Functional traits in macrophyte studies: Current trends and future research agenda

Review Paper

Title: **Functional traits in macrophyte studies: current trends and future research agenda**

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Abstract

The use of functional traits (FTs) can provide quantitative information to explain macrophyte ecology more effectively than traditional taxonomic-based methods. This research aims to elucidate the trait-based approaches used in recent macrophyte studies to outline their applications, shortcomings, and future challenges. A systematic literature review focused on macrophytes and FTs was carried out on Scopus database (last accessed May 2020). The latest 520 papers published from 2010 to 2020, which represent 70% of the whole literature selected since 1969, were carefully screened. Reviewed studies mainly investigated: 1) the role of FTs in shaping communities; 2) the responses of macrophytes to environmental gradients; 3) the application of FTs in monitoring anthropic pressures; and 4) the reasons for success of invasive species. Studied areas were concentrated in Europe (41%) and Asia (32%), overlooking other important biodiversity hotspots, and only 6.2% of the world macrophytes species were investigated in dedicated single species studies. The FTs most commonly used include leaf economic and morphological traits, and we noticed a lack of attention on root traits and in general on spatial traits patterns, as well as a relatively poor understanding of how FTs mediate biotic interactions. High-throughput techniques, such as remote sensing, allow to map fine-scale variability of selected traits within and across systems, helping to clarify multiple links of FTs with ecological drivers and processes. We advise to promote investigations on root traits, and to push forward the integration of multiple approaches to better clarify the role of macrophytes at multiple scales.

Keywords: macrophytes, anthropic pressures, leaf economics, root traits, remote sensing, aquatic environments

1. Introduction

The concept of functional traits is a relatively recent research approach that is rapidly establishing in ecology and is taking the place of purely taxonomic studies because of its high potential in exploring multi-scale environmental issues. Functional traits are defined as any morphological or phenological characteristic that is measurable at the individual level (Díaz et al., 1998; Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013), and can mirror the relationships of a species to its habitat conditions, thus revealing the interactions of the plant with the environment (Fu et al., 2015). Moreover, a supplementary advantage of functional trait-based studies is that findings can be compared among different regions, since the different specific community composition does not represent a barrier anymore, thus allowing investigations at wider scales (Schoelynck and Struyf, 2016; Iversen et al., 2019).

The use of functional traits is of particular interest for aquatic ecosystems, which are environments of major concern when considering the threats posed by anthropic pollution, habitat degradation (land use change), and the introduction of non-native species, leading to a change in the community composition in terms of reduced biodiversity and functional homogenization (Bresciani et al., 2012; Phillips et al., 2016; Cantonati et al., 2020; Lindholm et al., 2020). The concern for biodiversity conservation is a critical concern for aquatic plants (O'Hare et al., 2018), which show a high diversity in sub-tropical to low tropical latitudes (Murphy et al., 2019), and in lowlands with higher water availability at the regional scale, coinciding with the strongest presence of anthropic activities (Bolpagni et al., 2018; Guareschi et al., 2020).

Aquatic plants are crucial in maintaining water transparency by absorbing nutrients from the water column and from the sediment, thus competing with phytoplankton for both nutrients and light (Scheffer, 1999), by releasing allelopathic substances that can inhibit the growth of phytoplankton (Hilt and Gross, 2008) and by favoring sediment stability and reducing resuspension (Van Donk and Van de Bund, 2002). Besides, macrophytes can influence hydrologic features of the water body, especially in lotic systems, by reducing water velocity and enhancing sedimentation of suspended particles (Rolland et al., 2015). They can also influence the chemical processes in the rhizosphere by releasing oxygen and other exudates from the roots

(Soana and Bartoli, 2013). Moreover, their presence creates structure in the water column and offer habitat for zooplankton and fish (Schriver et al., 1995; Perrow et al., 1999) and finally, aquatic plants represent an important food source for a range of different organisms, as invertebrates, amphibians, fish, birds and mammals (Wood et al., 2017). Because of all these reasons, the presence of macrophytes promotes complex feedbacks that help maintaining the ecosystem stability (Bakker et al., 2013), but at the same time they can also trigger dystrophic events (Bolpagni et al., 2007) As the multiple pivotal roles of macrophytes in influencing the structure and the dynamics of the ecosystem have been widely recognized in the literature (e.g., Ozimek et al., 1990; Scheffer et al., 1993; Van Donk and Van de Bund, 2002), a deeper understanding in their functionality and interactions with the other components of aquatic systems should be a prerequisite for developing effective management actions.

The study of aquatic and terrestrial plants has long been based on a taxonomic approach in order to detect changes in the community species composition, using indexes like species richness or beta diversity (McGill, et al., 2006; Lindholm et al., 2020). However, researchers have recently documented the use of functional traits for investigating important topics like the mechanisms explaining the structuring of the community (Van Gerven et al., 2015; Eckert et al., 2016; García-Girón et al., 2019a), the response of species and communities to environmental gradients (Zhang et al., 2018; Sebilian Wittyngham et al., 2019), the influence of anthropic activities and climate change (Huang et al., 2017; Yu et al., 2018), the design of effective restoration actions (Pereira et al., 2017; Pietrini et al., 2019), the spread of invasive species (Thiébaut et al., 2016; Villa et al., 2017), and the role of traits in determining biotic interactions (Grutters et al., 2016; Sun et al. 2018). The implementation of trait-based approaches has resulted in an increasingly abundant literature and in the institution of online databases containing plant functional traits values accessible to the scientific community (e.g., www.try-db.org, www.leda-traitbase.org, www.icestes.github.io). Nevertheless, a systematic and general synthesis on the use of functional traits in aquatic macrophytes studies is still missing. Given the high interest on these studies and the wide spectrum of application fields, we intend to answer the need of scrutiny for which functional traits, species and topics have been investigated so far in the context of aquatic macrophytes (Pan et al., 2019). We believe that this review has become necessary in order to evaluate what fields have been exhaustively researched and what other fields deserve further insight and to promote the standardization of procedures so that comparisons among studies are facilitated. For this reason, we aim to propose a research agenda highlighting the most critical aspects regarding trait-based approaches tackled so far and indicating what should be the next steps in this field.

2. Research strategy and analysis of articles

The systematic paper research was carried out on the Scopus database (www.scopus.com; last access 15th May 2020), addressing the words that identify aquatic plants and confining the research to functional traits. The string used was: TITLE-ABS-KEY ("aquatic plant*" OR macrophyte* OR hydrophyte* OR helophyte* OR pleustophyte* OR "water plant*") AND TITLE-ABS-KEY (trait* OR "functional trait*"). We are aware that by using only the word "trait" we omitted a number of studies that investigated plant characteristics or attributes, though not explicitly referred to as "functional traits" (e.g., Fornoff and Gross, 2014; Marzocchi et al., 2019). However, we intended to delineate our research to studies that refer to a specific and homogeneous field of research (trait-oriented), adopting a consistent use of terminology. A total of 738 papers resulted from the research, published from 1969 onwards. Only papers published between 2010 and 2020 were taken into consideration for this review, in order to focus on recent developments and current trends on the topic of functional traits applied to macrophytes, for a total of 520 papers (equal to 70% of the selected papers). The papers were examined to check for relevance following the "matrix method" approach by Klopper et al. (2007). This method involves the creation of a matrix that summarizes the information found in the papers using a series of parameters of interest. The research was open to any macrophyte growth form and aquatic habitat, including estuarine and marine ecosystems.

Papers were considered relevant if they included the measurement of functional traits on one or more macrophyte species (primary studies) or the use of already measured traits from the literature (secondary studies) in order to address any ecological question. During the elaboration of results, we made no distinction between these two types of studies. Previous reviews on specific traits or topics related to macrophyte functional traits were also included, however none of these offered a wide-ranging overview as the present review. The TRY database list for functional traits (www.try-db.org) was consulted to check for consistency of the traits considered by the papers. The matrix of revision contained 10 parameters: *Geographic distribution*, *Habitat type*, *Study type*, *Macrophyte type*, *Name of the species*, *Species number*, *Functional trait category*, *Shoot/root functional traits*, *Environmental variables*, and *Main topic*, as listed in Table 1.

The first feature *Geographic distribution* is informative of the place where the study was conducted at the macro-spatial scale (e.g., continent), for both field investigations and/or laboratory experiments. *Habitat type* refers to where macrophytes were either measured in the field or collected for further analyses or experiments in the laboratory. Here we distinguished between i) lentic environments like lakes, ponds, and wetlands, including the small-standing water ecosystems *sensu* Bolpagni et al. (2019) that are characterized by a larger variability in the water regime as ephemeral systems, ii) lotic environments, including rivers, streams and canals, and iii) marine environments. The tag *Any* was assigned to studies not restricted to a single habitat type and can include more than one habitat where the target macrophyte species were present and investigated. The parameter *Macrophyte type* includes the three main growth forms, i.e. submerged, free-floating, and emergent (Fu et al., 2019a; García-Girón et al., 2019b); rooted emergent (e.g., *Nelumbo nucifera*) and rooted floating leaved (e.g., *Nuphar lutea*, *Nymphaea alba*) were grouped together because often there was no clear distinction in some of the papers examined. The tag *Any* was given to papers analyzing the whole community including more than one macrophyte growth form present in the study area. Under *Study type*, *field/lab* refers to whether traits were measured from samples of plants grown under natural conditions (field) or grown in manipulated conditions (laboratory). Reviews were listed separately (e.g., Colmer et al., 2011; Heino et al., 2015). For *Species number* we chose three categories defined based on preliminary check of the selected papers, in order to distinguish those papers addressing specific questions to single or very few species (tag *1to3*), papers considering a limited number of species (*4to6*) and lastly papers studying more than 6 species (tag *>6*), which may be representative of the whole community.

The *Functional traits* considered by the papers where classified into 10 categories: *Growth form*, when this was considered as a variable relevant for the issue investigated; *Morphology*, including measures of the size and plant structure (e.g., height, stem diameter, root length); *Productivity*, related to fresh and dry weight and biomass allocation, together with growth rates measured on a biomass basis; *Physiology* includes traits related to physiological processes like photosynthesis, respiration and enzyme activity (pigment content is also included in this group); *Biochemistry* refers to the elemental composition of tissues, namely content of C, N, P or other elements; the traits included in *Reproduction* concern any feature related to vegetative or sexual reproduction (e.g., number of flowers, seed size, number of vegetative propagules); *Ecological preferences* take into consideration indexes like the Ellenberg indicator values applied to identify the plant niche along environmental gradients (Ellenberg et al., 2003); the category *Biomechanical* traits includes plant features linked to the resistance to mechanical stress, like wind, waves or water flow velocity. Typical measured traits are flexural rigidity and flexural strain (Łoboda et al., 2018, 2019). *Biotic interactions* identify traits related to the nutrient uptake strategy facilitated by other organisms, which may be mycorrhizal fungi or bacteria (see Cornelissen et al., 2003). In this category we did not include traits that can determine other types of interactions, such as the elemental composition of tissues or the dry matter content, which are already mentioned in previous groups. The last category (*Other*) includes all other traits.

Shoot or root FTs points out whether the papers dealt with only aboveground or belowground traits or with both types: belowground traits were those measured specifically on roots or rhizomes, while aboveground traits were those measured on stems, leaves and reproductive organs. As for pleustophytes, when biomass was provided, it was considered a shoot trait unless a distinction between shoot and root biomass was made. Papers were also scanned for *Main environmental variables* that were measured and related to the functional traits. They were in turn classified into: *Water*, including physical and chemical parameters of the water column like temperature, pH or nutrient concentration; *Sediment* characteristics such as granulometry or organic matter content; *Climate*, concerning meteorological variables together with changes in the atmospheric composition (e.g., increased CO_2); *Anthropic* refers to the influence of anthropic activities, for example land use and pollution; the tag *Depth/light* addresses specifically the effect of a reduction of available radiation both because of shading or increased water depth, while *Hydrology/topography* includes the information on the hydrologic regime or physical habitat characteristics. Papers were finally assigned to one or more of the seven *Main topic* categories: *Environmental gradients* groups papers addressing how community or species traits vary with relation to one or more environmental variable; *Community structure* studies include questions on the mechanisms that rule the interactions among plant species and how different species occupy space within the community; *Anthropic pressure* refers to the studies that investigate the effect of pollution, habitat degradation and climate change on plant traits; the topic *Biotic interactions* explores the effect of plant traits on other organisms both above and belowground, including phytoplankton, bacteria and fungi, as well as interactions with herbivores; *Invasiveness* clearly refers to studies investigating relationships between traits and potential invasiveness and management implications; *Species characteristics* is a broad category that was assigned to studies investigating relationships among functional traits of single or few species, without the aim of finding any relation with other variables. The last topic (*Other*) includes all other questions.

3. General findings

The first functional trait-based studies on macrophytes were published in the late 1960s and the trend is so far considerably increasing, with the majority of the papers being published in the last ten years (520 out of 738, equal to 70% of total publications; Fig. 1). In this review, the papers published between 2010 and 2020 were screened for relevance. Of these, 296 papers were considered relevant and included in this study (40% of initial set of papers; Tables S1, S2). Most of the studies were carried out in Europe (41.4% of the total amount of papers considered) and Asia (31.5%), followed by North and South America, and only very little attention was given to this topic in Oceania and Africa (Fig. 2a). As for the habitat type, lakes are the most investigated (30%), but also lotic environments and wetlands received considerable attention (21.1% and 20%, respectively) (Fig. 2b). Authors dedicated most of their attention specifically to submerged (39.0%) and emergent macrophytes (29.9%) rather than free-floating ones (8.8%). However, there is a noticeable number of papers (71 papers, 22.3%), which dealt with all three growth forms (Fig. 3a). Studies were equally divided into field and lab studies (44% and 42.3%, respectively) and 16 studies used a combined approach of controlled and field experiments (Fig. 3b). Within the period considered in this study, 24 review papers concerning some delineated aspects of functional traits were published (ID number highlighted in bold in Table S3). However, the aim of these papers was not to provide a general framework as in this review.

Besides, considering the number of species studied in each paper, the vast majority of the studies focused on 1 to 3 species (57.3%), and about a third (32.5%) on more than 6 species.

The most investigated functional traits categories are *Morphology* (27.7% of the papers), *Productivity* (22.6%), *Reproduction* (13.7%) and *Physiology* (12.2%; Fig. 4a). Traits are measured in most cases on the aboveground portion of the plant (57.4%) and often also on belowground organs (38.4%). Only 12 studies focused exclusively on *Root traits*. Among the environmental variables related to macrophyte traits, *Water* parameters are the most frequently studied (34.2%), followed by *Depth* and *Light* (17.7%), *Hydrology* and *Topography* parameters (15.2%) and sediment characteristics (14.1%) (Fig. 4b). As for the main topics, *Environmental gradients* have received by far the greatest attention (30.4%); other importantly explored topics are related to *Anthropic activities*, namely anthropic pressure (18.2%) and *Invasiveness* (14.7%).

4. Analysis of current research trends

4.1 Geographic distribution

Europe is the continent showing the greatest number of studies on macrophyte functional traits (Fig. 2a). Research groups are well spread around the countries and we can list examples from all Europe (e.g., Mermillod-Blondin and Lemoine (2010) in France; Anjum et al. (2013) in Portugal; Villa et al. (2017) in Italy; Lindholm et al. (2020) in Finland). The same cannot be said for Asia, the second continent for number of studies, where China accounts for most of the publications and very few studies have been carried out outside China (e.g., Kato and Kadono (2011) and Amano et al. (2012) in Japan; Bashir Shah et al. (2014) in India). The other continents lay far below in the list, but we noted emerging studies in the Brazilian wetlands present along the Amazon basin (e.g., Delatorre et al., 2019; Catian et al., 2018). Studies conducted in Oceania mainly concern the topic of invasive species, for example the research on effective management actions (Eller et al., 2015; Ellawala Kankanamge et al., 2019) or the impact of disturbance due to anthropic activities on native and invasive species (Mouton et al., 2019). Similar topics related to invasiveness can be found also in African studies (Venter et al., 2017), together with studies investigating community assembly rules in South African wetlands (Sieben and Le Roux, 2017).

4.2 Habitat type

Lakes result as the most studied habitat, which in part mirrors the wide number of studies conducted in Chinese lakes (e.g., Xing et al., 2016; Wang et al., 2017; Fu et al., 2018; Su et al., 2019; Fig. 2b). Here, shallow lakes have been chosen to investigate the effect of water depth on macrophyte population stability and traits intraspecific variability (Fu et al., 2018; Zhou et al., 2019) and wind disturbance combined with eutrophication effects on traits (Zhu et al., 2018a), or the drivers influencing functional diversity in different macrophyte communities (Fu et al., 2019a,b). After lakes, lotic environments and wetlands are roughly equally studied. In both environments, aspects related to the hydrologic regime are particularly investigated, namely the effects of water level changes and water flow disturbance on biomechanical or life history traits (e.g., Colmer et al., 2011; Miler et al., 2014) or the relationship between sediment properties and plant performance (Sutton-Grier and Megonigal, 2011). Papers belonging to the category *Any habitat* include some reviews (e.g., the review by Schultz and Dibble, 2012), focusing on how invasive macrophytes may influence fish and macroinvertebrates communities, the paper by Eckert et al. (2016) on the consequences of clonal and sexual reproduction for aquatic plants, or the review by Schoelynck and Struyf (2016) exploring the role of silicon as a trait for aquatic vegetation, and many studies on single species, in which samples are collected for trait measurements in several environments where the species of interest was found (e.g., Efremov et al., 2015; Kwong et al., 2017).

4.3 Macrophyte type

All macrophyte growth forms (e.g., Korol and Ahn, 2016; Dong et al., 2017; Huang et al., 2018) have been well represented in the trait-based studies we analyzed, except for a lower number of studies regarding free floating species, a result that could be expected due to the relatively lower number of species included in this group (Chambers et al., 2008; Fig. 3a). These species have mainly been used to investigate responses to water contamination and possible uses of these plants in phytoremediation (Mesa et al., 2017; Pietrini et al., 2019) or aspects related to the dispersal and proliferation of highly invasive species like *Eichhornia crassipes* or *Pistia stratiotes* (Gao et al., 2012; Fan et al., 2013; Venter et al., 2017). On the other hand, submerged macrophytes represent the most studied growth form. They have been investigated for a variety of purposes, and in particular they were selected to investigate the responses to and effects on sediment properties (Lemoine et al., 2012; Zhu et al., 2012), or to explore the use of different forms of inorganic carbon to support underwater photosynthesis (Hussner and Jahns, 2014; Eller et al., 2015). Emergent macrophytes have also been widely explored, especially with a focus on trait plasticity in relation to water parameters and water level fluctuation (Demetrio et al., 2014; Stander et al., 2018) and responses to disturbance by wind or water flow (Cao et al., 2016; Wang et al., 2010).

4.4 Study type

Studies carried out under natural conditions or under controlled conditions (*field* and *laboratory* studies) are equally abundant in this research, however laboratory studies include almost exclusively papers considering only few species (Fig. 3b), and often try to explain the adaptation (i.e., intraspecific trait variability) of a species trait to changes in a certain environmental condition determined by biotic or abiotic factors (Nuttens et al., 2016; Silveira and Thiébaut, 2017; Thouvenot et al., 2017). Field studies tend to bypass intraspecific variability, and more often aim at detecting changes in the community trait composition, thus determined by a different species composition and relative abundance rather than due to variability at the species level (Fu et al., 2014a; Lindholm et al., 2020). 16 studies have used a dual approach to compare results obtained in the two experimental conditions or combine information from different kinds of experiments. For example, Kordyum et al. (2017) compared the aerenchyma formation and enzyme biosynthesis in two emergent species (*Sium latifolium* and *S. sisaroideum*), under natural and experimental conditions, and Paz et al. (2019) analyzed palatability traits to herbivores for three macrophyte species (*Egeria densa, Gymnocoronis spilanthoides, Ludwigia peploides*) in the laboratory, and later transplanted them in the field to assess actual consumption under natural conditions. Among the 24 reviews scrutinized, the topic of invasive species is very common: traits were used to explain the effects of invasive species on the ecosystem and on interactions among the components (Strayer, 2010) or for the redaction of risk assessments based on functional traits (Gordon et al., 2012; Azan et al., 2015). Other topics debated in these reviews are linked to specific questions such as the response of aquatic vegetation to abiotic factors (Bornette and Puijalon 2011), the role of silica in aquatic plants (Schoelynck and Struyf, 2016) or effects of water level fluctuations (Carmignani and Roy, 2017). Root functional traits were taken into consideration in 11 out of 24 review papers: Fusconi and Mucciarelli (2017) explored arbuscular mycorrhiza, while the most extensive review we found on root functional traits is by Ali et al. (2019), focusing on nutrients and heavy metal abatement.

4.5 Trait category

We observed that *Morphology* and *Productivity* traits are the most investigated among the analyzed papers and show an increasing trend in the last four years (Fig. 4a). Many of these traits are considered "soft traits", relatively cheap and easy to measure in the field, such as leaf area or plant height (Cornelissen et al., 2003), which make them a good choice for field studies at the community level, and are also available for many species in online databases. They are often used to compute indices that synthetize functional characteristics within a community, such as the "functional trait diversity" index (FD_Q) and functional beta diversity, the "community weighted means" index (CWM), the SES_{MPD}, namely the standardized effect size of abundance-weighted mean pairwise distances between species for each trait (Fu et al., 2014a, 2019b; Lukács et al., 2019). These metrics all take into consideration both trait values and species abundance within the community. In this sense, researchers are not interested in catching the trait variability at the species level, rather they use traits as an indication of the mean species characteristics, thus revealing the function of the species at the community scale: at this scale intraspecific variability is believed to have a negligible influence (e.g., Fu et al., 2014a; García-Girón et al., 2019b). *Morphology* and *Productivity* traits often appear together in studies, because they include traits describing the leaf and plant economic spectrum, along with elemental composition (e.g. Specific Leaf Area, Leaf Area, Leaf Dry Matter Content, Leaf Nitrogen Content, Specific Root Length, Leaf Area Index) (e.g., Pierce et al., 2012; Li et al., 2019a). The economic spectrum is considered explicative of existing trade-offs between, for example, growth and tissue construction; its strength may vary along an environmental gradient and in turn it influences the ecosystem functions (Díaz et al., 2004, 2016). These trait categories have been applied to the most disparate research purposes other than the insight into community assembly rules and community responses to environmental conditions, such as in the response to anthropic activities like the introduction of invasive species and pollution. For instance, Chmura and Molenda (2012) evaluated the phenology and growth response of three emergent species (*Phragmites australis*, *Scirpus sylvaticus*, and *Typha latifolia*) to thermally polluted water, and Thiébaut et al. (2017) used these morphology and productivity traits, along with tissues elemental composition, to assess palatability to gammarid herbivores in two invasive species, *Elodea canadensis* and *E. nuttallii*. Such studies addressing more specific ecological questions often take into consideration also the trait plasticity, as mentioned above, in order to understand what are the factors that determine the variability at the species level (e.g., Xie and Yu, 2011b; Glover et al., 2015). *Reproduction* traits have been widely used to investigate dispersal abilities, how they are affected by environmental conditions and how they influence the community structure (Qian et al., 2014). In this context, Chmara et al. (2015) found a strong relationship between traits (including *Reproduction* and *Morphology* traits) and the acidity gradient, demonstrating the importance of carbon availability in determining aquatic plants performance. *Reproduction* and growth-related traits have also been used to detect differences in growth strategies and resource allocation between sexes in the dioecious species *Vallisneria spinulosa* (Li et al., 2019b). *Physiology* traits are very often measured in what we defined *laboratory* studies, because they are often more expensive and time-consuming to measure directly in the field (e.g., Saha et al., 2016; Tang et al., 2018). Besides, physiology-related measurements are very sensitive to changes in environmental conditions, which can be difficult to control when in the field and bias the response of plants to defined treatments, e.g., photosynthesis efficiency under different levels of CO_2 (Hyldgaard and Brix, 2012). Again, a widespread purpose for the use of these traits was the assessment of effects of pollution and climate change: photosynthetic and enzymatic responses to specific pollutants like cadmium (Huang et al., 2017; Liu et al., 2017), copper (Roubeau Dumont et al., 2019), herbicides (Nuttens et al., 2016) and perfluoroalkyl substances (Pietrini et al., 2019) were investigated. *Physiology* traits and especially photosynthesis-related traits and allelopathic activity have been used to understand the advantages of invasive species that lead to their successful competition against natives, in the context of increasing temperatures and CO_2 availability (Thouvenot et al., 2015; Gillard et al., 2017). To this regard, the recent development of innovative instruments (i.e., more portable and less expensive) for measuring chlorophyll fluorescence (Kuhlgert et al., 2016; Chen et al., 2019; Gomez-Sanchez et al., 2019) should enable the collection of larger amount of data on some synthetic metric of physiological performance (e.g., photosynthetic yield) allowing for the extent of physiology traits studies. Interactions with herbivores were often studied using a combination of traits that describe the palatability of a species: usually these traits include the elemental composition of tissues, the phenolic content, and the Plant Dry Matter Content or Leaf Dry Matter Content, in order to detect differences in the response to herbivores between native and invasive species and outline a possible management solution against invasive species, and understand the reasons for their successful competition (Grutters et al., 2016; Thiébaut et al., 2017), or to determine the effects of the introduction of invasive herbivores, so that the choice of poorly palatable species in restoration action can prevent the spread of herbivores (Yam et al., 2016). Similarly, relations with herbivores and palatability traits are used to identify the most suitable (e.g., less palatable) species to introduce in constructed wetlands and other restoration actions (Paz et al., 2019). On the other hand, the least investigated traits directly describing *Biotic interactions* in terms of relations with bacteria and fungi as an uptake strategy. We found only four papers focusing on this subject, of which three are reviews that discuss the role and importance of traits describing the interactions with bacteria (Bornette and Puijalon, 2011) or mycorrhiza (Fusconi and Mucciarelli, 2018; Ali et al., 2019). The only study we found that experimentally measured bacterial associations is by Rejmánková et al. (2011), who attempted to explore plant strategies for phosphorus uptake and related phosphatase activity to bacteria associated to roots. In general, as we mentioned above, root traits have been quite understudied. Within our research there are several papers (n = 111) that deal with combined shoot and root traits, however, most of the time they principally concern root biomass, to calculate the root-shoot ratio (e.g., Fu et al., 2013; Hussner and Jahns, 2014; Dong et al., 2017).

4.6 Multi-scale trait patterns

Exploring plant functional variability at different scales in both spatial (from community to ecosystem, up to landscape) and temporal (from daily to seasonal dynamics, up to long-term changes) dimensions requires an approach that is at the same time effective and feasible (Abelleira Martinez et al., 2016; Anderson, 2018). Remote sensing provides high-throughput data and techniques that can be translated into quantitative metrics related to vegetation features and overcome logistic and economic constraints of directly measuring most of the plant species inhabiting all biomes (Jetz et al., 2016; Gamon et al., 2019). Remote sensing applications to trait-based vegetation studies have shown an increasing trend during the last couple of decades (Homolová et al., 2013; Wang and Gamon, 2019), with a particular focus on terrestrial plant communities, especially in forest and grassland ecosystems (e.g., Asner et al., 2015; Schneider et al., 2017; Schweiger et al., 2018), but some studies on aquatic plants have recently emerged, implementing and extending *in situ* measurements (Villa et al., 2014, 2017).

In our research, we found 9 papers applying remote sensing techniques to macrophyte studies, focusing in particular on floating and emergent growth forms. Interactions between light and plant canopy elements, in particular reflectance and transmittance due to leaves, shape vegetation spectral response; these interactions result in a strong link between anatomical and biochemical properties (Leaf Pigments Content, Specific Leaf Area, Leaf Tissue Density) and optical properties (Klančnik et al., 2014; Klančnik and Gaberščik, 2016), which in turn can be exploited to model the performance and productivity of macrophytes stands (Liu et al., 2011). For example, Wang et al. (2012) used indices obtained from multispectral remote sensing data (Normalized Difference Vegetation Index and Vegetation-Water Index) to classify vegetation functional types in relation to water level dynamics. An approach based on remote sensing has found application also in the determination of traits favoring invasion success: Santos et al. (2012) used airborne imaging data to compare pigments and light use efficiency of native and non-native submerged species, and Tóth et al. (2019) characterized morphological and physiological traits with leaf reflectance for autochthonous and allochthonous emergent species. The contribution of remote sensing data in this context allows for a larger scale sampling and a prompter evaluation of seasonal variability of the macrophytes stands (Tóth et al., 2019). Reflectance and transmittance spectra of floating-leaved species were also measured as specific traits that influence light availability in the water column and then alter the environmental conditions underneath the water surface, and these properties can be explained by species exhibiting different morphological and biochemical leaf traits (Klančnik et al., 2018).

4.7 Species covered

The papers included in our review have applied functional traits to a total amount of 1124 aquatic *taxa*, which were in most cases identified to the species level, but for few studies the identification reached only the genus level (e.g., Molnár et al., 2015; Cao et al., 2016; Cornacchia et al., 2019). Some papers included also terrestrial species (Zhang et al., 2017; Dalle Fratte et al., 2019), but they were not considered in the evaluation of the diversity of species studied in this review. The world macrophyte species diversity has been estimated to count on 3457 species (Murphy et al., 2019), so our study revealed that in the last ten years about one third of the total macrophyte diversity has been explored in terms of functional traits. However, if we consider only the two categories of papers that focused on up to six species, the *taxa* investigated are only 213. This suggests that specific ecological questions have been asked only on a very limited portion of the total macrophyte diversity, while most of the diversity is explored in the context of vast community studies (e.g., Monção et al., 2012; Török et al., 2013), in which mainly "soft traits" are used (e.g., morphology traits), even if it is "hard traits" (e.g., physiology traits) that could be more explicative of plant functionality (*sensu* Hodgson et al., 1999; Cornelissen et al., 2003), although more difficult and expensive to measure. According to our results, the ten most studied species are: *Myriophyllum spicatum* (63 papers), *Ceratophyllum demersum* (52 papers), *Potamogeton crispus* (41 papers), *Stuckenia pectinata* (40 papers), *P. australis* (39 papers), *E. canadensis* (35 papers), *Potamogeton perfoliatus* (31 papers), *Lemna minor* (30 papers), *Hydrilla verticillata* (28 papers) and *Persicaria amphibia* (28 papers). Common applications of traits for these species include the research of features determining plant palatability, physiological adaptations in response to eutrophication and the presence of contaminants, and plant adaptations to hydrological stress (Table 1, Table S4). Most of these species were well represented both in community studies and in specialized experimental studies: for *M. spicatum* see Thouvenot et al. (2019) and Fu et al. (2020); for *C. demersum* see Fu et al. (2017) and Sun et al. (2018); for *P. australis* see Yam et al. (2016) and Sikorska et al. (2017). However, species belonging to the genus *Potamogeton*, including *S. pectinata*, although widely spread across aquatic plant communities, were very poorly represented in the latter category of studies (3, 2, and 1 papers, respectively; Amano et al., 2012; Gillard et al., 2017; Riis et al., 2018; Zhu et al., 2018a; Zhang et al., 2019; Pätzig et al., 2020), indicating a need for further examination of their functionality.

4.8 Connections among topics

If we consider how papers are connected with each other in terms of the examined categories and topics, it is quite difficult to observe distinct clusters of narrative trends: most subjects are quite evenly linked with each other (Fig. 5). However, it is still possible to detect at least one strong narrative trend, which, to some extent, had already emerged in the above discussed paragraphs: studies that investigate the topic of environmental gradients mainly use morphology and productivity traits measured in field, with a notable portion of laboratory studies on submerged species (and less frequently on emergent ones), and relate these traits to water parameters especially in lakes, covering sites located in Asia and Europe. This pattern is consistent with the most studied features observed for each category (Figs. 2 to 4). The works of a group of scientists of the Chinese Academy of Sciences from Wuhan and Beijing are emblematic of this trend (e.g., Fu et al., 2013; Zhu et al., 2018a,b; Su et al., 2019). For example, Su et al. (2019) investigated how plant size and biomass of submerged species could establish feedbacks determining water transparency in subtropical shallow lakes. In this case, they found that small, bottom dwelling macrophytes were more effective in maintaining water transparency because they impeded more efficiently sediment resuspension, and released more oxygen to the water column, thus probably contributing to phosphorus immobilization. Overall, the pattern of connections among features shows that the topic of environmental gradients has been exhaustively explored and linked to nearly all the subjects we considered in this review (Fig. 5). Other topics do not show the same amount of coverage: for instance, "anthropic pressure" and "invasiveness" are strongly linked only to water parameters, among all environmental variables. Nevertheless, sediment or hydrology characteristics, have been demonstrated to be fundamental in determining the variability of root (Ali et al., 2019) and shoot traits (Zhu et al., 2018a), and therefore plant function in the ecosystem, especially in the context of invasive species (Venter et al., 2017). On the other hand, we mentioned root traits received far less attention than shoot traits, and we therefore suggest implementing the integration between root traits and sediment characteristics in future studies. At the same time, the topic of invasiveness has been studied mainly from the point of view of morphology and productivity traits, setting aside reproduction traits. Although vegetative propagation seems to be the main mechanism of spreading of aquatic invasive species (Bashir Shah et al., 2014; Urban and Dwyer, 2016), sexual reproduction may also be important in spreading dynamics. This could either lead to loss of genetic diversity, due to hybridization with native species, or higher vigor to hybrids in case of hybridization with non-natives, as observed for *Ludwigia* spp. in Brazil (Thouvenot et al., 2013b). Moreover, Kwong et al. (2017) found that fruit weight and fruit number in *Sagittaria platyphylla* was higher in introduced ranges than in native habitats, due to the absence of specialist herbivores. This work suggests the importance of evaluating the effects of biotic interactions on various traits categories and not only on biochemistry and productivity, as in most papers analyzed here (e.g., Grutters et al., 2016; Jiménez-Ramos et al., 2018). Reproduction traits resulted the third most studied trait category, however it does not keep the same position as for number of links, being related mainly only to the topics of environmental gradients and anthropic pressure (Fig. 5). Finally, we observed that the two continents that count the highest number of papers are not equally connected to all the subjects considered in this review: on one side Asian studies mostly stick to the most common pattern of lake studies on plant responses to water parameters, and on the other European studies basically encompass all the other subjects; the rest of continents are extremely underrepresented.

5. A research agenda

What emerges from this systematic review is that the use of functional traits in aquatic botany studies enormously increased in recent years (almost doubling in the last 5 years compared to the period 1969-2014). Indeed, researchers have long been dealing with macrophytes functional characteristics: see for example the works on the macrophyte productivity by Hogeland and Killingbeck (1985) or plant strategies by Murphy et al. (1990). However, only recently this research field has benefited from a standardization of measurements and a sharing of the information collected in online databases. Although so far, studies have been very heterogeneous in their purposes and methods, highlighting the vast range of the research fields that can be investigated using a functional trait approach, here we tried to offer a unified perspective. This allows researchers to identify a few aspects that can be represent a starting point for future developments in studying traits applied to macrophytes:

i. In the papers examined in this review, sediment characteristics have been associated to traits almost as often as other parameters like hydrology or water depth and light availability, confirming the importance of substrate type influencing plant traits (Xie and Yu, 2011a; Anjum et al., 2015) and performance (Bolpagni and Pino, 2017). Roots of aquatic plants colonize the sediment and so they represent the plant interface between the water column and the rhizosphere, and although aquatic plants are able to absorb nutrients from shoots as well, roots are not only passive organs in charge of ensuring anchorage to the substrate, but they have an active role in determining plant performance (Huang et al., 2018; Moe et al., 2019). However, we noticed a consistent lack of interest towards root traits, except for root biomass and number (e.g., Glover et al., 2015; Silveira and Thiébaut, 2017), whereas much less attention has been given to anatomy and physiology traits such as root lacunal volume and different tissues proportions, elemental composition, exudates and uptake strategies, which could reveal crucial implications for a deeper understanding of macrophytes functions (Kordyum et al., 2017; Ali et al., 2019). Again, we believe that traits related to root biotic interactions (we refer to bacterial and mycorrhizal associations) should receive further attention, because of their potential in influencing plant functioning (Rejmánková et al., 2011; Fusconi and Mucciarelli, 2019). It has been demonstrated that structural and physiological root traits play an important role in influencing other levels of biotic interactions, so their collection should be implemented: for example, root density was related to plant ability to regrow after herbivores damage (Wood et al., 2018). Therefore, we would like to stress the need of further collection and processing of macrophytes root traits and the study of the relationships with sediment characteristics, in view of a change of perspectives, which will see plant roots as major actors of life dynamics and not only as shoot subordinates.

ii. A main goal for future studies in this field will be to effectively capture the complexity that is intrinsic in natural systems dynamics, especially in aquatic ecosystems. The environmental heterogeneity characterizing macrophytes habitat, connected with their high phenotypic plasticity (Vivian-Smith, 1997), results in fine-scale patchiness of aquatic plant communities, and disentangling trait variability among and within species in more than few ecosystems would require an amount of data impossible to collect in the field using traditional data collection techniques. Integrating remote sensing into the functional measurements and monitoring pipeline can enable the effective upscaling of some relevant community traits (Anderson, 2018), especially for emergent or floating-leaved species, thus helping to study the spatial variability of functional traits across systems, and its links with ecological processes (Funk et al., 2017). Furthermore, for submerged macrophytes acoustic systems (i.e., side-scan sonar, echo sounders, and multibeam sonar) can expand the range of application of optical methods providing high-resolution, 3D data to delineate the underwater patterns of macrophytes (Bučas et al., 2016; Mizuno et al., 2018). The multiple roles of macrophytes are well known and they state that macrophytes, as primary producers, do not live in isolation but they constantly interact with the other biotic and abiotic components (O'Hare et al., 2018). It will be essential to deepen our understanding of these interactions by applying traits-oriented frameworks, e.g., the Biodiversity-Ecosystem Functioning approach (Tilman and Dowing, 1994), in order to have a more complete view of ecosystems functioning, avoiding separating different compartments during the assessment.

iii. Invasive species represent one of the main threats to biodiversity and ecosystem functioning that aquatic habitats are facing in recent years (Strayer, 2010; Bolpagni et al., 2015; Rumlerová et al., 2016). Biological invasions correspond indeed to one of the most investigated topics among the papers we analyzed; however, we noticed some research gaps in this field, related to the type of traits studied and the environmental parameters associated. We promote the extension of these studies to other functional traits besides morphology, productivity and elemental composition, since there is evidence that also physiological and reproduction traits play an important role in non-native species establishment and colonization success (Kwong et al., 2017; Tóth et al., 2019). Moreover, the role of traits in invasive species has seldom been associated to environmental variables other than water chemical and physical parameters, although other parameters have been demonstrated relevant effects, such as light availability, in driving competition with native species, especially in the first phases of establishment (Ellawala Kankanamge et al., 2019), and hydrology parameters, in determining important consequences in propagule dispersion and plant resistance to variable water regimes (Urban and Dwyer, 2016; Zhang et al., 2016). Remotely sensed data, allowing quantitative, standardized measures of specific traits (Tóth et al., 2019), can make the allochthonous *vs*. autochthonous species comparison feasible across scales and sites, thus facilitating the assessment of environmental drivers for invasiveness (Rocchini et al., 2015; Niphadkar and Nagendra, 2016), at least for floating and emergent plants. We also encourage the investigation of invasive species and their biotic interactions, focusing in detail on the effects of specialist herbivores rather than generalists and on their foraging strategy (e.g., foraging on meristems and flowering organs rather than on mature leaves), which could be more effective in the control of invasive alien aquatic plants (Grutters et al., 2016).

iv. One of the main purposes of trait-based studies should be to allow for comparisons at multiple scales, as wide as possible. However, our review highlights how most of the recent research in the context of aquatic macrophytes has been carried out in Europe and China, while entire continents like Africa and Oceania have been almost neglected. Besides, very little attention has been given to some important hotspots of macrophyte biodiversity, like Brazil, which alone hosts more than one fifth of the global macrophyte species pool (Murphy et al., 2019). The same study from Murphy et al. (2019) divided the globe into squares of 10x10° latitude x longitude in order to evaluate global macrophyte diversity, and it states the urgency of not neglecting any part of the world, since all the squares contained at least 55 different species. It is then clear how global research on macrophyte functional traits is omitting some of the regions hosting the highest diversity. In this context, collaboration within the scientific community is essential in order to share the expertise and reach a faster advance in macrophyte functional traits research. The pledge of favoring a wider and immediate collaboration has already been launched in the context of carbon emissions from inland aquatic habitats (Marcé et al., 2019), and we believe that this concept is particularly fitting our field as well. Moreover, mapping data retrieved from remote sensing can increase the resolution of current knowledge we have on plant diversity, by improving the spatial scale of analysis where trait data available are already abundant, and providing a mean to fill gaps where species or traits data are scarce (Jetz et al., 2016).

Authors' statement

ADV and RB conceptualized the study. Literature inspection was carried out by ADV. All authors discussed the results. ADV led the writing of the original draft. All authors contributed critically to the drafts and gave final approval for publication. Alice Dalla Vecchia (ADV), Paolo Villa (PV), Rossano Bolpagni (RB)

Supplementary data

Table S1 – Summary analysis data matrix of the 296 reviewed papers. Table S2 – Revision matrix summarizing the information obtained from the 296 papers analysed. The absolute and relative representativeness of each category within each feature is presented. Table S3 - List of the 296 papers analysed for the review. The identification number (ID, first column) and the year of publication (second column) are used in the summary matrix provided in Table S1. Reviews IDs are highlighted in bold. Table S4 – Extension of Table 1 showing the functional traits and applications for the ten most studied species, including references. On the same line, traits and corresponding ecological questions addressed are marked. Only paper studying *1to3* species were included in this table.

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References

Abelleira Martínez, O.J., Fremier, A.K., Günter, S., Ramos Bendaña, Z., Vierling, L., Galbraith, S.M., Bosque-Pérez, N.A., Ordoñez, J.C., 2016. Scaling up functional traits for ecosystem services with remote sensing: concepts and methods. Ecol. Evol. 6, 4359–4371. https://doi.org/10.1002/ece3.2201

Ali, F., Jilani, G., Fahim, R., Bai, L., Wang, C., Tian, L., Jiang, H., 2019. Functional and structural roles of wiry and sturdy rooted emerged macrophytes root functional traits in the abatement of nutrients and metals. J. Environ. Manage. 249, 109330. https://doi.org/10.1016/j.jenvman.2019.109330

Amano, M., Iida, S., Kosuge, K., 2012. Comparative studies of thermotolerance: Different modes of heat acclimation between tolerant and intolerant aquatic plants of the genus *Potamogeton*. Ann. Bot. 109, 443–452. https://doi.org/10.1093/aob/mcr300

Anderson, C.B., 2018. Biodiversity monitoring, earth observations and the ecology of scale. Ecol. Lett. 21, 1572–1585. https://doi.org/10.1111/ele.13106

Anjum, N.A., Ahmad, I., Válega, M., Figueira, E., Duarte, A.C., Pereira, E., 2013. Phenological development stages variation versus mercury tolerance, accumulation, and allocation in salt marsh macrophytes *Triglochin maritima* and *Scirpus maritimus* prevalent in Ria de Aveiro coastal lagoon (Portugal). Environ. Sci. Pollut. Res. 20, 3910–3922. https://doi.org/10.1007/s11356-012-1336-8

Anjum, N.A., Ahmad, I., Válega, M., Pacheco, M., Figueira, E., Duarte, A.C., Pereira, E., 2012. Salt marsh macrophyte *Phragmites australis* strategies assessment for its dominance in mercury-contaminated coastal lagoon (Ria de Aveiro, Portugal). Environ. Sci. Pollut. Res. 19, 2879–2888. https://doi.org/10.1007/s11356-012-0794-3

Armitage, D.W., Jones, S.E., 2019. Negative frequency-dependent growth underlies the stable coexistence of two cosmopolitan aquatic plants. Ecology 100, 1–12. https://doi.org/10.1002/ecy.2657

Asner, G.P., Martin, R.E., Anderson, C.B., Knapp, D.E., 2015. Quantifying forest canopy traits: Imaging spectroscopy versus field survey. Remote Sens. Environ. 158, 15–27. https://doi.org/10.1016/j.rse.2014.11.011

Molnár, V.A., Tóth, J.P., Sramkó, G., Horváth, O., Popiela, A., Mesterházy, A., Lukács, B.A., 2015. Flood induced phenotypic plasticity in amphibious genus *Elatine* (*Elatinaceae*). PeerJ 3, e1473. https://doi.org/10.7717/peerj.1473

Azan, S., Bardecki, M., Laursen, A.E., 2015. Invasive aquatic plants in the aquarium and ornamental pond industries: A risk assessment for southern Ontario (Canada). Weed Res. 55, 249–259. https://doi.org/10.1111/wre.12135

Bakker, E.S., Sarneel, J.M., Gulati, R.D., Liu, Z., van Donk, E., 2013. Restoring macrophyte diversity in shallow temperate lakes: biotic versus abiotic constraints. Hydrobiologia 710, 23–37. https://doi.org/10.1007/s10750-012-1142-9

Barks, P.M., Laird, R.A., 2015. Senescence in duckweed: Age-related declines in survival, reproduction and offspring quality. Funct. Ecol. 29, 540–548. https://doi.org/10.1111/1365-2435.12359

Bashir Shah, A., Reshi, Z.A., Shah, M.A., 2014. Clonal trait diversity in relation to invasiveness of alien macrophytes in two Himalayan Ramsar sites. J. Veg. Sci. 25, 839–847. https://doi.org/10.1111/jvs.12143

Boiché, A., Lemoine, D.G., Barrat-Segretain, M.H., Thiébaut, G., 2011. Resistance to herbivory of two populations of *Elodea canadensis* Michaux and *Elodea nuttallii* Planchon St. John. Plant Ecol. 212, 1723–1731. https://doi.org/10.1007/s11258-011-9944-9

Bolpagni, R., Pino, F. 2017. Sediment nutrient drivers of the growth dynamics of the rare fern *Marsilea quadrifolia*. Hydrobiologia 792, 303–314. https://doi.org/10.1007/s10750-016-3064-4.

Bolpagni, R., Laini, A., Stanzani, C., Chiarucci, A., 2018. Aquatic plant diversity in Italy: Distribution, drivers and strategic conservation actions. Front. Plant Sci. 9, 116. https://doi.org/10.3389/fpls.2018.00116

Bolpagni, R., Laini, A., Soana, E., Tomaselli, M., Nascimbene, J., 2015. Growth performance of *Vallisneria spiralis* under oligotrophic conditions supports its potential invasiveness in mid-elevation freshwaters. Weed Res. 55, 185–194. https://doi.org/10.1111/wre.12128

Bolpagni, R., Poikane, S., Laini, A., Bagella, S., Bartoli, M., Cantonati, M., 2019. Ecological and conservation value of small standing-water ecosystems: A systematic review of current knowledge and future challenges. Water 11, 402. https://doi.org/10.3390/w11030402

Bolpagni, R., Pierobon, E., Longhi, D., Nizzoli, D., Bartoli, M., Tomaselli, M., Viaroli, P., 2007. Diurnal exchanges of CO_2 and CH_4 across the water–atmosphere interface in a water chestnut meadow (*Trapa natans* L.). Aquat. Bot. 87, 43–48. https://doi.org/10.1016/j.aquabot.2007.02.002

Bornette, G., Puijalon, S., 2011. Response of aquatic plants to abiotic factors: A review. Aquat. Sci. 73, 1–14. https://doi.org/10.1007/s00027-010-0162-7

Bresciani, M., Bolpagni, R., Braga, F., Oggioni, A., Giardino, C., 2012. Retrospective assessment of macrophytic communities in southern Lake Garda (Italy) from in situ and MIVIS (Multispectral Infrared and Visible Imaging Spectrometer) data. J. Limnol. 71, 180-190. https://doi.org/10.4081/jlimnol.2012.e19

Bučas, M., Šaškov, A., Šiaulys, A., Sinkevičienė, Z., 2016. Assessment of a simple hydroacoustic system for the mapping of macrophytes in extremely shallow and turbid lagoon. Aquat. Bot. 134, 39-46. https://doi.org/10.1016/j.aquabot.2016.06.009

Cantonati, M., Poikane, S., Pringle, C.M., Stevens, L.E., Turak, E., Heino, J., Richardson, J.S., Bolpagni, R., Borrini, A., Cid, N., Čtvrtlíková, M., Galassi, D.M.P., Hájek, M., Hawes, I., Levkov, Z., Naselli-Flores, L., Saber, A.A., Cicco, M.D., Fiasca, B., Hamilton, P.B., Kubečka, J., Segadelli, S., Znachor, P., 2020. Characteristics, Main Impacts, and Stewardship of Natural and Artificial Freshwater Environments: Consequences for Biodiversity Conservation. Water 12, 260. https://doi.org/10.3390/w12010260

Cao, Q.J., Liu, N., Wang, L., 2016. Relative response to mechanical stress of co-existing aquatic species, floating-leaved *Nymphoides peltata* and submerged *Myriophyllum spicatum*. Pakistan J. Bot. 48, 935–943.

Carmignani, J.R., Roy, A.H., 2017. Ecological impacts of winter water level drawdowns on lake littoral zones: a review. Aquat. Sci. 79, 803–824. https://doi.org/10.1007/s00027-017-0549-9

Catian, G., da Silva, D.M., Súarez, Y.R., Scremin-Dias, E., 2018. Effects of Flood Pulse Dynamics on functional diversity of macrophyte communities in the Pantanal wetland. Wetlands 38, 975–991. https://doi.org/10.1007/s13157-018-1050-5

CESTES. URL: https://icestes.github.io/ (accessed 06/07/2020)

Chambers, P.A., Lacoul, P., Murphy, K.J., Thomaz, S.M., 2008. Global diversity of aquatic macrophytes in freshwater. Hydrobiologia 595, 9–26. https://doi.org/10.1007/s10750-007-9154-6

Chen, S., Guo, Y., Sirault, X., Stefanova, K., Saradadevi, R., Turner, N.C., Nelson, M.N., Furbank, R.T., Siddique, K.H.M., Cowling, W.A., 2019. Nondestructive Phenomic Tools for the Prediction of Heat and Drought Tolerance at Anthesis in Brassica Species 2019.

Chmara, R., Banaś, K., Szmeja, J., 2015. Changes in the structural and functional diversity of macrophyte communities along an acidity gradient in softwater lakes. Flora Morphol. Distrib. Funct. Ecol. Plants 216, 57–64. https://doi.org/10.1016/j.flora.2015.09.002

Chmura, D., Molenda, T., 2012. Influence of thermally polluted water on the growth of helophytes in the vicinity of a colliery waste tip. Water. Air. Soil Pollut. 223, 5877–5884. https://doi.org/10.1007/s11270-012-1323-1

Colmer, T.D., Winkel, A., Pedersen, O., 2011. A perspective on underwater photosynthesis in submerged terrestrial wetland plants. AoB Plants 11, 1–15. https://doi.org/10.1093/aobpla/plr030

Cornacchia, L., Licci, S., Nepf, H., Folkard, A., van der Wal, D., van de Koppel, J., Puijalon, S., Bouma, T.J., 2019. Turbulence-mediated facilitation of resource uptake in patchy stream macrophytes. Limnol. Oceanogr. 64, 714–727. https://doi.org/10.1002/lno.11070

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380. https://doi.org/10.1071/BT02124

Dalle Fratte, M., Brusa, G., Pierce, S., Zanzottera, M., Cerabolini, B.E.L., 2019. Plant trait variation along environmental indicators to infer global change impacts. Flora Morphol. Distrib. Funct. Ecol. Plants 254, 113–121. https://doi.org/10.1016/j.flora.2018.12.004

Delatorre, M., da Cunha, N.L., Rodrigues, R.B., Damasceno-Júnior, G.A., Ferreira, V.L., 2019. Trait-environment relationship of aquatic vegetation in a tropical pond complex system. Wetlands. https://doi.org/10.1007/s13157-019-01189-0

Demetrio, G., Barbosa, M., Coelho, F., 2014. Water level-dependent morphological plasticity in *Sagittaria montevidensis* Cham. and Schl. (*Alismataceae*). Brazilian J. Biol. 74, S199–S206. https://doi.org/10.1590/1519-6984.26912

Díaz, S., Cabido, M., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. J. Veg. Sci. 9, 113–122. https://doi.org/10.2307/3237229

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., De Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-

Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg. Sci. 15, 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Dong, B., Qin, B., Li, W., Gao, G., 2017. Growth and community composition of submerged macrophytes in Lake Taihu (China): assessment of changes in response to sediment characteristics. Wetlands 37, 233–243. https://doi.org/10.1007/s13157-016-0861-5

Eckert, C.G., Dorken, M.E., Barrett, S.C.H., 2016. Ecological and evolutionary consequences of sexual and clonal reproduction in aquatic plants. Aquat. Bot. 135, 46–61. https://doi.org/10.1016/j.aquabot.2016.03.006

Efremov, A.N., Filonenko, A. V., Sviridenko, B.F., 2015. Anatomy and morphology of reproductive organs of *Stratiotes aloides* L. (*Hydrocharitaceae*). Inl. Water Biol. 8, 334–344. https://doi.org/10.1134/S1995082915040057

Ellawala Kankanamge, C., Matheson, F.E., Riis, T., 2019. Shading constrains the growth of invasive submerged macrophytes in streams. Aquat. Bot. 158, 103125. https://doi.org/10.1016/j.aquabot.2019.06.004

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., 2003. Zeigerwerte von Pflanzen in Mitteleuropa. Datenbank. Scripta Geobot. 18, 1-258.

Eller, F., Alnoee, A.B., Boderskov, T., Guo, W.Y., Kamp, A.T., Sorrell, B.K., Brix, H., 2015. Invasive submerged freshwater macrophytes are more plastic in their response to light intensity than to the availability of free CO_2 in air-equilibrated water. Freshw. Biol. 60, 929–943. https://doi.org/10.1111/fwb.12547

Fan, S., Liu, C., Yu, D., Xie, D., 2013. Differences in leaf nitrogen content, photosynthesis, and resource-use efficiency between *Eichhornia crassipes* and a native plant *Monochoria vaginalis* in response to altered sediment nutrient levels. Hydrobiologia 711, 129–137. https://doi.org/10.1007/s10750-013-1471-3

Fu, H., Yuan, G., Jeppesen, E., 2020. Trait-based community assembly of submersed macrophytes subjected to nutrient enrichment in freshwater lakes: Do traits at the individual level matter? Ecol. Indic. 110, 105895. https://doi.org/10.1016/j.ecolind.2019.105895

Fu, H., Yuan, G., Zhong, J., Cao, T., Ni, L., Xie, P., 2013. Environmental and ontogenetic effects on intraspecific trait variation of a macrophyte species across five ecological scales. PLoS One 8, e62794. https://doi.org/10.1371/journal.pone.0062794

Fu, H., Zhong, J., Yuan, G., Ni, L., Xie, P., Cao, T., 2014a. Functional traits composition predict macrophytes community productivity along a water depth gradient in a freshwater lake. Ecol. Evol. 4, 1516–1523. https://doi.org/10.1002/ece3.1022

Fu, H., Yuan, G., Li, W., Ge, D., Zou, D., Huang, Z., 2019a. Environmental effects on community productivity of aquatic macrophytes are mediated by species and functional composition. Ecohydrology 12, 1–9. https://doi.org/10.1002/eco.2147

Fu, H., Yuan, G., Lou, Q., Dai, T., Xu, J., Cao, T., Ni, L., Zhong, J., Fang, S., 2018. Functional traits mediated cascading effects of water depth and light availability on temporal stability of a macrophyte species. Ecol. Indic. 89, 168–174. https://doi.org/10.1016/j.ecolind.2018.02.010

Fu, H., Yuan, G., Jeppesen, E., Ge, D., Li, W., Zou, D., Huang, Z., Wu, A., Liu, Q., 2019b. Local and regional drivers of turnover and nestedness components of species and functional beta diversity in lake macrophyte communities in China. Sci. Total Environ. 687, 206–217. https://doi.org/10.1016/j.scitotenv.2019.06.092

Fu, H., Zhong, J., Yuan, G., Guo, C., Lou, Q., Zhang, W., Xu, J., Ni, L., Xie, P., Cao, T., 2015. Predicting changes in macrophyte community structure from functional traits in a freshwater lake: A test of maximum entropy model. PLoS One 10, e0131630. https://doi.org/10.1371/journal.pone.0131630

Fu, H., Zhong, J., Yuan, G., Xie, P., Guo, L., Zhang, X., Xu, J., Li, Z., Li, W., Zhang, M., Cao, T., Ni, L., 2014b. Trait-based community assembly of aquatic macrophytes along a water depth gradient in a freshwater lake. Freshw. Biol. 59, 2462–2471. https://doi.org/10.1111/fwb.12443

Fu, H., Zhong, J., Fang, S., Hu, J., Guo, C., Lou, Q., Yuan, G., Dai, T., Li, Z., Zhang, M., Li, W., Xu, J., Cao, T., 2017. Scale-dependent changes in the functional diversity of macrophytes in subtropical freshwater lakes in south China. Sci. Rep. 7, 8294. https://doi.org/10.1038/s41598-017-08844-8

Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, G.J., Cavender-Bares, J., Firn, J., Laughlin, D.C., Sutton-Grier, A.E., Williams, L., Wright, J., 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biol. Rev. 92, 1156–1173. https://doi.org/10.1111/brv.12275

Fusconi, A., Mucciarelli, M., 2018. How important is arbuscular mycorrhizal colonization in wetland and aquatic habitats? Environ. Exp. Bot. 155, 128–141. https://doi.org/10.1016/j.envexpbot.2018.06.016

Gamon, J.A., Somers, B., Malenovský, Z., Middleton, E.M., Rascher, U., Schaepman, M.E., 2019. Assessing Vegetation Function with Imaging Spectroscopy. Surv. Geophys. 40, 489–513. https://doi.org/10.1007/s10712-019-09511-5

Gao, L., Liu, W.Y., Shen, Y.X., Liu, W.J., 2012. Trade-off responses of the clonal plant water lettuce (*Pistia Stratiotes* L.) to the allelopathy of crofton weed (*Eupatorium Adenophorum* Spreng). Isr. J. Ecol. Evol. 58, 313–324. https://doi.org/10.1560/IJEE.58.4.313

García-Girón, J., Wilkes, M., Fernández-Aláez, M., Fernández-Aláez, C., 2019a. Processes structuring macrophyte metacommunities in Mediterranean ponds: Combining novel methods to disentangle the role of dispersal limitation, species sorting and spatial scales. J. Biogeogr. 46, 646–656. https://doi.org/10.1111/jbi.13516

García-Girón, J., Fernández-Aláez, C., Fernández-Aláez, M., Alahuhta, J., 2019b. Untangling the assembly of macrophyte metacommunities by means of taxonomic, functional and phylogenetic beta diversity patterns. Sci. Total Environ. 693, 133616. https://doi.org/10.1016/j.scitotenv.2019.133616

Gillard, M., Thiébaut, G., Rossignol, N., Berardocco, S., Deleu, C., 2017. Impact of climate warming on carbon metabolism and on morphology of invasive and native aquatic plant species varies between spring and summer. Environ. Exp. Bot. 144, 1–10. https://doi.org/10.1016/j.envexpbot.2017.09.009

Glover, R., Drenovsky, R.E., Futrell, C.J., Grewell, B.J., 2015. Clonal integration in *Ludwigia hexapetala* under different light regimes. Aquat. Bot. 122, 40–46. https://doi.org/10.1016/j.aquabot.2015.01.004

Gomez-Sanchez, A., Gonzalez-Melendi, P., Santamaria, M.E., Arbona, V., Lopez-Gonzalvez, A., Garcia, A., Hensel, G., Kumlehn, J., Martinez, M., Diaz, I., 2019. Repression of drought-induced cysteine-protease genes alters barley leaf structure and responses to abiotic and biotic stresses. J. Exp. Bot. 70, 2143–2155. https://doi.org/10.1093/jxb/ery410

Gordon, D.R., Gantz, C.A., Jerde, C.L., Chadderton, W.L., Keller, R.P., Champion, P.D., 2012. Weed risk assessment for aquatic plants: Modification of a New Zealand system for the United States. PLoS One 7, e40031. https://doi.org/10.1371/journal.pone.0040031

Grutters, B.M.C., Gross, E.M., Bakker, E.S., 2016. Insect herbivory on native and exotic aquatic plants: phosphorus and nitrogen drive insect growth and nutrient release. Hydrobiologia 778, 209–220. https://doi.org/10.1007/s10750-015-2448-1

Guareschi, S., Laini, A., P. Viaroli, Bolpagni, R., 2020. Integrating habitat- and species-based perspectives for wetland conservation in lowland agricultural landscapes. Biol. Conserv. 29, 153–171. https://doi.org/ 10.1007/s10531-019-01876-8

Hart, S.P., Turcotte, M.M., Levine, J.M., 2019. Effects of rapid evolution on species coexistence. Proc. Natl. Acad. Sci. U.S.A. 116, 2112–2117. https://doi.org/10.1073/pnas.1816298116

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., Virtanen, R., 2015. A comparative analysis of metacommunity types in the freshwater realm. Ecol. Evol. 5, 1525–1537. https://doi.org/10.1002/ece3.1460

Hidding, B., Klaassen, M., de Boer, T., de Vries, P.P., Nolet, B.A., 2012. Aquatic plant shows flexible avoidance by escape from tuber predation by swans. Basic Appl. Ecol. 13, 50–58. https://doi.org/10.1016/j.baae.2011.11.002

Hilt, S., Gross, E.M., 2008. Can allelopathically active submerged macrophytes stabilise clear-water states in shallow lakes? Basic Appl. Ecol. 9, 422–432. https://doi.org/10.1016/j.baae.2007.04.003

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P., Thompson, K., 1999. Allocating C-S-R plant functional types: A soft approach to a hard problem. Oikos 85, 282–294. https://doi.org/10.2307/3546494

Hogeland, A.M., Killingbeck, K.T., 1985. Biomass, productivity and life history traits of *Juncus militaris* Bigel. In two Rhode Island (U.S.A.) freshwater wetlands. Aquat. Bot. 22, 335–346. https://doi.org/10.1016/0304-3770(85)90008-7

Homolová, L., Malenovský, Z., Clevers, J.G.P.W., García-Santos, G., Schaepman, M.E., 2013. Review of optical-based remote sensing for plant trait mapping. Ecol. Complex. 15, 1–16. https://doi.org/10.1016/j.ecocom.2013.06.003

Huang, W., Shao, H., Zhou, S., Zhou, Q., Li, W., Xing, W., 2017. Modulation of cadmium-induced phytotoxicity in *Cabomba caroliniana* by urea involves photosynthetic metabolism and antioxidant status. Ecotoxicol. Environ. Saf. 144, 88–96. https://doi.org/10.1016/j.ecoenv.2017.06.003

Huang, X., Shen, N., Guan, X., Xu, X., Kong, F., Liu, C., Yu, D., 2018. Root morphological and structural comparisons of introduced and native aquatic plant species in multiple substrates. Aquat. Ecol. 52, 65–76. https://doi.org/10.1007/s10452-017-9645-0

Hussner, A., Jahns, P., 2014. European native *Myriophyllum spicatum* showed a higher HCO3-use capacity than alien invasive *Myriophyllum heterophyllum*. Hydrobiologia 746, 171–182. https://doi.org/10.1007/s10750-014-1976-4

Hyldgaard, B., Brix, H., 2012. Intraspecies differences in phenotypic plasticity: Invasive versus non-invasive populations of *Ceratophyllum demersum*. Aquat. Bot. 97, 49–56. https://doi.org/10.1016/j.aquabot.2011.11.004

Hyldgaard, B., Sorrell, B., Olesen, B., Riis, T., Brix, H., 2012. Geographically distinct *Ceratophyllum demersum* populations differ in growth, photosynthetic responses and phenotypic plasticity to nitrogen availability. Funct. Plant Biol. 39, 774–783. https://doi.org/10.1071/FP12068

Iversen, L.L., Winkel, A., Baastrup-Spohr, L., Hinke, A.B., Alahuhta, J., Baattrup-Pedersen, A., Birk, S., Brodersen, P., Chambers, P.A., Ecke, F., Feldmann, T., Gebler, D., Heino, J., Jespersen, T.S., Moe, S.J., Riis, T., Sass, L., Vestergaard, O., Maberly, S.C., Sand-Jensen, K., Pedersen, O., 2019. Catchment properties and the photosynthetic trait composition of freshwater plant communities. Science 366, 878–881. https://doi.org/10.1126/science.aay5945

Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F.W., Asner, G.P., Guralnick, R., Kattge, J., Latimer, A.M., Moorcroft, P., Stahl, U., Ustin, S.L., 2016. Monitoring plant functional diversity from space. Nat. Plants 2. https://doi.org/10.1038/NPLANTS.2016.24

Jiménez-Ramos, R., Brun, F.G., Egea, L.G., Vergara, J.J., 2018. Food choice effects on herbivory: Intra-specific seagrass palatability and inter-specific macrophyte palatability in seagrass communities. Estuar. Coast. Shelf Sci. 204, 31–39. https://doi.org/10.1016/j.ecss.2018.02.016

Kato, R., Kadono, Y., 2011. Seed germination traits of *Trapella sinensis* (*Trapellaceae*), an endangered aquatic plant in Japan: Conservation implications. Aquat. Bot. 95, 258–261. https://doi.org/10.1016/j.aquabot.2011.08.002

Klančnik, K., Gaberščik, A., 2016. Leaf spectral signatures differ in plant species colonizing habitats along a hydrological gradient. J. Plant Ecol. 9, 442–450. https://doi.org/10.1093/jpe/rtv068

Klančnik, K., Iskra, I., Gradinjan, D., Gaberščik, A., 2018. The quality and quantity of light in the water column are altered by the optical properties of natant plant species. Hydrobiologia 812, 203–212. https://doi.org/10.1007/s10750-017-3148-9

Klančnik, K., Pančić, M., Gaberščik, A., 2014. Leaf optical properties in amphibious plant species are affected by multiple leaf traits. Hydrobiologia 737, 121–130. https://doi.org/10.1007/s10750-013-1646-y

Klopper, R., Lubbe, S., Rugbeer, H., 2007. The matrix method of literature review. Alternation 14, 262–276. ISSN 1023-1757

Kočić, A., Horvatić, J., Jelaska, S.D., 2014. Distribution and morphological variations of invasive macrophytes *Elodea nuttallii* (Planch.) H. St. John and *Elodea canadensis* Michx in Croatia. Acta Bot. Croat. 73, 437–446. https://doi.org/10.2478/botcro-2014-0011

Kordyum, E., Kozeko, L., Ovcharenko, Y., Brykov, V., 2017. Assessment of alcohol dehydrogenase synthesis and aerenchyma formation in the tolerance of *Sium* L. species (*Apiaceae*) to water-logging. Aquat. Bot. 142, 71–77. https://doi.org/10.1016/j.aquabot.2017.07.001

Korol, A.R., Ahn, C., 2016. Dominance by an obligate annual affects the morphological characteristics and biomass production of a planted wetland macrophyte community. J. Plant Ecol. 9, 187–200. https://doi.org/10.1093/jpe/rtv041

Kuhlgert, S., Austic, G., Zegarac, R., Osei-Bonsu, I., Hoh, D., Chilvers, M.I., Roth, M.G., Bi, K., TerAvest, D., Weebadde, P., Kramer, D.M., 2016. MultispeQ Beta: A tool for large-scale plant phenotyping connected to the open photosynQ network. R. Soc. Open Sci. 3. https://doi.org/10.1098/rsos.160592

Kwong, R.M., Sagliocco, J.L., Harms, N.E., Butler, K.L., Green, P.T., Martin, G.D., 2017. Biogeographical comparison of the emergent macrophyte, *Sagittaria platyphylla* in its native and introduced ranges. Aquat. Bot. 141, 1–9. https://doi.org/10.1016/j.aquabot.2017.05.001

Lastrucci, L., Gigante, D., Vaselli, O., Nisi, B., Viciani, D., Reale, L., Coppi, A., Fazzi, V., Bonari, G., Angiolini, C., 2016. Sediment chemistry and flooding exposure: A fatal cocktail for *Phragmites australis* in the Mediterranean basin? Ann. Limnol. 52, 365–377. https://doi.org/10.1051/limn/2016023

LEDA. URL http://www.leda-traitbase.org/ (accessed 03.06.2020).

Lemoine, D.G., Mermillod-Blondin, F., Barrat-Segretain, M.H., Massé, C., Malet, E., 2012. The ability of aquatic macrophytes to increase root porosity and radial oxygen loss determines their resistance to sediment anoxia. Aquat. Ecol. 46, 191–200. https://doi.org/10.1007/s10452-012-9391-2

Li, F., Qin, Y., Zhu, L., Xie, Y., Liang, S., Hu, C., Chen, X., Deng, Z., 2016. Effects of fragment size and sediment heterogeneity on the colonization and growth of *Myriophyllum spicatum*. Ecol. Eng. 95, 457–462. https://doi.org/10.1016/j.ecoleng.2016.06.097

Li, Y., He, Q., Ma, X., Wang, H., Liu, C., Yu, D., 2019a. Plant traits interacting with sediment properties regulate sediment microbial composition under different aquatic DIC levels caused by rising atmospheric CO_2. Plant Soil 445, 497–512. https://doi.org/10.1007/s11104-019-04312-6

Li, L., Ding, M., Lan, Z., Zhao, Y., Chen, J., 2019b. Light availability and patterns of allocation to reproductive and vegetative biomass in the sexes of the dioecious macrophyte *Vallisneria spinulosa*. Front. Plant Sci. 10, 572. https://doi.org/10.3389/fpls.2019.00572

Li, Z., Lu, W., Yang, L., Kong, X., Deng, X., 2015. Seed weight and germination behavior of the submerged plant *Potamogeton pectinatus* in the arid zone of northwest China. Ecol. Evol. 5, 1504–1512. https://doi.org/10.1002/ece3.1451

Lindholm, M., Alahuhta, J., Heino, J., Hjort, J., Toivonen, H., 2020. Changes in the functional features of macrophyte communities and driving factors across a 70-year period. Hydrobiologia in press. https://doi.org/10.1007/s10750-019-04165-1

Liu, H., Cao, Y., Li, W., Zhang, Z., Jeppesen, E., Wang, W., 2017. The effects of cadmium pulse dosing on physiological traits and growth of the submerged macrophyte *Vallisneria* *spinulosa* and phytoplankton biomass: a mesocosm study. Environ. Sci. Pollut. Res. 24, 15308–15314. https://doi.org/10.1007/s11356-017-9155-6

Liu, K., Zhao, W., Guo, X., Wang, Y., Miao, Q., 2011. Determination the nitrogen status of wetlands using emergent macrophytes leaf spectral reflectance. Int. Geosci. Remote Sens. Symp. 2161–2164. https://doi.org/10.1109/IGARSS.2011.6049594

Łoboda, A.M., Karpiński, M., Bialik, R.J., 2018. On the relationship between aquatic plant stem characteristics and drag force: Is a modeling application possible? Water 10, 540. https://doi.org/10.3390/w10050540

Łoboda, A.M., Bialik, R.J., Karpiński, M., Przyborowski, Ł., 2019. Two simultaneously occurring *Potamogeton* species: Similarities and differences in seasonal changes of biomechanical properties. Polish J. Environ. Stud. 28, 237–253. https://doi.org/10.15244/pjoes/85202

Lukács, B.A., E-Vojtkó, A., Erős, T., Molnár V., A., Szabó, S., Götzenberger, L., 2019. Carbon forms, nutrients and water velocity filter hydrophyte and riverbank species differently: A trait-based study. J. Veg. Sci. 30, 471–484. https://doi.org/10.1111/jvs.12738

Marcé, R., Obrador, B., Gómez-gener, L., Catalán, N., Koschorreck, M., Isabel, M., Singer, G., Schiller, D. Von, 2019. Earth-Science Reviews Emissions from dry inland waters are a blind spot in the global carbon cycle. Earth-Science Rev. 188, 240–248. https://doi.org/10.1016/j.earscirev.2018.11.012

Marzocchi, U., Benelli, S., Larsen, M., Bartoli, M., Glud, R.N., 2019. Spatial heterogeneity and short-term oxygen dynamics in the rhizosphere of *Vallisneria spiralis*: Implications for nutrient cycling. Freshw. Biol. 64, 532–543. https://doi.org/10.1111/fwb.13240

McCann, M.J., 2016. Response diversity of free-floating plants to nutrient stoichiometry and temperature: Growth and resting body formation. PeerJ 4, e1781. https://doi.org/10.7717/peerj.1781

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/https://doi.org/10.1016/j.tree.2006.02.002

Mermillod-Blondin, F., Lemoine, D.G., 2010. Ecosystem engineering by tubificid worms stimulates macrophyte growth in poorly oxygenated wetland sediments. Funct. Ecol. 24, 444–453. https://doi.org/10.1111/j.1365-2435.2009.01624.x

Mesa, L.M., Lindt, I., Negro, L., Gutierrez, M.F., Mayora, G., Montalto, L., Ballent, M., Lifschitz, A., 2017. Aquatic toxicity of ivermectin in cattle dung assessed using microcosms. Ecotoxicol. Environ. Saf. 144, 422–429. https://doi.org/10.1016/j.ecoenv.2017.06.016

Miler, O., Albayrak, I., Nikora, V., O'Hare, M., 2014. Biomechanical properties and morphological characteristics of lake and river plants: implications for adaptations to flow conditions. Aquat. Sci. 76, 465–481. https://doi.org/10.1007/s00027-014-0347-6

Moe, T.F., Hessen, D.O., Demars, B.O.L., 2019. Functional biogeography: Stoichiometry and thresholds for interpreting nutrient limitation in aquatic plants. Sci. Total Environ. 677, 447–455. https://doi.org/10.1016/j.scitotenv.2019.04.366

Monção, F.S., Dos Santos, A.M., Bini, L.M., 2012. Aquatic macrophyte traits and habitat utilization in the Upper Paraná River floodplain, Brazil. Aquat. Bot. 102, 50–55. https://doi.org/10.1016/j.aquabot.2012.04.008

Mouton, T.L., Matheson, F.E., Stephenson, F., Champion, P.D., Wadhwa, S., Hamer, M.P., Catlin, A., Riis, T., 2019. Environmental filtering of native and non-native stream macrophyte assemblages by habitat disturbances in an agricultural landscape. Sci. Total Environ. 659, 1370–1381. https://doi.org/10.1016/j.scitotenv.2018.12.277

Murphy, K.J., Rørslett, B., Springuel, I., 1990. Strategy analysis of submerged lake macrophyte communities: an international example. Aquat. Bot. 36, 303–323. https://doi.org/10.1016/0304-3770(90)90048-P

Murphy, K., Efremov, A., Davidson, T.A., Molina-navarro, E., Fidanza, K., Camila, T., Betiol, C., Chambers, P., Tapia, J., Varandas, S., Springuel, I., Kennedy, M., Paulo, R., Dibble, E., Hofstra, D., András, B., Gebler, D., Baastrup-spohr, L., Urrutia-estrada, J., 2019. World distribution, diversity and endemism of aquatic macrophytes. Aquat. Bot. 158, 103127. https://doi.org/10.1016/j.aquabot.2019.06.006

Nakamura, M., Nakamura, T., Tsuchiya, T., Noguchi, K., 2013. Functional linkage between N acquisition strategies and aeration capacities of hydrophytes for efficient oxygen consumption in roots. Physiol. Plant. 147, 135–146. https://doi.org/10.1111/j.1399-3054.2012.01643.x

Niphadkar, M., Nagendra, H., 2016. Remote sensing of invasive plants: incorporating functional traits into the picture. Int. J. Remote Sens. 37, 3074–3085. https://doi.org/10.1080/01431161.2016.1193795

Nuttens, A., Chatellier, S., Devin, S., Guignard, C., Lenouvel, A., Gross, E.M., 2016. Does nitrate co-pollution affect biological responses of an aquatic plant to two common herbicides? Aquat. Toxicol. 177, 355–364. https://doi.org/10.1016/j.aquatox.2016.06.006

O'Hare, M.T., Aguiar, F.C., Asaeda, T., Bakker, E.S., Chambers, P.A., Clayton, J.S., Elger, A., Ferreira, T.M., Gross, E.M., Gunn, I.D.M., Gurnell, A.M., Hellsten, S., Hofstra, D.E., Li, W., Mohr, S., Puijalon, S., Szoszkiewicz, K., Willby, N.J., Wood, K.A., 2018. Plants in aquatic ecosystems: current trends and future directions. Hydrobiologia 812, 1–11. https://doi.org/10.1007/s10750-017-3190-7

Ozimek, T., Gulati, R.D., van Donk, E., 1990. Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. Hydrobiologia 200-201, 399–407. https://doi.org/10.1007/BF02530357

Pan, Y., Cieraad, E., van Bodegom, P.M., 2019. Are ecophysiological adaptive traits decoupled from leaf economics traits in wetlands? Funct. Ecol. 33, 1202–1210. https://doi.org/10.1111/1365-2435.13329

Pätzig, M., Geiger, F., Rasche, D., Rauneker, P., Eltner, A., 2020. Allometric relationships for selected macrophytes of kettle holes in northeast Germany as a basis for efficient biomass estimation using unmanned aerial systems (UAS). Aquat. Bot. 162, 103202. https://doi.org/10.1016/j.aquabot.2020.103202

Paz, L.E., Ferreira, A.C., Simonetti, M.A., Capítulo, A.R., 2019. Selection of macrophytes by a generalist invertebrate herbivore and potential impacts for stream rehabilitation. Aquat. Bot. 158, 103121. https://doi.org/10.1016/j.aquabot.2019.05.006

Pereira, F.J., De Castro, E.M., Pires, M.F., De Oliveira, C., Pasqual, M., 2017. Anatomical and physiological modifications in water hyacinth under cadmium contamination. J. Appl. Bot. Food Qual. 90, 10–17. https://doi.org/10.5073/JABFQ.2017.090.003

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter

Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. https://doi.org/10.1071/BT12225

Perrow, M.R., Jowitt, A.J.D., Stansfield, J.H., Phillips, G.L., 1999. The practical importance of the interactions between fish, zooplankton and macrophytes in shallow lake restoration. Hydrobiologia 395-396, 199–210. https://doi.org/10.1007/978-94-017-3282-6_19

Phillips, G., Willby, N., Moss, B., 2016. Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? Aquat. Bot. 135, 37–45. https://doi.org/10.1016/j.aquabot.2016.04.004

Pierce, S., Brusa, G., Sartori, M., Cerabolini, B.E.L., 2012. Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies. Ann. Bot. 109, 1047–1053. https://doi.org/10.1093/aob/mcs021

Pietrini, F., Passatore, L., Fischetti, E., Carloni, S., Ferrario, C., Polesello, S., Zacchini, M., 2019. Evaluation of morpho-physiological traits and contaminant accumulation ability in *Lemna minor* L. treated with increasing perfluorooctanoic acid (PFOA) concentrations under laboratory conditions. Sci. Total Environ. 695, 133828. https://doi.org/10.1016/j.scitotenv.2019.133828

Qian, C., You, W., Xie, D., Yu, D., 2014. Turion morphological responses to water nutrient concentrations and plant density in the submerged macrophyte *Potamogeton crispus*. Sci. Rep. 4, 1–6. https://doi.org/10.1038/srep07079

Radulović, O., Petrić, M., Raspor, M., Tadić, V., Jovanović, P., Zečević, V., 2019. Assessment of in vitro multiplication of *Lemna minor* in the presence of phenol: Plant/bacteria system for potential bioremediation – part I. Polish J. Environ. Stud. 28, 803–809. https://doi.org/10.15244/pjoes/84921

Rejmánková, E., Sirová, D., Carlson, E., 2011. Patterns of activities of root phosphomonoesterase and phosphodiesterase in wetland plants as a function of macrophyte species and ambient phosphorus regime. New Phytol. 190, 968–976. https://doi.org/10.1111/j.1469-8137.2011.03652.x

Richter, D., Gross, E.M., 2013. *Chara* can outcompete *Myriophyllum* under low phosphorus supply. Aquat. Sci. 75, 457–467. https://doi.org/10.1007/s00027-013-0292-9

Riis, T., Olesen, A., Jensen, S.M., Alnoee, A.B., Baattrup-Pedersen, A., Lauridsen, T.L., Sorrell, B.K., 2018. Submerged freshwater plant communities do not show species complementarity effect in wetland mesocosms. Biol. Lett. 14, 10–14. https://doi.org/10.1098/rsbl.2018.0635

Rocchini, D., Andreo, V., Förster, M., Garzon-Lopez, C.X., Gutierrez, A.P., Gillespie, T.W., Hauffe, H.C., He, K.S., Kleinschmit, B., Mairota, P., Zorer, R., Neteler, M., 2015. Potential of remote sensing to predict species invasions: A modelling perspective. Prog. Phys. Geogr. 39, 283–309. https://doi.org/10.1177/0309133315574659

Rolland, D.C., Haury, J., Marmonier, P., 2015. Effect of macrophytes on flow conditions and deposition of suspended particles in small streams: an experimental study using artificial vegetation. Revue des sciences de l’eau 28, 231–245.

Roubeau Dumont, E., Larue, C., Lorber, S., Gryta, H., Billoir, E., Gross, E.M., Elger, A., 2019. Does intraspecific variability matter in ecological risk assessment? Investigation of genotypic variations in three macrophyte species exposed to copper. Aquat. Toxicol. 211, 29–37. https://doi.org/10.1016/j.aquatox.2019.03.012

Roubeau Dumont, E., Larue, C., Michel, H.C., Gryta, H., Liné, C., Baqué, D., Gross, E.M., Elger, A., 2020. Genotypes of the aquatic plant *Myriophyllum spicatum* with different growth strategies show contrasting sensitivities to copper contamination. Chemosphere 245. https://doi.org/10.1016/j.chemosphere.2019.125552

Rumlerová, Z., Vilà, M., Pergl, J., Nentwig, W., Pyšek, P., 2016. Scoring environmental and socioeconomic impacts of alien plants invasive in Europe. Biol. Invasions 18, 3697-3711. https://doi.org/10.1007/s10530-016-1259-2

Saha, C., Mukherjee, G., Agarwal-Banka, P., Seal, A., 2016. A consortium of non-rhizobial endophytic microbes from *Typha angustifolia* functions as probiotic in rice and improves nitrogen metabolism. Plant Biol. 18, 938–946. https://doi.org/10.1111/plb.12485

Santos, M.J., Hestir, E.L., Khanna, S., Ustin, S.L., 2012. Image spectroscopy and stable isotopes elucidate functional dissimilarity between native and nonnative plant species in the aquatic environment. New Phytol. 193, 683–695. https://doi.org/10.1111/j.1469-8137.2011.03955.x

Scheffer, M., 1999. The effect of aquatic vegetation on turbidity; how important are the filter feeders? Hydrobiologia 408, 307–316. https://doi.org/10.1023/A:1017011320148

Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8, 275-279. https://doi.org/10.1016/0169-5347(93)90254-M

Schneider, F.D., Morsdorf, F., Schmid, B., Petchey, O.L., Hueni, A., Schimel, D.S., Schaepman, M.E., 2017. Mapping functional diversity from remotely sensed morphological and physiological forest traits. Nat. Commun. 8. https://doi.org/10.1038/s41467-017-01530-3

Schoelynck, J., Struyf, E., 2016. Silicon in aquatic vegetation. Funct. Ecol. 30, 1323–1330. https://doi.org/10.1111/1365-2435.12614

Schriver, P., Bøgestrand, J., Jeppesen, E., Søndergaard, M., 1995. Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. Freshw. Biol. 33, 255–270. https://doi.org/10.1111/j.1365-2427.1995.tb01166.x

Schultz, R., Dibble, E., 2012. Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: The role of invasive plant traits. Hydrobiologia 684, 1–14. https://doi.org/10.1007/s10750-011-0978-8

Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R., Tilman, D., Gamon, J.A., 2018. Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. Nat. Ecol. Evol. 2, 976–982. https://doi.org/10.1038/s41559-018-0551-1

Scopus. URL https://www.scopus.com/ (accessed 03.06.2020).

Sebilian Wittyngham, S., Moderan, J., Boyer, K.E., 2019. Temperature and salinity effects on submerged aquatic vegetation traits and susceptibility to grazing. Aquat. Bot. 158, 103119. https://doi.org/10.1016/j.aquabot.2019.05.004

Sieben, E.J.J., le Roux, P.C., 2017. Functional traits, spatial patterns and species associations: what is their combined role in the assembly of wetland plant communities? Plant Ecol. 218, 433–445. https://doi.org/10.1007/s11258-017-0701-6

Sikorska, D., Papierowska, E., Szatyłowicz, J., Sikorski, P., Suprun, K., Hopkins, R.J., 2017. Variation in leaf surface hydrophobicity of wetland plants: the role of plant traits in water retention. Wetlands 37, 997–1002. https://doi.org/10.1007/s13157-017-0924-2

Silveira, M.J., Thiébaut, G., 2017. Impact of climate warming on plant growth varied according to the season. Limnologica 65, 4–9. https://doi.org/10.1016/j.limno.2017.05.003

Soana, E., Bartoli, M., 2013. Seasonal variation of radial oxygen loss in *Vallisneria spiralis* L.: An adaptive response to sediment redox? Aquat. Bot. 104, 228–232. https://doi.org/10.1016/j.aquabot.2012.07.007

Standen, K.M., Chambers, P.A., Culp, J.M., 2018. Arrowhead (*Sagittaria cuneata*) as a bioindicator of nitrogen and phosphorus for prairie streams and wetlands. Wetl. Ecol. Manag. 26, 331–343. https://doi.org/10.1007/s11273-017-9576-5

Strayer, D.L., 2010. Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. Freshw. Biol. 55, 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Su, H., Chen, Jun, Wu, Y., Chen, Jianfeng, Guo, X., Yan, Z., Tian, D., Fang, J., Xie, P., 2019. Morphological traits of submerged macrophytes reveal specific positive feedbacks to water clarity in freshwater ecosystems. Sci. Total Environ. 684, 578–586. https://doi.org/10.1016/j.scitotenv.2019.05.267

Sun, J., Wang, L., Ma, L., Huang, T., Zheng, W., Min, F., Zhang, Y., Wu, Z., He, F., 2018. Determinants of submerged macrophytes palatability to grass carp *Ctenopharyngodon idellus*. Ecol. Indic. 85, 657–663. https://doi.org/10.1016/j.ecolind.2017.11.023

Sutton-Grier, A.E., Megonigal, J.P., 2011. Plant species traits regulate methane production in freshwater wetland soils. Soil Biol. Biochem. 43, 413–420. https://doi.org/10.1016/j.soilbio.2010.11.009

Szabó, S., Peeters, E.T.H.M., Várbíró, G., Borics, G., Lukács, B.A., 2019. Phenotypic plasticity as a clue for invasion success of the submerged aquatic plant *Elodea nuttallii*. Plant Biol. 21, 54–63. https://doi.org/10.1111/plb.12918

Tabou, T.T., Baya, D.T.B., Liady, M.N.D., Eyul'Anki, D.M.E.A., Vasel, J.L., 2014. Apport du traitement d'images dans le suivi de l'influence des teneurs en nutriments sur la croissance des lentilles d'eau (*Lemna minor*). Biotechnol. Agron. Soc. Environ. 18, 37–48. https://popups.uliege.be:443/1780-4507/index.php?id=10776

Tang, X., Zhang, X., Cao, T., Ni, L., Xie, P., 2018. Reconstructing clear water state and submersed vegetation on behalf of repeated flocculation with modified soil in an in situ mesocosm experiment in Lake Taihu. Sci. Total Environ. 625, 1433–1445. https://doi.org/10.1016/j.scitotenv.2018.01.008

Thiébaut, G., Boiché, A., Lemoine, D., Barrat-Segretain, M.H., 2017. Trade-offs between growth and defense in two phylogenetically close invasive species. Aquat. Ecol. 51, 405–415. https://doi.org/10.1007/s10452-017-9625-4

Thiébaut, G., Gillard, M., Deleu, C., 2016. Growth, regeneration and colonisation of *Egeria densa* fragments: the effect of autumn temperature increases. Aquat. Ecol. 50, 175–185. https://doi.org/10.1007/s10452-016-9566-3

Thiébaut, G., Thouvenot, L., Rodríguez-Pérez, H., 2018. Allelopathic effect of the invasive *Ludwigia hexapetala* on growth of three macrophyte species. Front. Plant Sci. 9, 1835. https://doi.org/10.3389/fpls.2018.01835

Thouvenot, L., Deleu, C., Berardocco, S., Haury, J., Thiébaut, G., 2015. Characterization of the salt stress vulnerability of three invasive freshwater plant species using a metabolic profiling approach. J. Plant Physiol. 175, 113–121. https://doi.org/10.1016/j.jplph.2014.11.007

Thouvenot, L., Gauzens, B., Haury, J., Thiébaut, G., 2019. Response of macrophyte traits to herbivory and neighboring species: Integration of the functional trait framework in the context of ecological invasions. Front. Plant Sci. 9, 1981. https://doi.org/10.3389/fpls.2018.01981

Thouvenot, L., Haury, J., Pottier, G., Thiébaut, G., 2017. Reciprocal indirect facilitation between an invasive macrophyte and an invasive crayfish. Aquat. Bot. 139, 1–7. https://doi.org/10.1016/j.aquabot.2017.02.002

Thouvenot, L., Haury, J., Thiebaut, G., 2013b. A success story: Water primroses, aquatic plant pests. Aquat. Conserv. Mar. Freshw. Ecosyst. 23, 790–803. https://doi.org/10.1002/aqc.2387

Thouvenot, L., Puech, C., Martinez, L., Haury, J., Thiébaut, G., 2013a. Strategies of the invasive macrophyte *Ludwigia grandiflora* in its introduced range: Competition, facilitation or coexistence with native and exotic species? Aquat. Bot. 107, 8–16. https://doi.org/10.1016/j.aquabot.2013.01.003

Thouvenot, L., Thiébaut, G., 2018. Regeneration and colonization abilities of the invasive species *Elodea canadensis* and *Elodea nuttallii* under a salt gradient: implications for freshwater invasibility. Hydrobiologia 817, 193–203. https://doi.org/10.1007/s10750-018-3576-1

Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. Nature 367, 363–365. https://doi.org/10.1038/367363a0

Török, P., Miglécz, T., Valkó, O., Tóth, K., Kelemen, A., Albert, Á. J., Matus, G., Molnár, V.A., Ruprecht, E., Papp, L., Deák, B., Horváth, O., Takács, A., Hüse, B., Tóthmérész, B., Deák, B., 2013. New thousand-seed weight records of the Pannonian flora and their application in analysing social behaviour types. Acta Bot. Hung. 55, 429–472. https://doi.org/10.1556/ABot.55.2013.3

Tóth, V.R., Villa, P., Pinardi, M., Bresciani, M., 2019. Aspects of invasiveness of *Ludwigia* and *Nelumbo* in shallow temperate fluvial lakes. Front. Plant Sci. 10, 647. https://doi.org/10.3389/fpls.2019.00647

TRY. URL http://www.try-db.org/ (accessed 03.06.2020).

Urban, R.A., Dwyer, M.E., 2016. Asexual reproduction and its potential influence on the distribution of an invasive macrophyte. Northeast. Nat. 23, 408–419. https://doi.org/10.1656/045.023.0308

Van Donk, E., Van de Bund, W.J., 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: Allelopathy versus other mechanisms. Aquat. Bot. 72, 261–274. https://doi.org/10.1016/S0304-3770(01)00205-4

Van Gerven, L.P.A., de Klein, J.J.M., Gerla, D.J., Kooi, B.W., Kuiper, J.J., Mooij, W.M., 2015. Competition for light and nutrients in layered communities of aquatic plants. Am. Nat. 186, 72–83. https://doi.org/10.1086/681620

Venter, N., Cowie, B.W., Witkowski, E.T.F., Snow, G.C., Byrne, M.J., 2017. The amphibious invader: Rooted water hyacinth's morphological and physiological strategy to survive stranding and drought events. Aquat. Bot. 143, 41–48. https://doi.org/10.1016/j.aquabot.2017.09.004

Villa, P., Bresciani, M., Braga, F., Bolpagni, R., 2014. Comparative assessment of broadband vegetation indices over aquatic vegetation. IEEE J-STARS 7, 3117-3127. https://doi.org/10.1109/JSTARS.2014.2315718

Villa, P., Pinardi, M., Tóth, V.R., Hunter, P.D., Bolpagni, R., Bresciani, M., 2017. Remote sensing of macrophyte morphological traits: Implications for the management of shallow lakes. J. Limnol. 76, 109–126. https://doi.org/10.4081/jlimnol.2017.1629

Vivian-Smith, G., 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. J. Ecol. 85, 71–82. https://doi.org/10.2307/2960628

Wang, L., Dronova, I., Gong, P., Yang, W., Li, Y., Liu, Q., 2012. A new time series vegetation-water index of phenological-hydrological trait across species and functional types for Poyang Lake wetland ecosystem. Remote Sens. Environ. 125, 49–63. https://doi.org/10.1016/j.rse.2012.07.003

Wang, R., Gamon, J.A., 2019. Remote sensing of terrestrial plant biodiversity. Remote Sens. Environ. 231. https://doi.org/10.1016/j.rse.2019.111218

Wang, Q., Yu, D., Xiong, W., Yu, L., Xie, D., 2010. Do freshwater plants have adaptive responses to typhoon-impacted regimes? Aquat. Bot. 92, 285–288. https://doi.org/10.1016/j.aquabot.2010.01.004

Wang, T., Hu, J., Liu, C., Yu, D., 2017. Soil type can determine invasion success of *Eichhornia crassipes*. Hydrobiologia 788, 281–291. https://doi.org/10.1007/s10750-016-3003-4

Wei, H., Cheng, S., Tang, H., He, F., Liang, W., Wu, Z., 2013. The strategies of morphology, reproduction and carbohydrate metabolism of *Hydrilla verticillata* (Linn.f.) Royle in fluctuating waters. Fresenius Environ. Bull. 22, 2590–2596.

Wong, P.K., Liang, Y., Liu, N.Y., Qiu, J.W., 2010. Palatability of macrophytes to the invasive freshwater snail *Pomacea canaliculata*: Differential effects of multiple plant traits. Freshw. Biol. 55, 2023–2031. https://doi.org/10.1111/j.1365-2427.2010.02458.x

Wood, K.A., O’Hare, M.T., McDonald, C., Searle, K.R., Daunt, F., Stillman, R.A., 2017. Herbivore regulation of plant abundance in aquatic ecosystems. Biol. Rev. 92, 1128–1141. https://doi.org/10.1111/brv.12272

Wood, K.A., Stillman, R.A., Clarke, R.T., Daunt, F., O’Hare, M.T., 2018. Water velocity limits the temporal extent of herbivore effects on aquatic plants in a lowland river. Hydrobiologia 812, 45–55. https://doi.org/10.1007/s10750-016-2744-4

Xie, D., Yu, D., 2011a. Size-related auto-fragment production and carbohydrate storage in auto-fragment of *Myriophyllum spicatum* L. in response to sediment nutrient and plant density. Hydrobiologia 658, 221–231. https://doi.org/10.1007/s10750-010-0475-5

Xie, D., Yu, D., 2011b. Turion production and nutrient reserves in *Potamogeton crispus* are influenced by sediment nutrient level. Aquat. Biol. 14, 21–28. https://doi.org/10.3354/ab00371

Xie, D., Yu, D., You, W.H., Wang, L.G., 2013. Morphological and physiological responses to sediment nutrients in the submerged macrophyte *Myriophyllum spicatum*. Wetlands 33, 1095–1102. https://doi.org/10.1007/s13157-013-0465-2

Xie, D., Yu, D., Yu, L.F., Liu, C.H., 2010. Asexual propagations of introduced exotic macrophytes *Elodea nuttallii*, *Myriophyllum aquaticum*, and *M. propinquum* are improved by nutrient-rich sediments in China. Hydrobiologia 655, 37–47. https://doi.org/10.1007/s10750-010-0402-9

Xie, D., Zhou, H., Zhu, H., Ji, H., Li, N., An, S., 2015. Differences in the regeneration traits of *Potamogeton crispus* turions from macrophyte-and phytoplankton-dominated lakes. Sci. Rep. 5, 1–11. https://doi.org/10.1038/srep12907

Xing, W., Shi, Q., Liu, H., Liu, G., 2016. Growth rate, protein:RNA ratio and stoichiometric homeostasis of submerged macrophytes under eutrophication stress. Knowl. Manag. Aquat. Ecosyst. 417, 25. https://doi.org/10.1051/kmae/2016012

Yam, R.S.W., Fan, Y.T., Wang, T.T., 2016. Importance of macrophyte quality in determining life-history traits of the apple snails *Pomacea canaliculata*: Implications for bottom-up management of an invasive herbivorous pest in constructed wetlands. Int. J. Environ. Res. Public Health 13, 1–17. https://doi.org/10.3390/ijerph13030248

Zhang, L., Ma, D., Xu, J., Quan, J., Dang, H., Chai, Y., Liu, X., Guo, Y., Yue, M., 2017. Economic trade-offs of hydrophytes and neighbouring terrestrial herbaceous plants based on plant functional traits. Basic Appl. Ecol. 22, 11–19. https://doi.org/10.1016/j.baae.2017.06.004

Zhang, P., Grutters, B.M.C., van Leeuwen, C.H.A., Xu, J., Petruzzella, A., van den Berg, R.F., Bakker, E.S., 2019. Effects of rising temperature on the growth, stoichiometry, and palatability of aquatic plants. Front. Plant Sci. 9, 1947. https://doi.org/10.3389/fpls.2018.01947

Zhou, Y., Li, L., Song, Z., 2019. Plasticity in sexual dimorphism enhances adaptation of dioecious *Vallisneria natans* plants to water depth change. Front. Plant Sci. 10, 826. https://doi.org/10.3389/fpls.2019.00826

Zhu, G., Di, G., Zhang, M., Cao, T., Ni, L., Fang, R., Yu, G., 2018b. Biomechanical response of a submerged, rosette-forming macrophyte to wave action in a eutrophic lake on the Yungui Plateau, China. Environ. Sci. Pollut. Res. 25, 34027–34045. https://doi.org/10.1007/s11356-018-3047-2

Zhu, G., Yuan, C., Di, G., Zhang, M., Ni, L., Cao, T., Fang, R., Wu, G., 2018a. Morphological and biomechanical response to eutrophication and hydrodynamic stresses. Sci. Total Environ. 622–623, 421–435. https://doi.org/10.1016/j.scitotenv.2017.11.322

Zhu, G., Zhang, M., Cao, T., Ni, L., Zhong, A., Fu, H., 2012. Effects of sediment type on stem mechanical properties of the submerged macrophyte *Hydrilla verticillata* (L.F.) Royle. Fresenius Environ. Bull. 21, 468–474.

Zuo, S., Fang, Z., Zhou, S., Ye, L., 2016. Benthic fauna promotes algicidal effect of allelopathic macrophytes on *Microcystis aeruginosa*. J. Plant Growth Regul. 35, 646–654. https://doi.org/10.1007/s00344-015-9566-x

Figures

Figure legends

Figure 1. Publication trend of the 738 macrophyte trait-based studies.

Figure 2. The number of papers conducted in different continents (*Geographic distribution*, A), South America (SAm), North America (NAm), and Global Studies (Global), and *Habitat type* (B). Stacked bars show the repartition in years of publication.

Figure 3. The number of papers focusing on different macrophyte *Growth forms* (A) and *Study type* (B). Study types include field studies (*field*), controlled-conditions experiments (*lab*), combined approaches (*lab and field*) and reviews.

Figure 4. Categories of functional traits that have been measured by the authors or acquired from the literature and used to reach the aim of the study (A) and main topics investigated (B). The categories of functional traits are: *Morphology* (Mor), *Productivity* (Pro), *Reproduction* (Rep), *Physiology* (Phys), *Biochemistry* (BioC), *Growth form* (GroF), *Ecological preferences* (EcoP), *Biomechanical* traits (Mec), *Other* (OthFT) and *Biotic interactions* (Bint). Main topics are: *Environmental gradients* (EnvG), *Anthropic pressure* (AntPr), *Invasiveness* (Inv), *Community structure* (ComS), *Biotic interactions* (BioI), *Specific characteristics* (SpCh) and *Other topics* (OthTop).

Figure 5. Diagram illustrating the major links among the features considered in this review. Arc width is representative of the strength of the link between two nodes, i.e., the number of papers including both nodes in the study, and circle size is proportional to how many connections the node installs with other nodes. For clarity links weaker than 15 (less than 15 studies showing that connection) are omitted, just as nodes not showing links of this strength.