Trends in
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Review

Global change and plant-ecosystem functioning in freshwaters

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Freshwater ecosystems are of worldwide importance for maintaining biodiversity and sustaining the provision of a myriad of ecosystem services to modern societies. Plants, one of the most important components of these ecosystems, are key to water nutrient removal, carbon storage, and food provision. Understanding how the functional connection between freshwater plants and ecosystems is affected by global change will be key to our ability to predict future changes in freshwater systems. Here, we synthesize global plant responses, adaptations, and feedbacks to present-day and future freshwater environments through trait-based approaches, from single individuals to entire communities. We outline the transdisciplinary knowledge benchmarks needed to further understand freshwater plant biodiversity and the fundamental services they provide.

Changing freshwater systems

Anthropogenic pressures are creating global shifts in freshwater permanency [1,2], increasing droughts in tropical and temperate regions [3] and, consequently, species extinction rates and freshwater ecosystem degradations are increasing [4]. Predicting freshwater ecosystem responses across landscapes and continents will be key to our ability to understand how these systems will develop under human-induced global change [5,6].

The past two decades have seen increased research efforts devoted to understanding plant structure–functioning relationships, which have substantially increased our knowledge on how terrestrial ecosystems are responding to the ongoing global change [7]. Functional traits underlie individual performance, community structure, and ecosystem functioning via their impacts on eco-physiological adaptations, intra- and interspecific interactions, and energy flow in ecosystems, thereby providing a promising tool for freshwater research that can be used as a proxy in large-scale and global estimations of functional changes in these systems and the services they provide [8]. However, until now, freshwater systems have been largely excluded from such efforts and an increased focus on the specific conditions and traits important for life in water is needed if we are to gain a sound understanding of how plant communities are changing and the reciprocal relationships between freshwater plant functions and the environment.

In this review, we synthesize global plant responses, adaptations, and feedbacks to present-day and future freshwater environments through trait-based approaches from single individuals to entire communities. From this, we outline the transdisciplinary knowledge benchmarks needed to further understand freshwater plant biodiversity and the fundamental services they provide. We also emphasize that concepts related to functional traits are greatly understudied in freshwaters compared with terrestrial systems and describe the research needed if we are to close this knowledge gap.

Highlights

Contrary to their terrestrial counterparts, freshwater plants are linked to flooding dynamics associated with their habitats in or around water.

Gas diffusivity, light availability, nutrient concentrations, and flow velocity select not only on freshwater eco-physiological adaptive traits but also on general plant functional traits, such as plant height or specific leaf area.

Emerging stressors under global change impact freshwater plant functions at different temporal and spatial scales via both trait–trait and trait–environment relationships.

Predicting how freshwater plant communities are changing and the reciprocal relationships between freshwater plant functions and the environment will require a focus on the specific conditions and traits important for a life in water.

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Plant adaptations to freshwaters and emerging ecosystem changes

Contrary to their terrestrial counterparts, freshwater plants are intrinsically linked to **flooding dynamics** (see Glossary) associated with their habitats in or around water (Box 1). Such watery environments impose a set of unique ecological pressures and thresholds for plants in terms of gas diffusivity, light availability, nutrient contents, and current stress.

Gas limitation

The diffusivity of gases, such as carbon dioxide (CO_2) and oxygen (O_2), is about 10^4-fold lower in surface waters than in the atmosphere. Due to such lower diffusion rates in inland waters, more than 12 times the air equilibrium CO_2 concentration is needed to reach saturated photosynthesis for submerged freshwater plants [9]. The general adaptations of freshwater plants to gas limitation include specialized morphological leaf traits to decrease the resistance to gas exchange [10], such as the development of a thin cuticle or submerged-induced plasticity in leaf mass area, while some plants are able to form gas films to enhance underwater gas exchange [11,12]. To maintain underwater photosynthesis when CO_2 accessibility is limited, many freshwater plants evolved **carbon concentration mechanisms (CCMs)** for photosynthesis [13,14]. Although some aquatic plants share the same crassulacean acid metabolism (the C_4 pathways) as terrestrial plants, the most widespread CCMs are access to CO_2 via uptake and exploitation of **bicarbonate (HCO_3^-)** [15–17]. Even though O_2 can be directly obtained through photosynthesis, the O_2 shortage may still pervade and especially be severe in plant root tissues in submerged and waterlogged substrates. Oxygen-sensing mechanisms, in response to ethylene accumulation induced by submergence and waterlogging, are therefore common in freshwater plants to prevent excessive activation of the anaerobic metabolism [18–20]. In particular, an internal hormonal cascade of ethylene, auxin, gibberellin, and abscisic acid regulates gene expression in the control of morphological changes, such as fast shoot elongation to reestablish contact with the atmosphere, to further enhance the adaptation to freshwater environments [21,22]. In addition, freshwater plants generally have special **aerenchyma tissues** in both stems and roots to facilitate the convective gas flow and internal aeration [23–25], and some plants can form a barrier to prevent oxygen release from root tissues [i.e., **radial oxygen loss (ROL)**] [26,27]. By breaking the water surface, species with emergent and floating leaves have access to aerial photosynthesis [28] (Box 1).

Box 1. Growth forms in freshwater plants

Plants growing in freshwater exhibit a variety of growth forms reflecting adaptations to the physical conditions they are living in (Figure I). Freshwater plants have typically been divided into four categories [126]. Emergent species, which grow rooted in the periodically or permanently waterlogged substrate but have aerial photosynthetic parts (above the water surface). Such species dominate shallow water and periodically inundate shorelines and develop leaves adapted to terrestrial photosynthesis and respiration conditions (Figure IA). Submerged species predominantly grow beneath the water surface. As a consequence of the support provided by water, submerged species invest less in physical structures and are characterized by having limited woody tissue and thin cuticles, which in return allow for greater gas exchange between the tissue and the surroundings (Figure IB,C). Many species, like *Cabomba caroliniana* (Figure IB), have finely dissected leaves with a large surface area optimizing gas exchange. Rooted floating-leaved species have leaves that float on the water surface and a stem rooted to the bottom. These species typically have rounded leaves, adaxial directed stomata, and waxy coating on the upper surface (Figure ID). The waxy coating prevents wetting and clogging of stomata. Free floating species are unrooted plants that are growing either submerged (e.g., bladderworts, *Utricularia*, Figure IE) or floating on the surface (e.g., duckweeds, *Spirodela*, Figure IF). These four growth forms help divide species into functional clusters, but distinctions can be arbitrary and some species exhibit different growth forms according to environmental conditions or specific life stages. During early submerged growth, many emergent species have thin and delicate leaves compared with the leaves they develop during aerial growth (Figure IA). Other species, like the water-crowfoots *Ranunculus*, develop a combination of submerged (Figure IC) and floating (Figure ID) leaves, an adaptation to varied surrounding conditions known as heterophylly. The ratio between different types of leaves depends on the physical environment the plants are exposed to. Photo copyright: © Lars L. Iversen.

Glossary

Aerenchyma tissues: a modification of the parenchyma to form a spongy tissue that creates spaces or air channels in the leaves, stems, and roots of some plants, which is widespread in aquatic and wetland plants to facilitate gas exchange.

Bicarbonate (HCO_3^-): the dominant form of dissolved inorganic carbon in sea water and in most freshwaters.

Carbon concentration mechanisms (CCM): CCMs overcome the limitations to freshwater plants imposed by reduced accessibility to CO_2 in water.

C:N ratios: the amount of carbon relative to the amount of nitrogen present in organic matter.

Ellenberg indicator values: estimates of species-specific ecological optima along main abiotic environmental gradients, such as light, temperature, continentality, moisture, nutrients, pH, and salinity.

Eutrophication: the condition of a gradual increase in the concentration of phosphorous, nitrogen, and other nutrients in water bodies.

Flooding dynamics: growing conditions in which part of a plant's ontogeny is completed in a submerged environment. Such flooding can be permanent or vary across the season or within hydrological rhythms.

Leaf economics spectrum: describes consistent correlations that constrain leaf traits to a single axis of variation in terms of investment and use of nutrients and other resources. Originally proposed by Wright *et al.* [105], the leaf economics spectrum consists of six key functional traits: dark respiration rates, leaf life span, leaf mass per area, leaf nitrogen content, leaf phosphorous content, and photosynthetic assimilation rates.

Radial oxygen loss (ROL): ROL is the oxygen released from root aerenchyma to the rhizosphere in the radial directions.

Vertical light attenuation: the exponential decrease in light intensity in the water column at increasing depths.
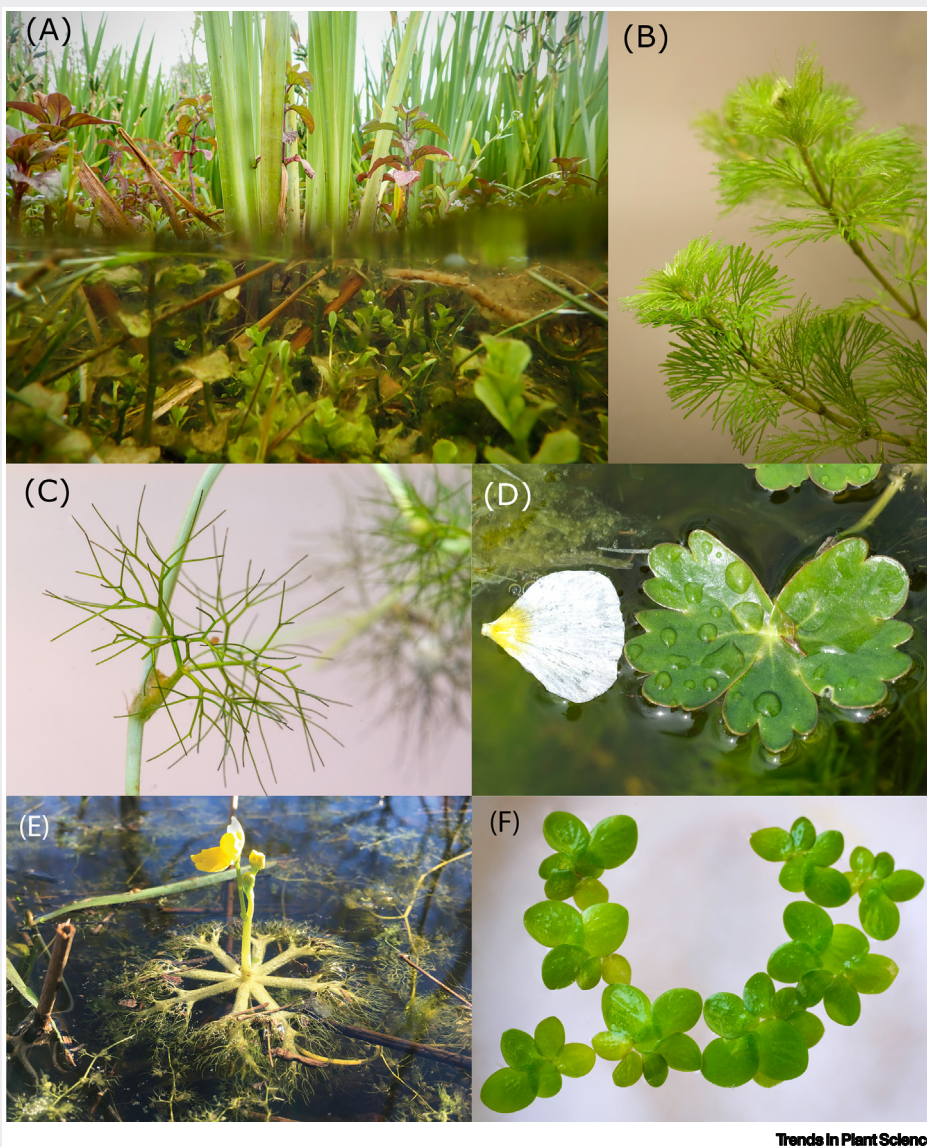
Figure I. Examples of freshwater plant growth forms reflecting adaptations to life in water.

Light

Light quantity and quality are changed through water surface reflection, scattering, and absorption, following an exponential decrease from the surface to deeper areas. Along the light spectrum, UV light is mostly scattered in water, whereas IR light is more quickly absorbed, which results in an increase of the red/far-red ratio [29]. The scattering and absorption of light are further enhanced by suspended materials, dissolved organic matter, and microalgae [30,31]. To achieve photosynthetic acclimation to **vertical light attenuation**, freshwater plants have favored widespread phenotypic plasticity mechanisms in terms of specific leaf area, leaf nitrogen, and phosphorus concentrations [32]. Such a 'plastic strategy' leads freshwater plants to develop higher specific leaf areas and thinner cuticles below the water surface, thereby enhancing both efficient light

utilization and gas exchange at low-light ranges [33,34]. These adaptations to light availability dynamics vary among different life forms (e.g., emergent vs. submerged vs. free-floating in Box 1), reflecting intrinsic species-specific differences in heterophylly, life cycles, and tolerance ranges [35,36] (i.e., whereas submerged plants are strongly dependent on underwater light conditions [29], emergent vegetation is only influenced by light attenuation during its early growth stages [36]).

Nutrient

Freshwater wetlands have a high nitrogen removal capacity through both nitrogen retention and denitrification processes. These mechanisms have been widely embraced in ecological engineering for water purification in artificial wetlands [37,38]. Nitrogen leaching (a process through which excess water drains soluble nitrogen below the root zone) may result in very infertile wetland habitats, such as bogs, where mixed-species *Sphagnum* associations are able to prosper and exclude other plants by maintaining low soil pH levels. Furthermore, in shallow freshwater wetlands, ROL can create microaerophilic conditions in the rhizosphere, leading to sediment phosphorous precipitation and inactivation [39,40]. Under such low-nutrient conditions, freshwater plants have developed various adaptive strategies, including increased energy allocation to root tissue [41] and carnivory [42]. For example, the rootless *Utricularia* develops numerous prey-capture bladders providing alternative and novel resources in nutrient-poor ecosystems [42,43]. In eutrophic waters, an excess of nutrients favors fast-growing organisms and subsequent algae outbreaks have been shown to structure freshwater plant distribution through light shading, competition, toxicity, and oxygen depletion [44]. Under such conditions, tall-growing and floating-leaved plants seem to be more tolerant compared with species with a fully submerged life cycle [45].

Flow velocity

For those plants that inhabit flowing waters in rivers and streams, as well as in lakes with wave-induced water motion, flow velocity creates varying levels of drag that select for certain types of plant architectural and mechanical properties and rooting abilities [46,47]. Low-flow regimes in near-lentic conditions may constrain the development and abundance of freshwater plants through resource limitation caused by enhanced heterotrophic activity in fine organic matter accumulation [48,49]. Fast-flow regimes, however, may cause physical destruction and damage to plant leaves and tissues, especially during their juvenile phases. The adaptive morphological responses of freshwater plants include the acquisition of more streamlined morphology and the development of an altered clonal architecture to enhance mechanical strength [50–52]. Furthermore, flow velocity impacts gas exchange and nutrient uptake by reducing the diffusive boundary layer between plant tissues and water, decreasing molecule concentration in the water column, increasing gas exchange with the atmosphere, and altering the vertical distribution of fine organic matter [53–55].

Flooding gradient

The flooding gradient provides an overview of the environmental stressors and habitat conditions mentioned earlier, which 'select' for a battery of trait combinations in freshwater plants. For example, trait compositions in terms of leaf phosphorus content, plant height, and specific leaf area vary accordingly between different growth forms distributed across a flooding gradient (Box 1 and Figure 1). The overlapping patterns in trait expressions across different growth forms also suggest that trade-offs and optimal trait combinations are different, depending on the varying habitat features along the flooding gradient (Figure 1C).

Freshwater plant adaptations can also serve as promising ecological indicators of the environment. Specifically, freshwater plants show multiple correlations between variations in their functional traits and a set of **Ellenberg indicator values** [56,57] (Figure 2A). The Ellenberg
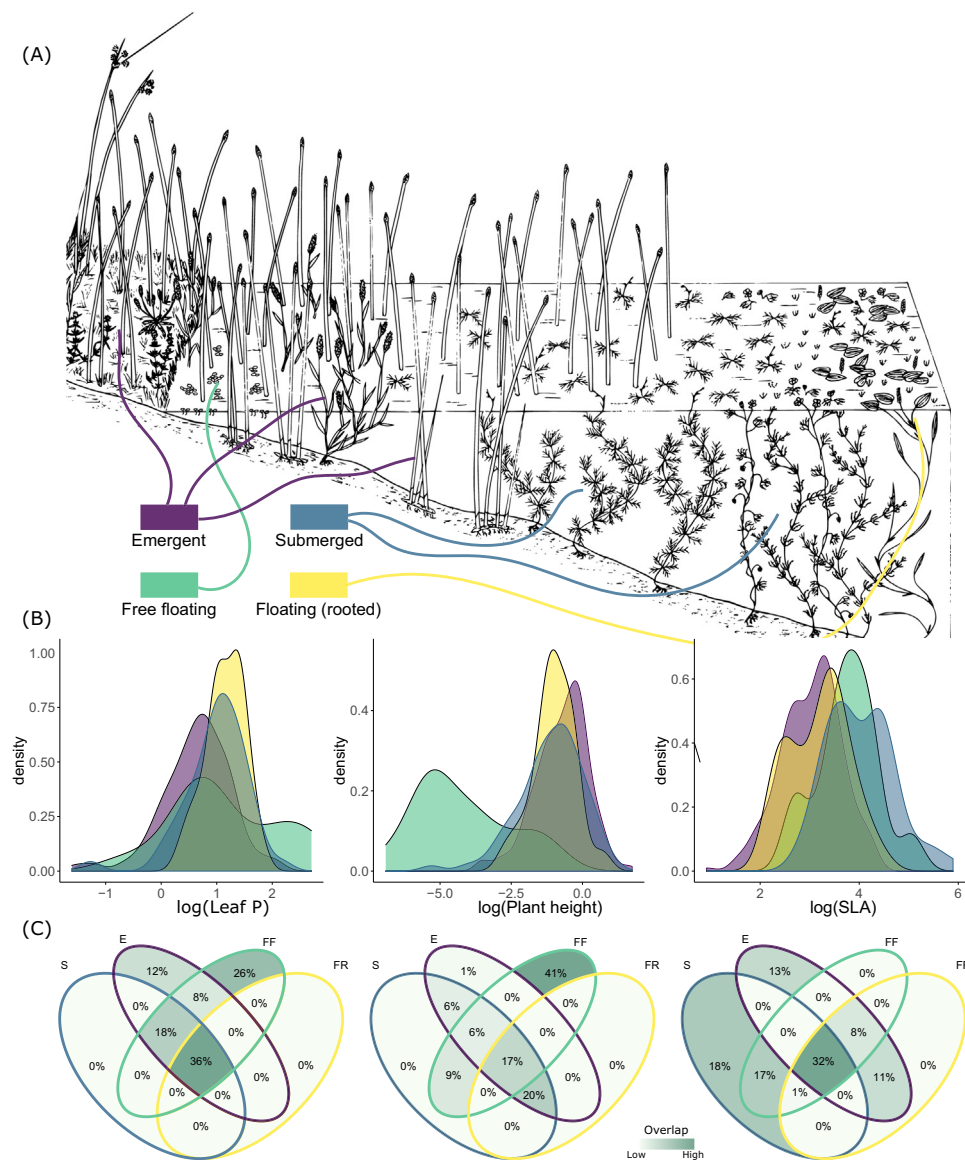
Figure 1. Plant functions across a flooding gradient. Trait variation of the four major growth forms in aquatic plants [emergent (E), submerged (S), free floating (FF), and rooted floating-leaved (FR)] representing a transition from emergent to fully submerged growth. Growth strategies have unique combinations of trait variations in leaf phosphorus (P) content, plant height, and specific leaf area (SLA). (A) Schematic overview of the different growth forms in a freshwater habitat. (B) Density distributions across three trait axes for plant growth forms. (C) Overlap in trait variation between growth forms. Overlaps are estimated based on the 95% quantiles for each growth form. Total sample size for leaf P = 243, plant height = 502, and SLA = 349. Trait and growth form data modified from [34,123,124]. Drawing credit: © Camino Fernández-Aláez. Data and code used to create Figure 1 are available via Zenodo data repository (https://doi.org/10.5281/zenodo.7415976).

indicator values in freshwater plants differ from their terrestrial counterparts along different environmental gradients, such as temperature, nutrients, light, and moisture (Figure 2B), reflecting a major divergence in environmental constraints between terrestrial and freshwater habitats. However, the complex correlations between different plant traits and habitat characteristics suggest that no single trait is able to provide a complete picture of ecological conditions. Rather,
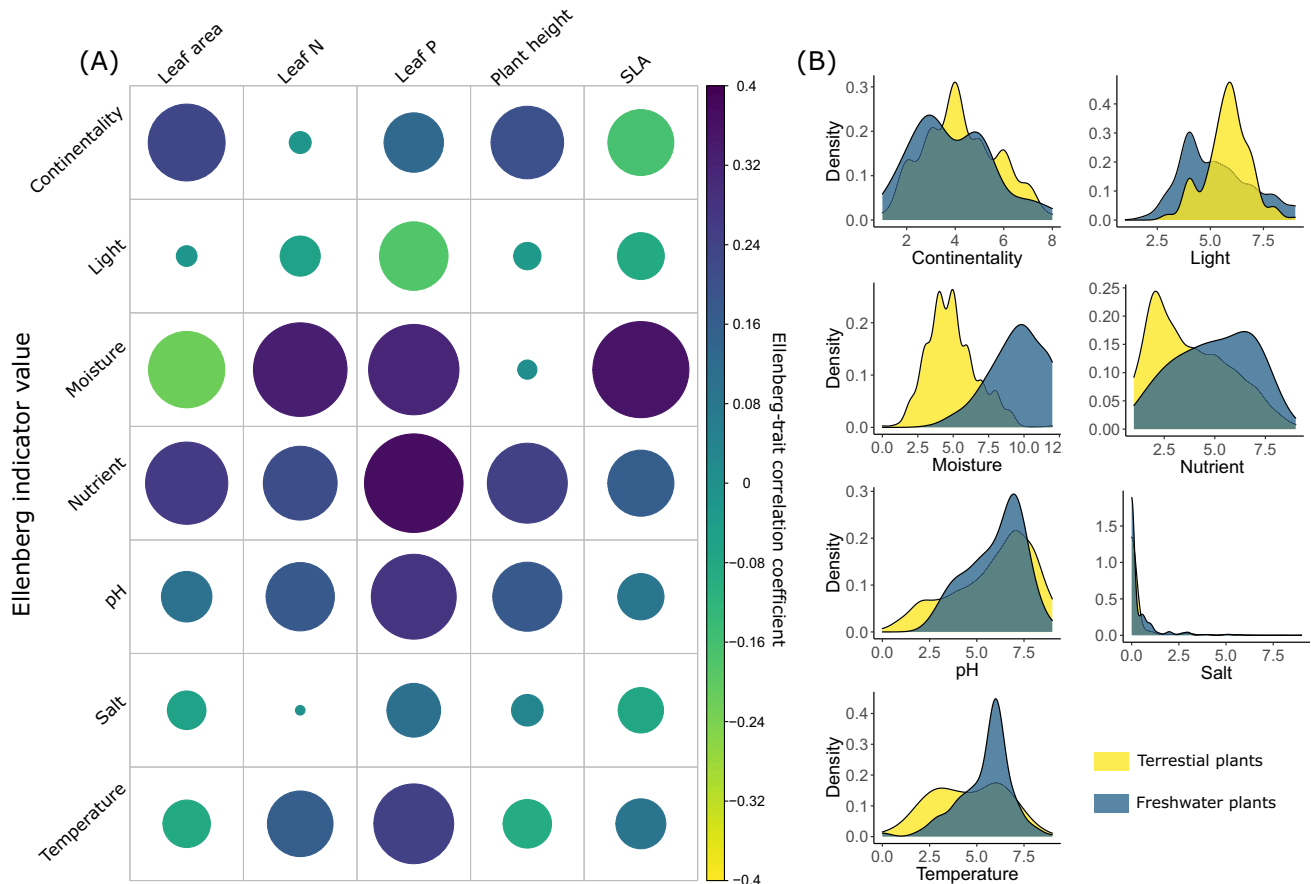
Figure 2. Freshwater plants as ecosystem indicators. Ellenberg indicator values for 281 freshwater species and their correlation with functional traits. (A) Bivariate correlations between Ellenberg indicator values and five functional traits. The size of the circles represents the amplitude of Pearson correlation coefficients. (B) Density distribution of Ellenberg indicators in terrestrial (n = 3592) and freshwater plants (n = 281). Data modified from [124]. Data and code used to create Figure 2 are available via Zenodo data repository (https://doi.org/10.5281/zenodo.7415976).

variation in species trait hypervolumes can only model and predict functional adaptations of freshwater plants to multiple environmental features [58–60].

Freshwater plant responses to emerging stressors under global change

The impacts of global change on freshwater ecosystems are multiscale and multivariate. For example, extreme weather events (droughts, heatwaves, and flooding) together with long-term global change drivers, such as increased atmospheric CO_2 level, sea level rising, and altered precipitation regimes, affect freshwater plants at different temporal and spatial scales. In this section, we highlight how global change impacts different freshwater plant functions from local to global scales.

Recent research has shown that freshwater systems are experiencing higher average temperatures [6,61] and more frequent and longer duration of heatwaves during the growing season [62–64]. Increasing temperatures have been linked to large-scale changes in lake mixing regimes via prolonged stratification periods [65,66]. In combination with anthropogenic land-use changes, these emerging stressors have contributed to disrupting patterns of natural flow in rivers

and streams via habitat destruction [67] and by changing the natural flow dynamics and flooding regimes [2,68]. In consequence, frequent flooding events can increase water turbidity and thereby decrease light availability for freshwater plants, especially for those with submerged leaves [33,69]. In addition, the increased current velocity in flooding water may exert more stress on freshwater plant leaves, which are generally thinner and more fragile than their terrestrial counterparts [10]. As a result, freshwater plant leaves require an extra mechanical resistance to tolerate stress caused by flooding events. In contrast to this, increased **eutrophication** reduces **C:N ratios** in freshwater plant leaves and thereby 'selects' against mechanical adaptations to flooding events by decreasing leaf strength and breaking stress [70]. For coastal areas, sea level rise and salt tide intrusion bring salinity stress (salt-forming ions, including Cl^-, NO_3^-, SO_4^{2-}, PO_4^{3-}) to freshwater plants in delta and shoreline wetlands. This boosts a rapid transition of plant communities through the selection of species tolerant to temporal variation in salinity and mineralization [71], although vertical sediment accretion and facilitation from early-colonizing species seem to alleviate this chemical stress in intertidal flats to mid-marsh ecosystems [72]. While some plants can adapt well to salinity stress with specialized salt excretion and resource allocation mechanism [73,74], most freshwater plant species are negatively affected by such changes. Even though saltwater can serve as a subsidy for phosphorus availability in karstic P-limited wetlands, its long-term impacts are also negative in these ecosystems, especially when it comes to belowground peat soil structure and plant root tissues [75].

Beyond the long-term climate change, extreme weather events, including heatwaves, droughts, and extreme rainfall-related flooding, cause pervasive impacts on freshwater plants. Even if freshwater plants are less impacted by temperature variation due to the large heat capacity of water, plant communities in shallow water bodies are still sensitive to heatwaves [76,77]. Increased temperatures also directly reduce the solubility of gases in water, causing changes in gas fluxes and carbon sources available for submerged photosynthesis [78]. In addition, increasing periods of droughts have been shown to increase the number of species with an annual emergent growth form and reduce perennial submerged species [79]. This dynamic transition is controlled by key regeneration strategies of opportunistic species linked to seed dormancy and the production of long-viable seeds in the local propagule bank [80]. In the presence of increasing flooding events, plant responses are linked to submerged conditions, either by accommodating leaf adaptations to underwater photosynthesis or by developing functional traits that allow species to emerge from the water, such as plant height and shoot elongation (Figure 1B; e.g., [81]).

Altered hydrological regimes by anthropogenic activities, including dam constructions and land-use changes, have impacted freshwater plant distributions and ecosystem metabolism of both inland waters and their surrounding catchments worldwide [2,82]. Dams reduce water level fluctuations in the riparian zone and limit the abundance of aquatic plants and wetland vegetation in general [83]. Damming and artificial river fragmentation not only change downstream habitat conditions, but also alter landscape connectivity by reducing dispersal via propagule drift [84]. In areas where hydropower plants create artificial high seasonal water level drawdowns, artificial stress on bank shores promotes annual and fast-growing plant species [83].

In addition to intensive anthropogenic activities and land-use changes, sewage input and eutrophication have led to reductions in freshwater plant geographical range sizes and local abundances [85–87]. Increasing eutrophication creates sequential changes in plant communities by creating environmental conditions that favor tall and fast-growing plants and planktonic microalgae at the expense of slow-growing, short-stemmed species [44,88–90]. Although eutrophication mostly operates locally, the combination of increasing global temperatures and water nutrients is globally selecting towards freshwater environments dominated by phytoplankton communities [6,91]. In

addition to reduced light reaching plant beds due to eutrophication, air pollution has also been shown to reduce incoming solar energy before it reaches the water surface, thereby changing the heating and photosynthetic processes in freshwater ecosystems [92]. By contrast, nocturnal irradiance from artificial urban light sources might counteract these effects by increasing photosynthetic rates and C:N ratios in aquatic plants [93]. However, it is not yet known how the potential reduction in incoming solar radiation will interact with elevated atmospheric CO_2 concentrations, rising air temperatures, and night-time light pollution, as well as their overall effects on plant photosynthesis in freshwaters.

Linkages between plant functional traits and freshwater ecosystem functioning under global change

Functional traits have multiscaled linkages to the individual performance, community structure, as well as the entire ecosystem functioning. In this part, we show how general trait–trait and trait–environment relationships are liable to be affected by freshwater global change scenarios and, in return, alter the environment through key ecosystem functioning.

The interactions between plant traits and their surrounding environment determine the performance of individual species and the composition and structure of their communities [94,95], which can be directly measured through trait–trait and trait–environment relationships [96,97]. From a global perspective, plant functional traits and climate are determinants of major ecosystem functions, including productivity, as well as water- and carbon-use strategies [98,99]. Climate and catchment-level pressures related to global change also have direct impacts on freshwater plants in terms of fitness, growth, survival, and competition [100,101], contributing to present-day delineations of their geographical distributions (Figure 3). As a consequence, the multivariate functional trait space of these plants can have profound effects on important ecosystem functions and associated ecosystem services of inland waters [102,103]. Understanding the quantitative feedbacks between plant traits and ecosystem functioning are therefore key to mitigating the impacts of global change.

For freshwater plants, different sets of functional traits are impacted by different aspects of global change. For example, flooding-induced eco-physiological adaptive traits can facilitate freshwater plants' survival through the amelioration of the oxygen deficiency caused by inundation and enhancement of underwater photosynthesis (as discussed in the plant adaptation paragraph earlier). However, trade-offs between the mechanical strength and the proportion of aerenchyma formation can jeopardize the resistance of freshwater plant roots to flow stress and other physical forces [104], thereby reducing the fitness of adapted freshwater plants to increasing flooding exposure. Since the **leaf economics spectrum** traits (e.g., leaf nitrogen, leaf phosphorus, photosynthetic rate, and leaf life span) are indicative of plants' strategies in terms of resource acquisition (mostly nutrients and water) and allocation [105,106], freshwater plants usually show fast-return strategies with higher leaf nitrogen and phosphorus due to their highly specialized leaf structure and eco-physiological adaptations [34]. Eutrophication has been found to significantly increase leaf nitrogen and phosphorus in freshwater plants worldwide [107]. However, the general shortage of biogeographically explicit studies on multidimensional trait distributions still hinders our ability to establish a general picture of the functional responses of freshwater plants to global change across different geographical and environmental settings [108].

Plant functional traits can be explicitly related to ecosystem functions through their effects on key ecological processes, which have been widely applied in ecological engineering of freshwaters for multiple restoration targets [2,109]. Regarding two significant ecosystem functions in freshwaters
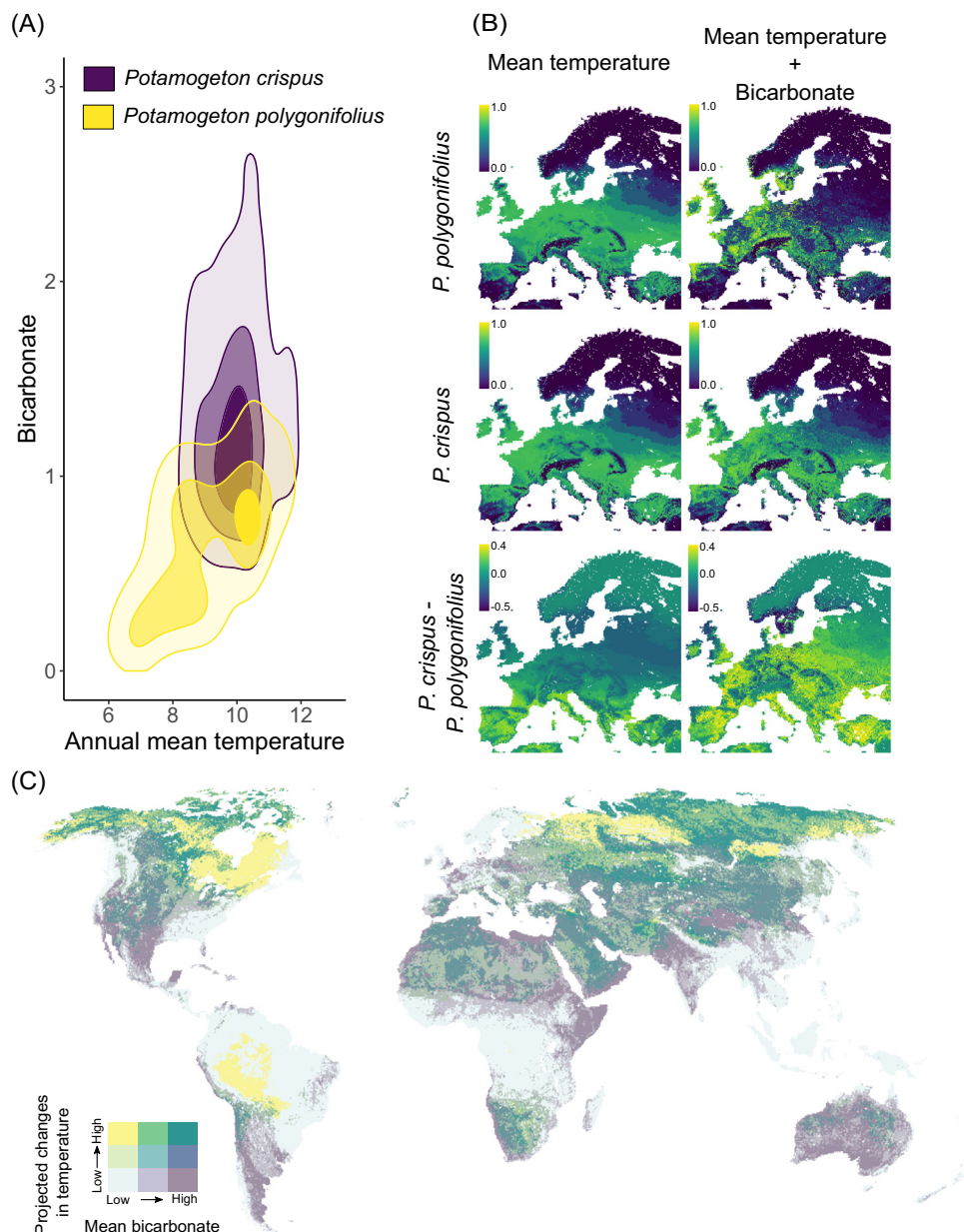
Figure 3. The interplay between climate and geology in shaping the distribution of freshwater plants.
(A) Temperature and bicarbonate preferences of two pondweed species with varying carbon concentrating abilities, *Potamogeton polygonifolius* Pourr. (obligate CO_2 user) and *Potamogeton crispus* L. (bicarbonate user) across the European continent. Lines represent approximate 25% quantiles. (B) Projected environmental suitability based on the realized niches of the two species when considering only temperature (left column) and temperature and bicarbonate together (right column). The scale bars show the probability of presence (top two rows) and differences between species probabilities (third row). The obligate CO_2 user (*P. polygonifolius*) is constricted to regions with low bicarbonate concentration compared with the bicarbonate user which can use both CO_2 and bicarbonate during photosynthesis. Consequently, the probability of species presence only separates between the two species when considering both temperature and bicarbonate. (C) The bivariate distribution of regions with high and low projected temperature change (2071–2100) and bicarbonate concentrations. Species distribution data were compiled from GBIF (https://www.gbif.org), climate data and projected climate data

(Figure legend continued at the bottom of the next page.)

(i.e., denitrification and methane production), connections between plant functional traits and ecosystem functioning originate from nutrient addition of plant litters and root exudates, as well as from changes in rhizosphere oxygen concentration through oxygen release from aerenchyma tissues [102,110,111]. Quantitative case studies on plant traits and their impacts on ecosystem functions thus provide a promising road towards improving ecological management aimed at supporting the provision of ecosystem services [112,113]. More broadly, different wetland ecosystem functions are directly impacted by global change (especially through CO_2 concentration, nitrogen deposition, precipitation, temperature, and land-use change) and indirectly modified through global change-induced plant community dynamics and phenotypic expressions [114–116].

Moving forward: freshwater plant traits under future scenarios

There is a need to understand how freshwater ecosystems will respond to global-change scenarios. Important in this process will be our ability to predict connections between ecosystem functions and freshwater plant adaptations and how such relationships may impact the services and biodiversity of inland waters.

A changing regime of flooding/drought frequency and severity

More fieldwork and modeling exercises are needed to understand the effects of changing hydrological regimes (including increased flooding/drought extremes and sea-level rise) on freshwater plant traits and associated ecosystem functioning (which is partly illustrated in Figure 3). Specifically, a global and coordinated effort is needed to understand freshwater plant community dynamics and functional trait expressions (including trait–trait tradeoffs) under such changing regimes. Key in this progress will be the availability of functional trait data for freshwater plants. Despite the long tradition of ecological research on freshwater flora [90,117], trait data collection of these plants is still in its infancy. Compared with terrestrial plants, the available functional information for freshwater plants is still limited and the few existing data are unbalanced among different growth forms (Box 2).

Trait-based modeling of freshwater plant distributions under climate change

Accurately modeling freshwater plant distributions is a fundamental prerequisite to understand the biogeography of freshwater plants. Trait-based perspectives could improve correlative niche-based, process-based, and Earth system models by: (i) including the specific effects of global change on trait–trait and trait–environment relationships in freshwater plants [8] (Figure 3); (ii) adding new trait-based freshwater plant modules by incorporating continuous trait data rather than traditional discrete plant functional types from classic terrestrial plant models [118]; and (iii) considering the unique mechanistic driving factors underlying trait expression in these freshwater plants across multiple spatial scales and biogeographical realms [108,119]. Overall, these novel lines of inquiry should be key in the context of global plant conservation efforts under the Post-2020 Global Biodiversity Framework of the Convention on Biological Diversity, among others.

Biodiversity in freshwater ecosystems

Most of the commonly recognized threats to freshwater biodiversity, including changing climate, invasive species, harmful algal blooms, and freshwater salinization, are a product of global change

(CMIP6 ISIMIP3, SSP5–8.5) were calculated by CHELSA [125]. Bicarbonate concentration was extracted from [15]. The predicted suitability maps (B) were estimated from polynomial logistic regression models, using GBIF records as species present-data and a balanced number of pseudoabsence points distributed randomly across the European continent. Data and code used to create Figure 3 are available via Zenodo data repository (https://doi.org/10.5281/zenodo.7415976).

[120]. Freshwater plant biodiversity has been shown as a surrogate for diversity in other freshwater organisms [121]. However, it remains unclear what combinations of plant functions are supporting freshwater biodiversity in general and how functional plant traits are linked to ecosystem resilience. It is also unknown if the macroecological overlap between freshwater plant diversity and overall freshwater biodiversity is a product of spatially correlated species pools or if these plants are supporting biodiversity via keystone processes. Modern spatial biodiversity models (e.g., latent variable models and joint-species distribution models [122]) can produce seamless pathway correlations between species distributions, functional traits, and the environment, thereby providing promising tools for differentiating between autocorrelated and keystone effects of plant traits on freshwater biodiversity. Such models could also support future research efforts documenting differences in plant functions across biogeographical realms (e.g., Neotropics vs. Palearctic) and identifying correlations between biodiversity hotspots and current centers of human impact.

The future of freshwater plant functional biogeography

Our ability to understand the distribution of plant trait–environment interactions will rely on a coordinated effort to collect the data needed to generate new synthesis. These efforts should include not only the collection and curation of single traits describing the form and functions of plants in general (Box 2), but also more system-specific data on unique adaptive traits and standardized monitoring data of freshwater plant communities and environmental conditions. A high priority should be given to large-scale collaborations linking the leaf economics spectrum (and leaf stoichiometry) to submerged photosynthetic capacities at different temperature and CO_2 levels, as well as inter- and intraspecific variation in aerenchyma formations and ROL. Understanding such linkages would provide key insights into the mechanism linking the leaf economics spectrum to the freshwater environment. Furthermore, existing data of functional traits and local community samples from strictly comparable field surveys should be harmonized into a common format providing a database for future research on plant functional responses to global change in freshwater systems.

Concluding remarks

The advancement of functional plant ecology in terrestrial systems has shown that species traits can be used to understand and predict how ecosystem functions are responding to the ongoing global change. This provides a promising tool for freshwater research and can be used as a proxy in large-scale and global estimations of functional changes in freshwater systems and the services they provide. However, an increased focus on the specific conditions and traits important for life in water is needed if we are to gain a sound understanding of how plant communities are changing and the reciprocal relationships between freshwater plant functions and the environment (see Outstanding questions).

Box 2. The data gap in freshwater plant functions

Global plant trait database compilation is an effective way to understand plant functional biogeography through quantitative analyses of the patterns and trends of plant performances along major environmental gradients. To date, the TRY database is one of the most comprehensive plant trait compilation campaigns worldwide [124]. Despite the overwhelming trait data compiled from terrestrial plants, freshwater plant traits are relatively scarce in terms of their current stage of compilation and public accessibility. For key leaf economic traits (Figure IA), only a fraction of the 3413 freshwater species has been mapped (colored), compared with the 46 085 vascular plant species used to define the global trait space for plants (black) [106]. Within freshwater plants, species with a fully submerged life stage are less often represented in the global trait databases compared with species with an emergent growth form. Figure IB shows the deviation in trait coverage across growth forms expressed as the differences between the proportional distribution of growth forms for the species covered by a single trait minus the proportional distribution of growth forms across all freshwater plants. Positive values indicate over-representations and negative values indicate under-representation of a growth form for a given trait. For freshwater plants, small-ranged species are more likely to be under-represented in global trait databases (Figure IC) and the same is true for species outside of North America and Europe (Figure ID). Consequently, the curation and subsequent publication of a comprehensive freshwater plant trait database is needed if we are to better understand their functions in a biogeographically explicit context, as well as their responses and feedbacks to different global change scenarios [8].
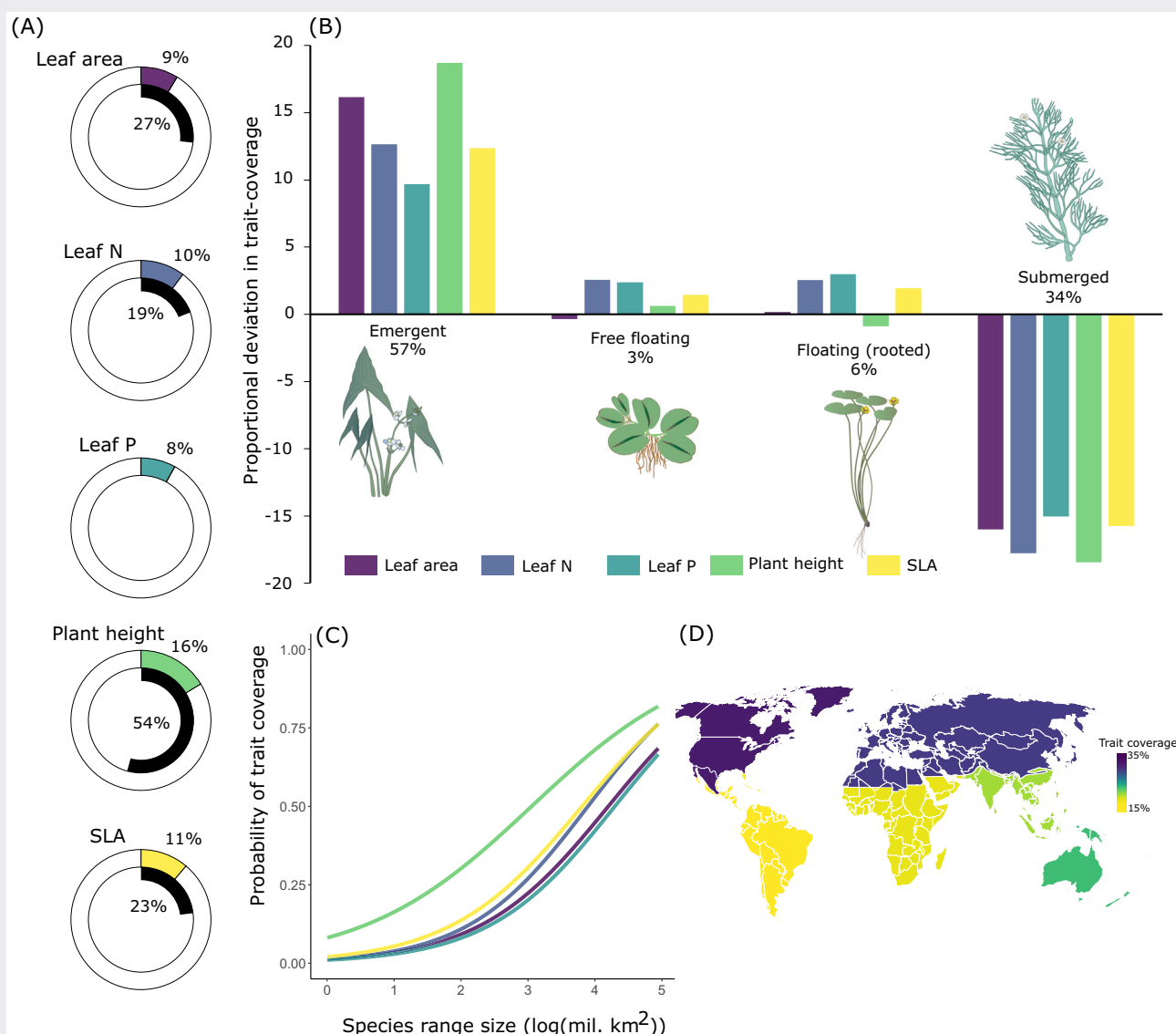
Figure I. Gaps in freshwater plant functional biogeography. Abbreviation: SLA, specific leaf area.

Declaration of interests

No interests are declared.

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