterns and their underlying mechanisms in freshwater plants. For example, terrestrial plants follow the latitudinal diversity gradient hypothesis, although anomalies to this positive trend exist regionally (Sabatini *et al.* 2022). For freshwater plants, species richness peaks in the sub-tropics (Murphy *et al.* 2019). Many other ecological hypotheses and theories lack clear evidence for freshwater plants, show incongruent patterns or are driven by different mechanisms compared with terrestrial plants. These inconsistencies originate from differences in accessibility to water and atmospheric gases between terrestrial and aquatic plants, which also experience less extreme temperatures in inland waters. Thus, catchment properties related to local environmental conditions are often highly important drivers of freshwater plant biodiversity (Iversen *et al.* 2019).

Contemporary climate and historical factors also contribute to distribution of freshwater plants, as found at northern latitudes (Figure 1). Regions with higher temperatures related to Gulf Stream dynamics in Central and northwestern Europe and eastern North America include more freshwater plant species than colder regions in the same latitudes (Murphy *et al.* 2019; Alahuhta *et al.* 2020), a pattern that is partly associated with the distribution of introduced and invasive freshwater plant species to these regions (Lobato-de Magalhães *et al.* 2023). Moreover, most northern latitudinal areas which were covered by ice sheets during the Last Glaciation Maximum have fewer plant species than ice-free areas located at the same or lower latitudes (Murphy *et al.* 2019). The number of endemic freshwater plant species also follows similar geographical patterns (Lobato-de Magalhães *et al.* 2024), the western Europe macroregion having many more ecozone-endemics (134 species) than northern Europe (72) or the Arctic macroregion of the Palaearctic as a whole (just 17 species). A similar trend is seen in the Nearctic, where eastern North America has many more endemic macrophyte species (129) than are present in the Arctic-Canadian Shield macroregion north of 50°N (56 endemic species). These endemism patterns are mostly explained by birds acting as dispersal vectors for freshwater plant species and historical factors (Lobato-de Magalhães *et al.* 2024). However, spatial patterns of rare freshwater plants at northern latitudes differ depending on definition of rarity and scale used for the study as well as the precise taxa set involved. For instance, García-Girón et al. (2021) studying hydrophytes in Europe and North America (50 km x 50 km grid cells) evidenced high rates of rarity in freshwater plants in Central Europe and northwestern Europe and in the US state of Florida and eastern coast areas. On the other hand, medium-sized levels of rarity were found in eastern and western coastal areas of Eurasia and North America for all freshwater plants at a resolution of 10° × 10° grid cells (Lobato-de Magalhães *et al.* 2024).

For invasive freshwater plant species, the current pattern of occurrence at high latitudes mirrors the overall diversity pattern seen in Figure 2. At present there are no invasive species in either the Nearctic or Palaearctic north of 70°N. In the 60-70°N band there are only four species invasive, in a limited set of localities in the Palaearctic (and one of these, *Elodea densa* in Arctic Iceland, is a special case, having been introduced there to naturally-heated thermal pools), while the Nearctic has only three invasive freshwater plant species in this latitude band. The biggest differences are seen in the 50-60° latitude band. There are six invasive freshwater plant species occurring in the Nearctic section of this latitude band, and a further three (all from the New World) invasive in the corresponding latitudes of the central and eastern Palaearctic. However, in the western Palearctic section of this latitude band, warmed by the influence of the Gulf Stream, no fewer than 15 invasive freshwater plant species occur, with the biggest numbers present in the Low Countries and British Isles. Together with the example of *Elodea densa* in Iceland, this perhaps gives notice of what might be expected to happen in high latitudes in response to global warming, in terms of the spread of invasive species.

Differences in three key macroecological patterns between terrestrial and freshwater plants

To further highlight differences but also similarities in broad-scale patterns and their underlying mechanisms between freshwater and terrestrial plants in general, we here focus on three well-known macroecological patterns: latitude-species richness gradient, Rapoport's rule and species turnover vs. nestedness components of beta diversity (Figure 2). As noted above, the patterns of species richness-latitude relationship differ between terrestrial and freshwater plants. Kreft & Jetz (2007) found that water-energy dynamics were among the most important drivers of latitudinal gradient in species richness in terrestrial plants. Similarly, Field *et al.* (2009) discovered in their meta-analysis that climate or productivity is generally the key driver of species richness patterns. Murphy *et al.* (2019) found that the presence of water (or lack of it) is an important contributor to the latitudinal gradient in species richness in freshwater plants, but altitude and land area are also important, highlighting the importance of catchment properties as found elsewhere (e.g. Iversen *et al.* 2019).

Rapoport's rule is an iconic macroecological pattern where species range size decreases from high to low latitudes (Stevens 1989). Yet, consensus over this gradient has been difficult to reach for both plant and animal groups, and our knowledge of the determinants driving these geographical patterns is limited in general (Sheth *et al.* 2020). For example, range sizes of terrestrial plants increased with latitude in North America and decreased in South America, with short- and long-term climate stability and availability of habitat area being the main drivers of the patterns (Morueta-Holme *et al.* 2013). Likewise, Alahuhta *et al.* (2020) reported support for Rapoport's rule in North America but found no evidence for it in Europe for freshwater plants. Both of these opposing patterns were determined by contemporary climate. In a recent global study, Murphy *et al.* (2020) provided strong evidence that Rapoport's rule applies to freshwater plants, though their global range size is also influenced by agricultural land-use, altitude and climate-change velocity. Differences between these findings likely originate from the use of different sets of species and spatial scale (both resolution and extent). With these differences in mind, it is evident that more research is needed on Rapoport's rule for both terrestrial and freshwater plants (e.g., Willig & Presley 2018).

Beta diversity describes compositional variation among communities across space (for a discussion on consistency in the terminology and interpretation of different aspects of beta diversity, see Heino et al. 2024), and is related to two processes (Legendre 2014): species turnover (i.e. where one species replaces another with no change in richness between localities) and nestedness (i.e. which is a type of richness difference pattern characterized by the species composition at a site being a strict subset of the species at a richer site). Pinto-Ledezma *et al.* (2018) found for terrestrial plants of North America that taxonomic beta diversity patterns vary strongly across the continent. Turnover was more influential in areas with higher species richness and greater environmental stability, whereas nestedness was more important in species-poor areas having high environmental variability. For freshwater plants, overall total beta diversity has either decreased or increased with latitude worldwide, depending on the data set and quantitative method used (Alahuhta *et al.* 2017; García-Girón *et al.* 2020a). Yet, species turnover is typically predominant over nestedness in explaining spatial beta diversity of freshwater plants (Alahuhta *et al.* 2017). Differences between terrestrial and freshwater plant beta diversity patterns emphasize the need to study both realms with equal efforts and harmonized data sets (*sensu* García-Girón *et al.* 2023b) for both basic and applied research, and further highlight the need for ecosystem- and region-specific assessments to guide conservation prioritization.

Ways forwards for freshwater plant macroecology

Examples of these three macroecological rules illustrate that mechanistic understanding of broad-scale diversity patterns of freshwater plants is far from complete. A challenge associated with macroecological studies of freshwater plants is the high degree of phenotypic plasticity. For example, a species recorded in a region may be characterized as a fully water-dependent freshwater plant, whereas the same species may grow on land in another region. The extreme of this is seen in the Cyperaceae, where all but 12 of the 556 species known to have macrophyte populations also have non-macrophyte populations growing in wetland, riparian or terrestrial habitats. This complicates our definition of which species are true freshwater plants, further possibly affecting observed macroecological patterns. Our knowledge of fundamental ecological phenomena is not only limited for taxonomic diversity patterns, but even more so for functional and phylogenetic dimensions of freshwater plant ecology (García-Girón *et al.* 2023b). In this regard, both high-quality trait and species-specific evolutionary data for freshwater plant species are, at best, patchy and often restricted to certain geographical areas and lineages (Iversen *et al.* 2022). First attempts to reveal functional and phylogenetic diversity patterns at broad scales suggest that processes acting along latitudinal and elevational gradients have left a strong footprint in the current diversity patterns of freshwater plants (García-Girón *et al.* 2020a). These intriguing findings emphasize the pressing need for efforts to extract well-curated distributional, functional and phylogenetic datasets of inland plants in different catchments, biomes and continents in order better to understand different biodiversity facets of freshwater plants (Alahuhta *et al.* 2021; García-Girón *et al.* 2023b; Pan *et al.* 2023). Such a research agenda is also of interest to environmental managers, conservation practitioners and policy makers aiming to reduce or halt the continued decline of plant species diversity in freshwaters and to sustain inland ecosystem services (e.g., Reid *et al.* 2019). These conservation targets would benefit from a metaecosystem approach, which integrates freshwater and surrounding terrestrial systems, as organisms, energy and matter flow from land to water, to better understand how different human-induced pressures affect freshwater biodiversity (e.g. Soininen *et al.* 2015). However, first we need to understand their macroecological patterns and determinants in spatially extended areas. By doing so, we should be able to forge an exciting new frontier in plant macroecology research that allows us to step forward from the shadows of the terrestrial domain and further bridge gaps between freshwater and terrestrial macroecology.

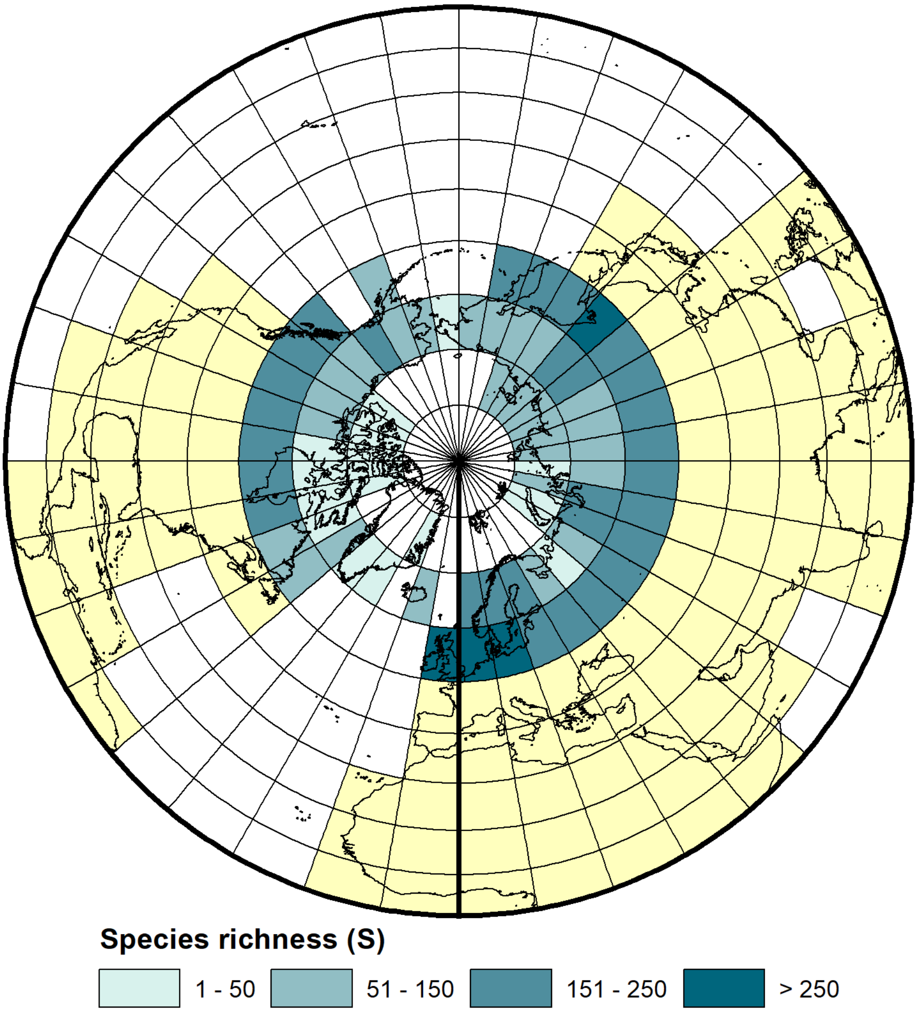

Figure 1. Map of species richness (in blue palette) in 10×10° latitude x longitude grid cells at northern latitudes (for more information on species data, see Murphy *et al.* 2019). Land areas are in yellow and oceans in white.

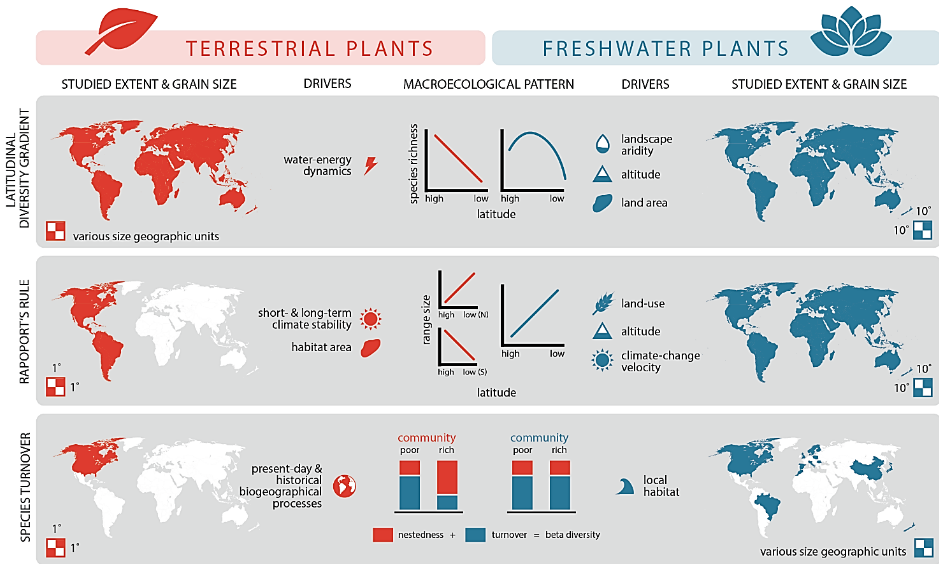

Figure 2. Examples of how terrestrial and freshwater plants decouple in their macroecological patterns and underlying mechanisms. These two groups differ in terms of the studied extent and grain size (data availability), detected patterns and underlying mechanism. Terrestrial and freshwater patterns presented are based on studies by Kreft & Jetz (2007) and Murphy *et al.* (2019) for latitudinal diversity gradient, Morueta-Holme *et al.* (2013) and Murphy *et al.* (2020) for Rapoport's rule, and Pinto-Ledezma *et al.* (2018) and Alahuhta *et al.* (2017) for species turnover, respectively.

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