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Towards linking freshwater plants and ecosystems via functional biogeography

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ABSTRACT

Functional biogeography has advanced the field of functional ecology into a more spatially—predictive science. However, freshwater plants are still underrepresented in these trait—based advancements. Here, we argue that there is a need for developing a functional biogeographical framework for freshwater plants and initiate global mapping efforts focusing on the form and function of freshwater plants. Specific attention should be given to (1) the placement of freshwater plants in the global plant trait space and show how this placement links to global trait—environment relationships; (2) the theoretical framework for major structural trait—trait correlations based on the physical constraints in aquatic ecosystems; (3) the evolutionary and environmental drivers underlying the global distribution of inter— and intra—specific variation in different life forms; and (4) the level of equilibrium between spatial and temporal trait—environment relationships in freshwater plants. By putting freshwater plants in the context of these spatial aspects, we could advance our understanding of freshwater plant adaptations and responses to environmental gradients, and thereby facilitate predicting the consequences of global changes for freshwater ecosystem functions and services.

Functional biogeography relates to the diversity of organismal forms and functions and puts these into a spatial—explicit context by linking responses of small and large—scale patterns of biodiversity to the environment (Violle et al., 2014). The emergence of functional biogeography has advanced the field of functional ecology into a more predictive science across biogeographical contexts and gradients (van Bodegom et al., 2014; Maire et al., 2015). In terrestrial systems, functional plant traits are now integrated into Earth system models (Wullschleger et al., 2014), accessible at high spatial resolutions in every corner of the world (Butler et al., 2017; Moreno-Martínez et al., 2018). These studies demonstrated the inherent potential of bridging plant forms and functions with georeferenced distributions for the ongoing exploration of large—scale ecological phenomena in our changing world. As a result of this unprecedented data collection effort, a new theoretical macroecological framework of plant traits is now emerging to help us understand how plants perform and adapt to environmental factors, and affect ecosystem functioning across organizational levels (Díaz et al., 2016; Kattge et al., 2020).

Although freshwater plants are not ignored (Moor et al., 2017), they are widely underrepresented in these trait—based advancements, and little attention has been given to understand the unique adaptations required for freshwater plant growth and persistence across geographical scales, e.g., bicarbonate uptake characters of freshwater plants as an alternative carbon source in water across catchments (Iversen et al., 2019). Therefore, we need to include freshwater plants in the context of functional biogeography, and initiate global mapping efforts focusing on the form and function of freshwater plants to achieve a better understanding of their global distribution patterns, ecological adaptive strategies, and how global change impacts freshwater systems via species functional responses.

In the slipstream of documenting global patterns of species richness and species' distributions, functional biogeography has emerged as a promising field bridging the link between biodiversity gradients and biogeochemical cycles, via ecosystem functional properties (Reichstein et al., 2014) and stoichiometry (Tian et al., 2019), thereby providing the framework for underlying mechanisms driving ecosystem services and

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functions (Violle et al., 2014). Within plants alone, empirical studies on global trait—environment relationships have outlined correlations between specific functional traits and global biochemical gradients such as water, nutrients, and energy (Reich and Oleksyn, 2004; Wright et al., 2004). Understanding such continuous relationships between functional traits and environmental drivers have pushed the field of functional biogeography into a predictive and applied science within the past decade. For example, by spatially modelling the balance of leaf energy inputs and outputs, the impacts of climate change have been used to predict changes in leaf size across the globe (Wright et al., 2017), and the relationships between bioclimatic drivers and functional trait variations have been used to predict the global vegetation distribution patterns under current and future climate regime (van Bodegom et al., 2014).

A key component in the advancement of functional biogeography within plant ecology has been the focus on selective functional traits (e.g., specific leaf area, leaf nitrogen content or plant size) linked to individual performance via their effects on growth, reproduction and survival (Violle et al., 2007; Gibert et al., 2016). Although freshwater plants are considered in the global synthesis of functional plant traits (Díaz et al., 2016), documenting macroecological correlations between these traits and the environment for aquatic species are still lacking. Of the *c.* 3420 freshwater plant species listed by Murphy et al. (2019), only 15% has data on plant height in TRY (the world's largest plant trait data portal). This is in stark contrast to the 54% coverage of plant height for the 46,085 species used to quantify the global plant trait space (Díaz et al., 2016). Such discrepancies become even greater when considering species with a predominantly submerged (8%) or free—floating (12%) life form. Recent reviews on the macroecology and functional traits of freshwater plant highlight that not only are freshwater plants largely absent in the global synthesis, but our knowledge within the group largely stems from studies in Europe and North America, and also rarely utilize the strength of continuous or experimentally quantified traits (Dalla Vecchia et al., 2020; Alahuhta et al., 2021).

Documenting and understanding the global trait space of freshwater plants goes beyond closing a knowledge gap. Freshwater plants, and wetland plants in general, have developed a suite of traits reflecting adaptations to a unique environment in terms of oxygen availability, nutrient cycles, pH and redox potential (Colmer and Voesenek, 2009; Pan et al., 2019). For example, the presence of leaf gas film counterbalances the low diffusion rate of molecules in water and improves O_2 and CO_2 exchange between submerged leaves and the surroundings (Colmer and Pedersen, 2008). Furthermore, many freshwater plants have developed aerenchyma formation (enlarged gas spaces within the plant tissue), supporting gas exchanges between roots and aboveground tissues (Evans, 2004). Invasive plant species have triggered an irreversible hysteric phenomenon in inland waters, excluding native species from their original functional space (Bolpagni, 2021), predicting potential invasion fronts via functional trait matching with local faunas could provide important insights into future spreads of invasive species and thereby support local ecosystem management. The interactions between above—mentioned freshwater adaptation traits and traits associated with the leaf economics spectrum and plant growth will be key in understanding the underlying mechanisms driving large—scale plant trait patterns in freshwater ecosystems (Moor et al., 2017; Pan et al., 2019; Fig. 1). In bivariate trait relationships between leaf nitrogen, leaf phosphorus, and leaf dry mass per area, plants living in freshwater ecosystems generally detached from terrestrial predictions at the acquisitive end of the leaf economics spectrum, showing higher leaf nitrogen/phosphorus and faster photosynthetic rates (Pan et al., 2020). However, we do not know if such trait—trait deviations are caused by limited functional niche space, affecting the potential trait variation in freshwater environments, or if they reflect a trade—off linked to traits unique for freshwater plants.

The few global studies suggest that the biogeography of functional traits in freshwater plants can follow both unique eco—physiological pathways and trends reported from terrestrial systems. The low diffusivity and potential depletion of CO_2 in freshwater ecosystems has indirectly linked plant photosynthesis strategies (and abilities to utilize alternative carbon sources, such as bicarbonate uptake) to large scale gradients in catchment geology; a link created by the local presence of bicarbonate (HCO_3^-) derived from mineral weathering of soils and rocks in the catchment (Iversen et al., 2019). While few freshwater plants have evolved Crassulacean Acid Metabolism (CAM) or C4–like pathways (Maberly and Gontero, 2017), CAM is a common characteristic of plant living in semiarid and arid terrestrial environments, linked to global temperature and precipitation patterns (Still et al., 2003; Yamori et al., 2014).

In another study, the global distribution of ploidy states in freshwater plants were predominantly driven by temperature, with the proportion of diploid vs. polyploid species decreasing when moving away from the equator (Lobato-de Magalhães et al., 2021). This reflects the patterns reported from terrestrial systems (Rice et al., 2019), suggesting that the drivers affecting plant cytotypes may be the same between terrestrial and freshwater systems. Attempts to extend these observations to global patterns of multidimensional trait variation in freshwater plants are still limited though. But, between local lake plant communities, functional trait variation has been shown to be dependent of both climate and environmental gradients, generating a global pattern of functional beta diversity between lakes in tropical, subtropical, temperate and boreal regions (García-Girón et al., 2020). However, these patterns are still subject to revision, not least because adjustments of functional traits in freshwater plants are constrained by plasticity in the development and ontogeny within (e.g., Fu et al., 2013) and between species (e.g., Chmara et al., 2019).

Functional biogeography can help advance our understanding of freshwater plant adaptations and responses to environmental gradients, and thereby facilitate predicting the consequences of global changes for freshwater ecosystem functions and services. With the rise of freshwater plant macroecology (Alahuhta et al., 2021) and the standing traditions of functional ecology in freshwater systems (Alahuhta et al., 2018; Martini et al., 2021), now is the time to start mapping and synthesising the global patterns of functional plant traits (see our MAP project website for details; http://www.lifeinmud.com/map). Such efforts should build on the existing work done in terrestrial systems while paving their own unique way forward. In order to do so future work should strive to:

- Outline the placement of freshwater plants in the global plant trait space and show how this placement links to global trait—environment relationships and trait—trait trade—offs. How much of the predictability in terrestrial trait—environment relationships can we transfer to freshwater ecosystems?
- Generate a theoretical framework for major structural trait—trait correlations based on the physical constraints in aquatic ecosystems. How does life in water alter species in terms of resource allocation, trade—offs for acclimation, adaptation, and trait expression?
- Understand the evolutionary and environmental drivers underlying the global distribution of inter— and intra—specific variation in different life forms. When and how do plants shift between submerged, floating and emergent life forms?
- Document the level of equilibrium between spatial and temporal trait—environment relationships in freshwater plants. To what extent do past climate and freshwater conditions shape contemporary trait—environment relationships and how do we achieve predictability of future response to global change?
- Understand how anthropogenic pressures shape the distribution and variation in freshwater plant traits. Do freshwater plant communities trend towards increasing functional homogenization in response to human disturbance or do they show functional resilience?

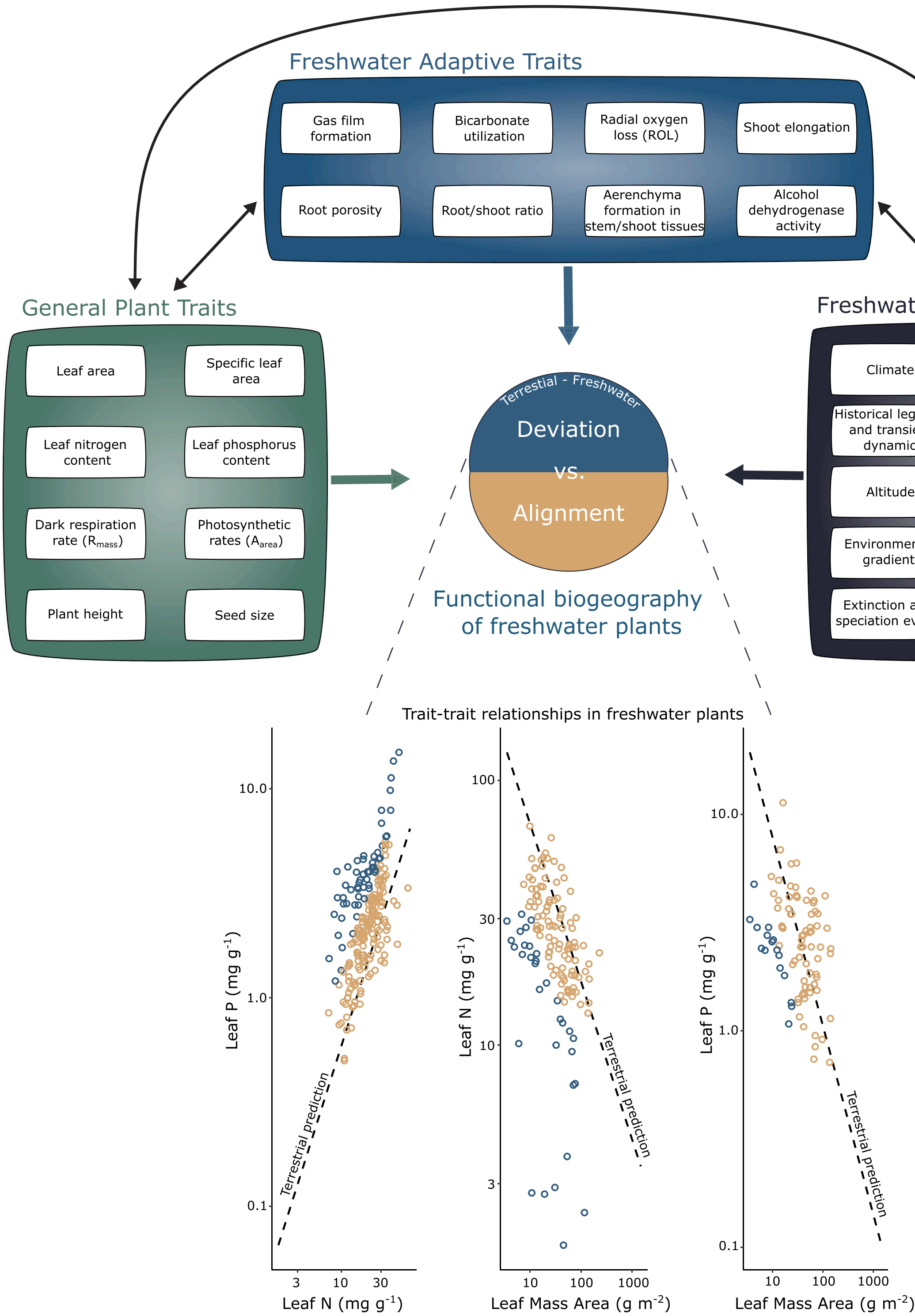

Fig. 1. The functional biogeography of freshwater plants is the outcome of the interplay between biogeography, functional traits related to the leaf economics spectrum and general plant structure, and freshwater adaptive traits. Each box highlights some of the important functional traits and biogeographical aspects in trait-space distributions in freshwater plants and plants in general. These components structure the functional biogeography directly or indirectly via complex linkages between trait-environment relationships and trait-trait associations (including facilitation and trade-offs, whose effects on trait expression are hypothesised to be modulated by species-driven changes in microhabitat conditions and resource limitation). Across functional and environmental gradients, variation within the trait space of freshwater plants will align or deviate from the terrestrial prediction. Understanding such discrepancies will be key in the development of a spatial framework of freshwater plant functions. The lower panels exemplify discrepancies (blue points) and alignments (yellow points) in bivariate leaf economic trait relationships between freshwater and terrestrial plants at the inter-specific level. Each point in the three scatter plots is a leaf from a freshwater plant species and the dotted line represent the predicted trait-trait relationship in terrestrial plants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article)
(Data from Pan et al., 2020).

CRediT authorship contribution statement

All authors contributed equally to the framing of the research questions, conducting the literature search, writing the manuscript, and creating the figure.

Declaration of Competing Interest

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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