Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Original Article
Acta Limnologica Brasiliensia, 2023, vol. 35, e20
https://doi.org/10.1590/S2179-975X4222
ISSN 2179-975X on-line version

A global review on invasive traits of macrophytes and their link to invasion success

Uma revisão global sobre traços funcionais de macrófitas invasoras e sua relação com o sucesso no processo de invasão

Leticia Siman Bora[1] and Andre Andrian Padial[1,2]*

[1]Laboratório de Análise e Síntese em Biodiversidade, Programa de Pós-graduação em Ecologia e Conservação, Departamento de Botânica, Setor de Ciências Biológicas, Universidade Federal do Paraná – UFPR, Av. Cel. Francisco H. dos Santos, 100, Jardim das Américas, CEP 81530-000, Curitiba, PR, Brasil

[2]Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura – Nupelia, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brasil

*e-mail: aapadial@gmail.com

Cite as: Bora, L.S. and Padial, A.A. A global review on invasive traits of macrophytes and their link to invasion success. *Acta Limnologica Brasiliensia*, 2023, vol. 35, e20.

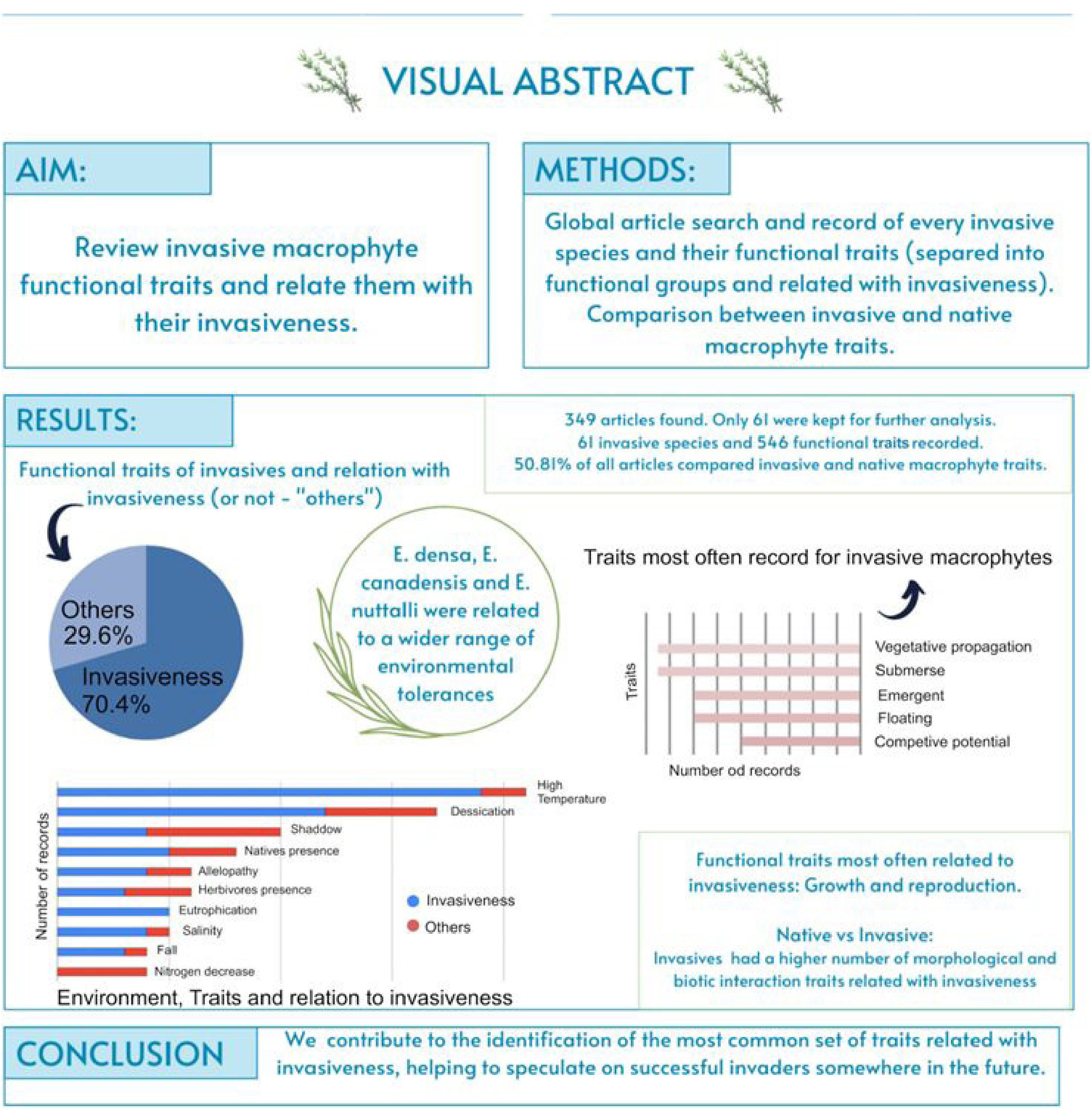
Abstract: Aim: Biological invasions by exotic macrophytes represent one of the main reasons for biodiversity and ecosystem changes in aquatic ecosystems. The reasons for their ability to succeed in new environments have been of ecological interest in the last years. We made a global review, aiming to describe functional traits related with invasiveness of macrophytes. **Methods:** Our search was performed using keywords regarding invasive macrophytes and functional traits. We related the group traits of invasive species with their probability of species invasion success in new localities (invasiveness). We also performed a nestedness analysis that helped us to see which species possessed the higher number of traits related to invasiveness, as well as which traits were more common among the invasive species. **Results:** Traits most often related to invasiveness were those indicating growth (94.5%) and reproduction (90.1%). Nearly 70.4% of invasive macrophytes traits were related with the probability of invasion success. Invasive species had a higher number of morphological and biotic interaction traits related with invasiveness than native species. Our nestedness analysis indicated a low degree of nestedness, but showed us that *Egeria densa*, *Elodea canadensis* and *Elodea nutalli* were the species with a wider range of environmental tolerances, explaining their invasibility across ecosystems. **Conclusions:** We summarized and complement existing reviews on the functional traits related to invasion success of macrophytes. We believe this review contributed to the identification of the most common set of traits related with invasiveness, helping to speculate on successful invaders in the future.

Keywords: biological invasion; aquatic plants; functional attributes; functional biodiversity; invasiveness.

Resumo: Objetivo: A invasão biológica por macrófitas exóticas é uma das maiores causas de perda de diversidade em ambientes aquáticos. Assim, o motivo para o seu sucesso em invadir novas localidades têm sido de interesse na ecologia. Fizemos uma revisão global, com o intuito de descrever os traços funcionais relacionados com o potencial invasor de macrófitas. **Métodos:** Realizamos a busca com palavras-chave relacionadas a macrófitas invasoras e traços funcionais. Relacionamos os grupos de traços de espécies invasoras com a sua probabilidade de sucesso de invasão em novas localidades. Também fizemos uma análise de aninhamento, que nos ajudou a constatar quais espécies possuem um maior número de traços relacionados com o potencial invasor, assim como quais traços funcionais são mais comuns entre as espécies invasoras. **Resultados:** Os traços mais frequentemente relacionados com o potencial invasor foram aqueles indicando crescimento (94,5%) e reprodução (90,1%). Aproximadamente 70,4% de todos os traços de espécies invasoras foram relacionados a com a probabilidade de sucesso de invasão. Espécies invasoras possuíram um maior número de traços morfológicos e reprodutivos relacionados com o potencial invasor do que espécies nativas. Nossa análise mostrou um baixo grau de aninhamento, mas nos mostrou que as espécies *Egeria densa*, *Elodea canadensis* e *Elodea nutalli* são as espécies com uma maior extensão de tolerâncias ambientais, explicando seu potencial invasor entre ecossistemas. **Conclusões:** Resumimos e complementamos revisões existentes sobre os traços funcionais relacionados com o potencial invasor de macrófitas. Acreditamos que esta revisão contribuiu para a identificação dos conjuntos de traços mais comumente relacionados com o potencial invasor, ajudando a especular sobre possíveis futuras invasoras.

Palavras-chave: invasão biólogica; plantas aquáticas; atributos funcionais; diversidade funcional; invasividade.

Graphical abstract



1. Introduction

Biological invasions are a major threat to natural environments, and therefore it would be useful to know if invasive species are better equipped by their functional traits to cope with the conditions of new environments, therefore aiming to prevent future invasions. Many works have tried to make a direct link between invasive macrophyte traits and the probability of invasion success (Alpert et al., 2000), however many results indicate that traits constantly associated with invasion are difficult to identify. On the other hand, there are other authors that claim that certain types of traits that related to invasion success are crucial for explaining and predicting invasion (Pyšek & Richardson, 2008). The number of articles working with invasive macrophyte traits is increasing over time, and there is relevant work being made. Recently, Hussner et al. (2021) reviewed traits associated with the most invasive macrophytes species and their relation to macrophytes' growth form.

It is often argued that some types of traits, such as the ability of vegetative reproduction, high growth rates, high seed production, and germination rates, short life cycles, and the production of allelopathic substances are usually linked to plant invasion success (Michelan et al., 2010; Hussner et al., 2021). Still, some native plants could possess such traits, and the question of what kind of traits differentiate successful invaders from natives or other unsuccessful invaders remains. The comparison between native and invasive species traits can shed some light on that matter, as has been shown in some previous works (Hamilton et al., 2005; Pyšek & Richardson, 2008), whereas invasion success may be influenced by differences in the functional traits of native communities, as already shown for fish (e.g. Azzurro et al., 2014; Skóra et al., 2015).

In this work, we reviewed the invasive macrophyte traits described in articles found in a global search and then related them with the possibility (or not) of invasion success (i.e. invasiveness). Also, as many articles compared invasive species traits with native traits, we added native species traits in our work as well, aiming to verify if there were any significant differences among traits between native and exotic species. Our main hypothesis here is that invasive species must have a higher number of traits associated with their invasiveness than native species, although it is very difficult to assume that one or more traits are exclusive to invaders. We must assume that when planning and executing this review, Hussner et al. (2021) published a very well-done review paper on invasive macrophytes and their traits of invasiveness. Here, we complement Hussner et al. (2021) work with a different approach. Indeed, we investigated a wider range of invasive species, comparing their traits with native species traits, and also investigated their success through different environmental conditions.

2. Methods

A scientometric analysis was also performed by measuring the number of articles resulting from the search, the increase in the number of articles involving invasive species and functional diversity over time, the location of the studies and the families of the species analyzed. The articles search was made through the ISI Web of Science database using the following keywords: (macrophyte* OR aquatic plant* OR aquatic vegetation* OR aquatic weed*) AND (biologic* invas* OR inva* OR introduced OR alien OR exotic OR non-native OR non-indigenous) AND (Function* Divers* OR function* trait* OR function* group* OR function* type*) in May of 2020. All articles obtained from this search were screened based on their titles and abstracts and later fully read. Only articles that studied (directly or indirectly) invasive macrophytes and related their functional traits with any ecological questions were selected. We reported all traits found in the articles and later related them with the possibility of invasion success. Invasion success traits were therefore any traits that would give an invasive species an advantage in new locations, such as high growth rates, allelopathy, or high competitive potential. The selected articles followed the PRISMA guidelines for reporting systematic reviews (Page et al., 2020) (Figure 1).

By functional trait, we consider any anatomical, morphological, or physiological behavior trait that is related to how these macrophytes affect and are affected by the environment and other individuals (Capers et al., 2010; Cardinale et al., 2012; Tilman, 2001). Different groups of traits were obtained by the article's search, such as physical, morphological, physiological, and response traits to environmental filtering and traits related to biotic interaction. Response traits are traits that measure how an individual responds to changes in the environment (Lavorel & Garnier, 2002) and biotic interaction traits are traits reflecting the interaction with other macrophyte species. Continuous attributes were included in the review as response/biotic interaction

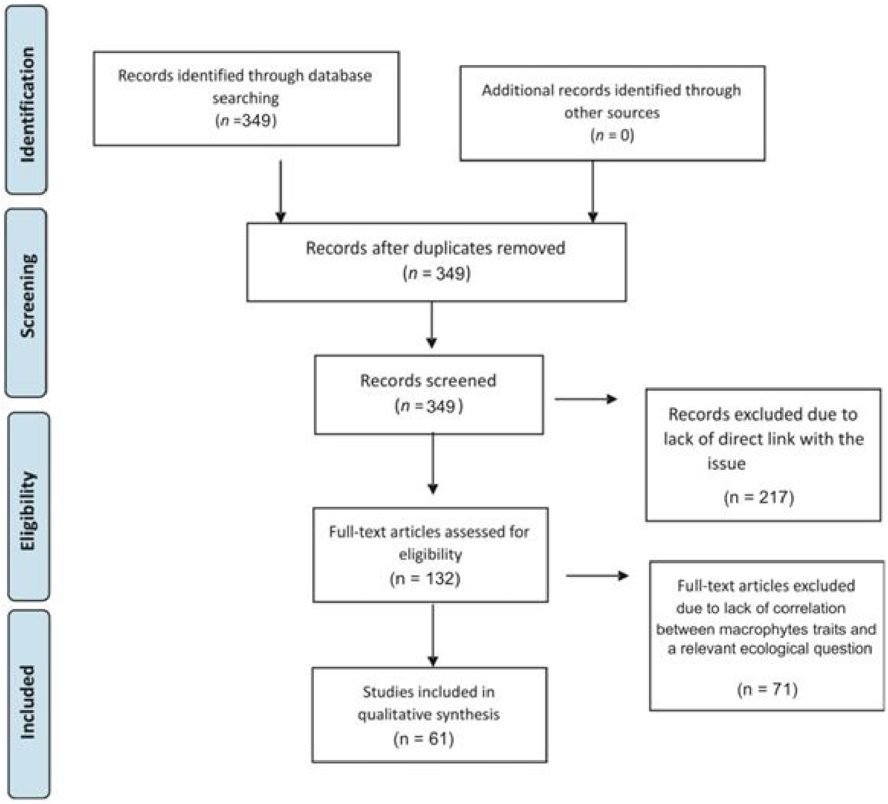


Figure 1. Prisma protocol (see Page et al., 2020) illustrating the steps of our search and review through ISI Web of Science database.

traits in a qualitative manner, for comparison between species.

Native species traits were also included in our review for means of comparison since many articles found in the search made a comparison between the traits of invasive and native macrophytes. By comparing with natives, we went further: if invasive and native species indeed possess different traits, functional traits could be better related to invasion processes.

For both invasive and native groups, functional traits obtained in the articles were separated as traits related to growth (such as type of growth, clump-forming for example, fast colonization or high growth rates), reproduction, and life cycle (such as vegetative propagation, life cycles, sexual or asexual reproduction), physiological processes (such as photosynthesis efficiency or nutrient concentration in their tissue), morphology (leaf morphology, height, canopy structure for example), effect traits (traits that alter ecosystem functions), life form (emergent, floating, submerged or emergent), trade-offs, competition potential, as response traits to environmental conditions (alterations in morphological, competition or any other traits that are affected by any type of environmental stress) and biotic interaction traits (any group traits that shows alterations in a scenario with the presence of new macrophyte species). Later, we related the reported traits to their indication of invasion success (invasiveness). Traits that did not indicate success are not necessarily a barrier to invasion; however, they cannot be immediately related to species' invasiveness.

The data concerning invasion success by invasive species in different environmental conditions (i.e. only response traits related to success in new environments) were compiled and analyzed through a network analysis (nestedness). This kind of analysis usually is performed with the interaction of two different sets of species, however, this analysis proved to be useful to us, since it allowed us to see graphically and statistically which conditions were more related to the invasive species, showing us these species and also what species were related to which conditions (or more than one condition). We used the NODF method and the analysis was performed through R software and with "bipartite" package.

3. Results

A total of 349 articles were found in the search. However, only 61 (17.47%) of them actually measured traits or made relationships between invasive macrophytes and functional traits. From those 61 articles, 31 (50.81%) compared invasive and native macrophyte traits. Invasive or native status depended on the studied region. Therefore, some species received both invasive and native status in our review, depending on the region where the study was performed. This was more clearly discussed after the comparison of native and invasive macrophyte traits in the 31 articles abovementioned.

There was a clear temporal increase in the interest of studies involving invasive macrophytes and functional diversity (Figure 2), with articles ranging from 1996 (n = 1; 1.63%) to 2019 (n = 14; 22.94%). Although our review is global and articles from many countries were found, there was a bias towards articles published in the United States (n = 22; 36.06%) and France (n = 10; 16.39%) (Figure 3).

In total, 61 invasive species (Table 1) were recorded and the most studied invasive macrophytes were *Egeria densa* Planch (11 studies) and *Elodea canadensis* Michx (10 studies). Hydrocharitaceae was the most common family of invasive species (n = 11; 14.7%), followed by Poaceae (n = 6; 9.8%). 94 native species (Table 1) were recorded in articles that compared invasive and native macrophyte traits, and the most common species studied were *Ceratophyllum demersum* L. (5 studies) and *Vallisneria americana Michx* (4 studies); the most common families of native's species were Potamogetonaceae (n = 18; 19. 6%) and Hydrocharitaceae (n = 17; 14.2%).

The majority of traits reported for invasive species were related to macrophyte responses to environmental conditions and biotic interactions, followed by morphological, reproductive, and life form traits (Table 2). From the traits regarding responses to environmental conditions, 70.4% (n = 86) indicated success in terms of responses to environmental changes or stresses. Considering invasive biotic interaction traits, 88.6% (n = 141) were related to invasiveness. Growth and reproductive invasive traits were the most related to invasiveness (94.5%, n = 35; and 90.1%, n = 46, respectively). Within competitive traits, only 10 traits were reported, all of them positively related to species invasiveness. Invasiveness, or probability of invasion success, was related to patterns such as high reproductive traits, better competition abilities than other species, or higher tolerance to stress (see Methods section). Given that native species could share some of these characteristics, we also related them to invasiveness, even when they can or cannot be considered invasive in their native ecosystem.

Vegetative propagation (reproduction trait) was the most recorded trait for invasive species, followed by submersed life form (life form trait - other life forms were also often recorded, such as emergent or floating), perennial life cycle (reproduction), formation of dense mats (growth), high competitive potential (competitive potential) and high growth rate (growth) (Figure 4). Many of these traits are often related with macrophyte invasion success. Also, other traits usually linked to invasiveness were often reported only for invasive species, such as high seed persistence, fast reproduction, and large leaves. Life form, although often described, is a difficult

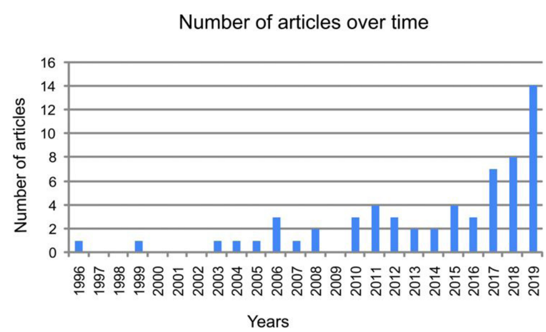


Figure 2. Temporal trend of the number of articles measuring and/or relating invasive macrophytes and functional traits found in ISI database following the Boolean operators described in methods.

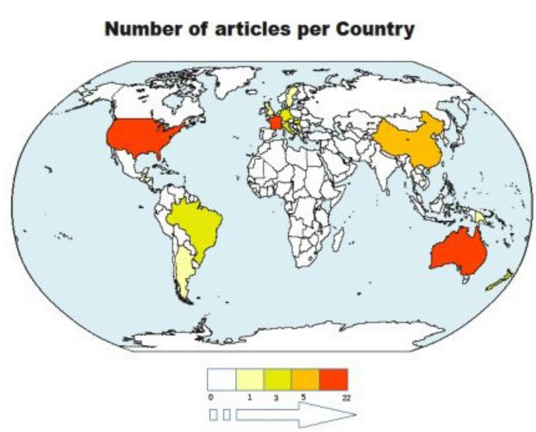


Figure 3. The number of articles measuring and/or relating invasive macrophytes and functional traits per country of study, found in ISI database following the Boolean operators described in methods.

Table 1. List of species studied in the articles analyzed (see methods for description of the search), and their respective status (native or invasive), family, region where the species is native or invasive and the number of articles that worked with the species.

Species	*Status*	Family	Region	N. of Studies
Alternanthera philoxeroides (Mart.) Griseb	Invasive	Amaranthaceae	China, United States, Australia	3
Apium nodiflorum (L.) Lag.	Invasive	Apiaceae	New Zealand	1
Arundo donax L.	Invasive	Poaceae	United States	1
Azolla caroliniana Willd	Invasive	Azollaceae	Serbia	1
Azolla filiculoides Lam.	Invasive	Azollaceae	Britain, Hungary, Italy, Serbia	3
Bacopa crenata (P.Beauv.) Hepper	Invasive	Scrophulariaceae	Hungary, Italy	1
Cabomba caroliniana A. Gray	Invasive	Cabombaceae	Hungary, Italy, Serbia	2
Callitriche stagnalis Scop.	Invasive	Callitrichaceae	New Zealand	1
Ceratophyllum demersum L.	Invasive	Ceratophyllaceae	New Zealand, Germany, New Zealand	3
Ceratopteris thalictroides (Linné) Brongniart	Invasive	Parkeriaceae	Hungary, Italy, New Zealand	1
Egeria densa Planch	Invasive	Hydrocharitaceae	New Zealand, France, United States, Australia, Hungary, Italy	11
Pontederia (Eichhornia) crassipes Mart. (Solms)	Invasive	Pontederiaceae	China, United States, Papua New Guinea, Guatemala, Australia	9
Elodea canadensis Michx	Invasive	Hydrocharitaceae	New Zealand, Germany, Hungary, France, Italy, Serbia, Sweden	10
Elodea nutallii (Planch.) H.St.J	Invasive	*Hydrocharitaceae*	Hungary, France, Italy, Serbia, Netherlands	7
Glyceria maxima (Hartm.) Holmb	Invasive	Poaceae	New Zealand	1
Gymnocoronis spilanthoides DC.	Invasive	Asteraceae	Australia	1
Hedychium coronarium J. König	Invasive	Zingiberaceae	Brazil	1
Hydrilla verticillata (L.f.) Royle	Invasive	Hydrocharitaceae	Germany, Guatemala, Hungary, Italy, United States	5
Hydrocotyle ranunculoides L.fil.	Invasive	Araliaceae	Europe, Asia, Africa	1
Hydrocotyle vulgaris L.	Invasive	Araliaceae	China	1
Lagarosiphon major (Ridl.) Moss	Invasive	Hydrocharitaceae	Netherlands, France, Alamanha, Hungary, Italy	6
Lemna minuta Kunth	Invasive	Araceae	Hungary, Italy	1
Ludwigia grandiflora (Michx.) Greuter & Burdet	Invasive	Onagraceae	France	2
Ludwigia hexapetala (Hook. & Arn.) Zardini et al.	Invasive	Onagraceae	France, Italy, Hungary, Italy, United States	6
Ludwigia peploides subsp. montevidensis (Spreng.) P.H.Raven.	Invasive	Onagraceae	United States	1
Lygodium microphyllum (Cav.) R.Br.	Invasive	Lygodiaceae	United States	1
Lythrum salicaria L.	Invasive	Lythraceae	Not informed	4
Myriophyllum aquaticum (Vell.) Verd.	Invasive	Haloragaceae	New Zealand, France, Hungary, Italy, United States, Australia	6
Myriophyllum heterophyllum Michx.	Invasive	Haloragaceae	Germany	1
*Myriophyllum salicaria**	Invasive	Haloragaceae	United States	1
Myriophyllum spicatum L.	Invasive	Haloragaceae	Germany, Netherlands, United States	7
Myriophyllum variifolium Hook.f.	Invasive	Haloragaceae	New Zealand	1
Najas flexilis (Willd.) Rostk. & Schmidt	Invasive	Hydrocharitaceae	Not informed	1
Nasturtium spp W.T.Aiton	Invasive	Brassicaceae	New Zealand	1
Nelumbo nucifera Gaertn.	Invasive	Nelumbonaceae	Hungary, Italy	2

*To our knowledge, there is no species named '*Myriophyllum salicaria*', this supposed species were cited in an article, but we do suspect that the correct species would be another one. **The authors **refer** to varieties of *Nymphaea* in their study, then we cited the genus author here.

Table 1. Continued...

Species	*Status*	Family	Region	N. of Studies
Nymphaea odorata Ait.	Invasive	Nymphaeaceae	Hungary, Italy	1
Nymphaea rubra Roxb	Invasive	Nymphaeaceae	Hungary, Italy	1
Nymphaea x "bluebird" L. **	Invasive	Nymphaeaceae	Hungary, Italy	1
Nymphaea x "purpurea" L. **	Invasive	Nymphaeaceae	Hungary, Italy	1
Nymphaea x marliacea L. **	Invasive	Nymphaeaceae	Hungary, Italy	1
Parthenium hysterophorus L.	Invasive	Asteraceae	Not informed	1
Paspalum distichum L.	Invasive	Poaceae	Serbia	1
Phalaris arundinacea L.	Invasive	Poaceae	United States	3
Phragmites australis (Cav.) Trin ex. Steud	Invasive	Poaceae	Australia (Native Invasive), United States	6
Pistia stratiotes L.	Invasive	Araceae	China, United States	3
Potamogeton crispus L.	Invasive	Potamogetonaceae	New Zealand, United States	4
Potamogeton pectinatus L.	Invasive	Potamogetonaceae	Not informed	1
Ranunculus flammula L.	Invasive	Ranunculaceae	New Zealand	1
Ranunculus trichophyllus Chaix ex Vill.	Invasive	Ranunculaceae	New Zealand	1
Rotala rotundifolia (Buch-Ham. ex Roxb) Koehne	Invasive	Lythraceae	Hungary, Italy	1
Salvinea molesta D.S.Mitch.	Invasive	Salviniaceae	Papua New Guinea, Australia	2
Tamarix ramosissima Ledeb	Invasive	Tamaricaceae	United States	1
Trapa natans L.	Invasive	Lythraceae	Hungary, Italy, United States	2
Typha angustifolia L.	Invasive	Typhaceae	United States	6
Typha domingensis (Pers.)	Invasive	Typhaceae	United States	1
Urochloa arrecta (Hack. ex T. Durand & Schinz) Morrone & Zuloaga	Invasive	Poaceae	Brazil	1
Utricularia gibba L.	Invasive	Lentibulariaceae	Hungary, Italy	1
Vallisneria americana Michx	Invasive	Hydrocharitaceae	Hungary, Italy	1
Vallisneria gigantea Graebn.	Invasive	Hydrocharitaceae	Hungary, Italy	1
Vallisneria spiralis L.	Invasive	Hydrocharitaceae	Hungary, Italy, Serbia	2
Veronica anagallis-aquatica L.	Invasive	Scrophulariaceae	New Zealand	1
Alternanthera denticulate R.Br.	Native	Amaranthaceae	Australia	1
Azolla filiculoides Lam.	Native	Salviniaceae	Australia	2
Callitriche obtusangula Le Gall.	Native	Callitrichaceae	Hungary, Italy	1
Callitriche platycarpa Kütz	Native	Callitrichaceae	Hungary, Italy	1
Ceratophyllum demersum L.	Native	Ceratophyllaceae	France, Hungary, Italy, United States	5
Chara globularis Thuill	Native	Characeae	Germany	1
Chara spp L.	Native	Characeae	Sweden	1
Comarum palustre L.	Native	Rosaceae	United States	1
Cyperus exaltatus Retz	Native	Cyperaceae	Australia	1
Dulichium arundinaceum L.	Native	Cyperaceae	United States	1
Eclipta prostrate L.	Native	Asteraceae	Australia	1
Pontederia (Eichhornia) azurea (Sw.) Kunth	Native	Pontederiaceae	Brazil	1
Elodea canadensis Michx	Native	Hydrocharitaceae	United States	1
Equisetum fluviatile L.	Native	Equisetaceae	United States	1
Hippuris vulgaris L.	Native	Hippuridaceae	Hungary, Italy	1
Hottonia palustris L.	Native	Primulaceae	Hungary, Italy	1
Typha x glauca Godr.	Native	Typhaceae	Not informed	1
Hydrilla verticillata (L.f.) Royle	Native	Hydrocharitaceae	Australia, China	2
Hydrocharis dubia (Bl.) Backer	Native	Hydrocharitaceae	China	1
Hydrocharis morsus-ranae L.	Native	Hydrocharitaceae	Hungary, Italy	1
Hydrocotyle ranunculoides L.fil.	Native	Araliaceae	United States	1
Hydrocotyle umbellata L.	Native	Araliaceae	United States	1
Iris versicolor L.	Native	Iridaceae	United States	1

*To our knowledge, there is no species named '*Myriophyllum salicaria*', this supposed species were cited in an article, but we do suspect that the correct species would be another one. **The authors **refer** to varieties of *Nymphaea* in their study, then we cited the genus author here.

Table 1. Continued...

Species	*Status*	Family	Region	N. of Studies
Isachne globosa (Thunb. ex Murray) Kuntze	Native	Poaceae	New Zealand	1
Lemna gibba L.	Native	Araceae	Hungary, Italy	1
Lemna minor L.	Native	Araceae	Hungary, Italy	2
Lemna trisulca L.	Native	Araceae	Hungary, Italy	1
Limnophila heterophylla (Roxb.) Benth.	Native	Plantaginaceae	China	1
Ludwigia peploides (Kunth) Raven *subsp. montevidensis* (Spreng) Raven	Native	Onagraceae	Australia	1
Marsilea quadrifolia L.	Native	Marsileaceae	Hungary, Italy	1
Mentha aquatic L.	Native	Lamiaceae	France	2
Monochoria cyanaea (F.Muell.) F.Muell.	Native	Pontederiaceae	Australia	1
Murdannia triquetra (Wall.) Bruckn	Native	Commelinaceae	China	1
Myosotis scorpioides L.	Native	Boraginaceae	France	1
Myriophyllum papillosum Orchard	Native	Haloragaceae	Australia	1
Myriophyllum propinquum A.Cunn.	Native	Haloragaceae	New Zealand	1
Myriophyllum spicatum L.	Native	Haloragaceae	France, China, Hungary, Italy	4
Myriophyllum verticillatum L.	Native	Haloragaceae	Hungary, Italy	1
Najas flexilis (Willd.) Rostk. & W.L.E. Schmidt	Native	Hydrocharitaceae.	United States	1
Najas marina L.	Native	Hydrocharitaceae.	Hungary, Italy	2
Najas minor All.	Native	Hydrocharitaceae.	China	1
Nitella sp. aff. cristata C. Agardh **	Native	Characeae	New Zealand	2
Nuphar lutea (L.) Sm	Native	Nymphaeaceae	Italy, Hungary	3
Nymphaea alba L.	Native	Nymphaeaceae	Italy, Hungary	3
Nymphoides peltatum (Gmel.) Kuntze	Native	Menyanthaceae	China	1
Ottelia alismoides (L.)	Native	Hydrocharitaceae	China	1
Ottellia ovalifolia (R.Br.) Rich.	Native	Hydrocharitaceae	Australia	1
Potamogeton epihydrus Raf.	Native	Potamogetonaceae	United States	1
Persicaria decipiens (R.Br.) Wilson	Native	Polygonaceae	New Zealand	1
Phragmites australis subsp. americanus Saltonst., P.M. Peterson & Soreng	Native	Poaceae	Not informed	1
Pontederia cordata L.	Native	Pontederiaceae	Not informed	1
Potamogeton berchtoldii Fieber	Native	Potamogetonaceae	Hungary, Italy	1
Potamogeton cheesemanii A.Benn.	Native	Potamogetonaceae	New Zealand	1
Potamogeton crispus L.	Native	Potamogetonaceae	Hungary, Italy, China	2
Potamogeton javanicus Hassk.	Native	Potamogetonaceae	Australia	1
Potamogeton lucens L.	Native	Potamogetonaceae	Hungary, Italy	1
Potamogeton maackianus A. Benn	Native	Potamogetonaceae	China	1
Potamogeton natans L.	Native	Potamogetonaceae	Hungary, Italy	1
Potamogeton nodosus Poir.	Native	Potamogetonaceae	Hungary, Italy	1
Potamogeton ochreatus Raoul	Native	Potamogetonaceae	New Zealand	1
Potamogeton pectinatus L.	Native	Potamogetonaceae	Hungary, Italy	1
Potamogeton perfoliatus L.	Native	Potamogetonaceae	Hungary, Italy, Netherlands	2
Potamogeton polygonifolius Pourr.	Native	Potamogetonaceae	Hungary, Italy	1
Potamogeton pusillus L.	Native	Potamogetonaceae	United States	1
Potamogeton richardsonii (A. Benn.) Rydb.	Native	Potamogetonaceae	United States	1

*To our knowledge, there is no species named '*Myriophyllum salicaria*', this supposed species were cited in an article, but we do suspect that the correct species would be another one. **The authors **refer** to varieties of *Nymphaea* in their study, then we cited the genus author here.

Table 1. Continued...

Species	*Status*	Family	Region	N. of Studies
Potamogeton robbinsii Oakes	Native	Potamogetonaceae	United States	1
Potamogeton sp. L.	Native	Potamogetonaceae	Sweden	1
Potamogeton suboblongus Hagstr.	Native	Potamogetonaceae	New Zealand	1
Potamogeton trichoides Cham. & Schltdl.	Native	Potamogetonaceae	Hungary, Italy	1
Ranunculus aquatilis L.	Native	Ranunculaceae	Hungary, Italy	1
Ranunculus fluitans Lam.	Native	Ranunculaceae	Hungary, Italy	1
Ranunculus trichophyllus Chaix	Native	Ranunculaceae	Hungary, Italy	2
Sagittaria trifolia L.	Native	Alismataceae	China	1
Salvinia natans L.	Native	Salviniaceae	Hungary, Italy	1
Schoenoplectus acutus (Muhl. ex Bigelow) Á. Löve & D. Löve	Native	Cyperaceae	Not informed	1
Schoenoplectus californicus (C.A.Mey.) Soják	Native	Cyperaceae	Guatemala	1
Schoenoplectus tabernaemontani (C. C. Gmel.) Palla	Native	Cyperaceae	United States	1
Sparganium emersum Rehmann	Native	Typhaceae	Hungary, Italy	1
Sparganium minimum (L.) Fr.	Native	Typhaceae	Hungary, Italy	1
Spirodela polyrrhiza (L.) Schleid.	Native	Araceae	Hungary, Italy	1
Trapa bispinosa Roxb. (OF)	Native	Lythraceae	China	1
Trapa natans L.	Native	Lythraceae	Italy, Hungary	2
Trapella sinensis Oliv.	Native	Plantaginaceae	China	1
Typha latifolia L.	Native	Typhaceae	United States	2
Typha orientalis C.Presl Bulrush	Native	Typhaceae	New Zealand	1
Typha spp L.	Native	Typhaceae	United States	1
Utricularia australis R.Br.	Native	Lentibulariaceae	Hungary, Italy	1
Utricularia vulgaris L.	Native	Lentibulariaceae	Hungary, Italy	2
Vallisneria americana Michx	Native	Hydrocharitaceae	United States	4
Vallisneria nana R.Br.	Native	Hydrocharitaceae	Australia	1
Vallisneria natans (Lour.) Hara	Native	Hydrocharitaceae	China	1
Vallisneria spiralis L.	Native	Hydrocharitaceae	Australia	1
Wolffia arrhiza (L.) Horkel ex Wimm.	Native	Araceae	Hungary, Italy	1
Zizania latifolia (Griseb.) Turcz. ex Stapf	Native	Poaceae	China	1

*To our knowledge, there is no species named '*Myriophyllum salicaria*', this supposed species were cited in an article, but we do suspect that the correct species would be another one. **The authors **refer** to varieties of *Nymphaea* in their study, then we cited the genus author here.

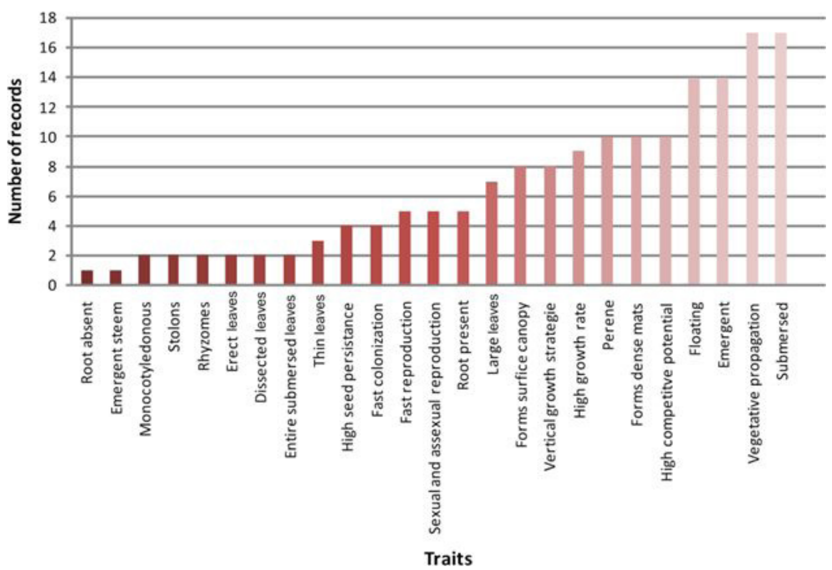


Figure 4. Most common traits recorded for invasive species in all articles analyzed after the search (see Methods for search details).

Table 2. Table of traits recorded in the articles (see the search in methods), separated by their group, number records, and their relation (or not) with invasion success.

Group traits	Nr. of records	Traits related to invasiveness	Invasiveness
Morphological	59	38	64.40%
Growth	37	35	94.59%
Life form	50	0	0%
Physiological	39	29	74.35%
Reproductive/life cycle	51	46	90.19%
Effects on ecosystem	3	1	33.33%
Competitive potential	10	10	100%
Trade-offs	6	4	66.66%
Response to environmental conditions	122	86	70.49%
Biotic interactions	159	141	88.67%
Total	536	390	72.76%

Table 3. Invasive and native macrophytes traits found in the 31 articles, divided by their trait group and related to invasiveness.

Trait Group	Invasives		Natives	
	Number of records	Invasiveness	Number of records	% Invasiveness
Morphological	19	57.89%	32	28.12%
Growth	17	64.7%	4	100%
Life form	47	0%	80	0%
Physiological	14	57.14%	12	58.33%
Reproductive	8	100%	4	100%
Competitive ability	1	100%	0	0%
Trade-offs	3	0%	0	0%
Response - environmental conditions	39	53.84%	37	78.37%
Biotic interactions	136	88.23%	35	31.42%
Total	284	57.97%	204	44.02%

group of traits to directly relate to invasion success. Therefore, we did not assume the relationship between life form and the possibility of invasion success in any case, since a more detailed analysis would be necessary (see also Hussner et al., 2021).

Biotic interaction traits were measured in different conditions and with the comparison of invasive macrophytes traits to natives or other invasive macrophytes traits. Most often for invasive species, traits were related to competition (n = 142; 89.3%) or tolerances (n = 4; 2.5%), and in general, 88.1% (n = 161) of traits indicated possible success in new environments.

The temperature increase was the most studied condition to measure response traits of invasive and native species, and for both invasives and natives, the success probability (invasiveness) was very high, indicating no particular advantage to invasive species. Desiccation and light limitations by shadow were also very studied, and for desiccation invasive macrophytes traits were mostly related to invasion success (70.5%), as for shadow this percentage was lower (40%, Figure 5).

When analyzing the 31 articles that compared invasive and native macrophytes traits, the main differences between the two groups can be seen in morphological, response and biotic interaction traits (Table 3). Invasive species had a higher proportion of morphological traits related to invasiveness (n = 11 out of 19; 57.8%), as well as biotic interaction traits (n = 120 out of 136; 88.2%). Native species had a lower proportion of morphological and biotic traits related to invasiveness, however, response traits were overall more related to invasiveness (n = 29 out of 37; 78.3%) than invasive species (n = 21 out of 39; 31.4%). Most traits recorded for native species involved macrophyte life form, mostly submersed, which as we pointed out, cannot be directly related to invasiveness without the understanding of the environment where the species are. Biotic interaction traits of native species were often related to competition (n = 24; 72.7%), followed by physiology (n = 6; 18.2%) and facilitation (n = 3; 9.1%).

The NODF analysis showed a low degree of nestedness (NODF = 19.77), and also the most

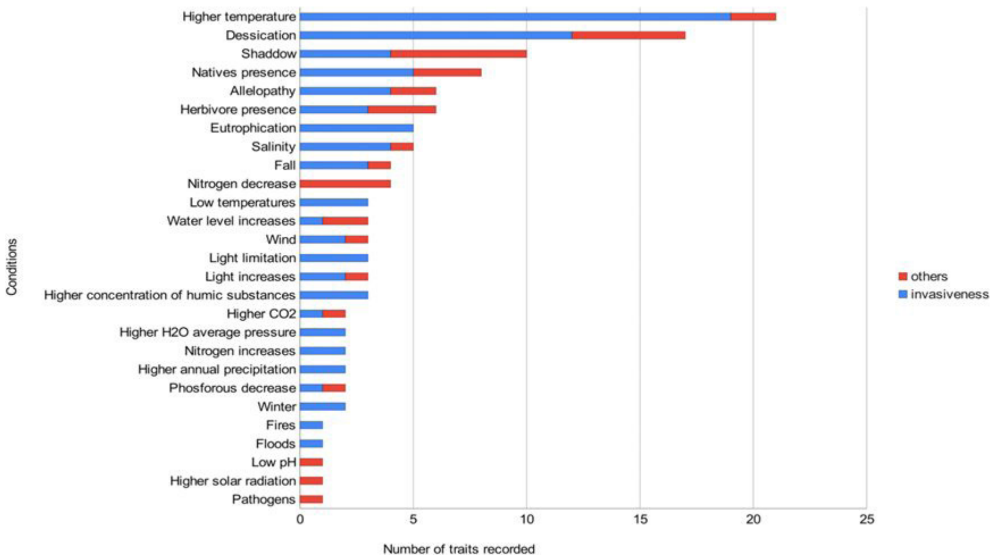


Figure 5. The number of traits recorded for invasive species (axis x), in different environmental conditions (axis y), related to invasiveness (probability of invasion success, color blue) or not (Others, color red).

recorded tolerance traits for each invasive species (Figure 6). *E. densa, E. canadensis* and *Elodea nutalli* (Planch.) H.St.J were the species connected to more environmental conditions, showing a wider range of environmental tolerances (Figure 6). Also, most species seemed more connected to high temperatures and desiccation conditions, indicating a vast range of invasive species tolerant to such conditions.

4. Discussion

The interest in studies involving invasive macrophytes and functional traits is clearly increasing and has gained popularity, being thoroughly studied throughout the years (see Figure 1). There are studies that go way back and already analyzed species traits, even without calling it so. The opposite is also true, in the sense that many articles claimed to work with species traits, but only discussed some species characteristics, without linking them with any ecological question. This raises the question of whether or not the concept of functional traits is being correctly used in studies. The concept is already very broad, and so if one really thinks about it, any species' characteristics could be a functional trait. However, this can really be a challenge when working with functional traits: what traits do you consider or not in your work? In a review, what traits are included or not? Here, we propose that a functional trait should be considered only when this particular trait is indeed related to an ecological function in the study. Therefore, studies should state the contingencies that define the use of functional traits. In that way, broad and meaningless characteristics are ruled out and the concept is narrowed.

Most articles were published in the United States, which makes sense since this is a developed country with many funding opportunities and researchers. France also published many articles, and even though France is geographically smaller than the United States, functional diversity research is very strong there (see CEFE, 2023).

The invasive species most recorded were *E. densa* and *E. canadensis*, both wide world invaders, and therefore very studied macrophytes. It is worth mentioning that both of them have a wide environmental tolerance (Figure 6) and both belong to the Hydrocharitaceae family, which was the most recorded family of invasive species in this study. Indeed, Hydrocharitaceae is a family with a high number of invasives, mostly submerged species, and the reasoning behind that fact is of interest in invasion studies. One of the traits that could help the members of this family to become invasive is allelopathy, a functional trait very present among the Hydrocharitaceae (Hussner et al., 2021). Through allelopathy, macrophytes species release chemical substances in the sediment or the water column, such as phenolics, which could hinder the development of other species, such as natives in new locations, and therefore may allow invasive colonization (Thiébaut et al., 2018). For instance, *E. nuttallii* and *E. canadensis* can produce flavonoids, which can affect other macrophytes and has shown to hinder cyanobacteria and herbivores' larvae growth as well (Erhard & Gross, 2005). As far as environmental tolerances, many invasive species

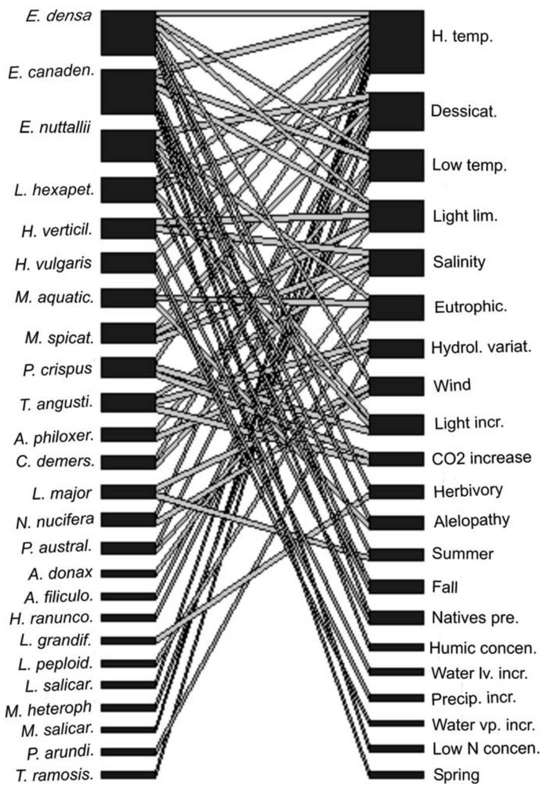


Figure 6. A plot of interactions between invasive macrophyte species and their tolerances to different environmental conditions. Each line corresponds to one connection (tolerance). Species subtitles (see authors names in Table 1): *E. canaden.* = *Elodea canadensis*; *L. hexapet.* = *Ludwigia hexapetala*; *H. vertical.* = *Hydrilla verticillata; M. aquatic.* = *Myriophyllum aquaticum; M. spicat* = *Myriophyllum spicatum; T. angusti.* = *Typha angustifolia;A. philoxer.* = *Alternantera philoxeroides; C. demers.* = *Ceratophyllum demersum; P. austral.* = *Phragmites australis; A. filiculo.* = *Azolla filiculoides; H. ranunco.* = *Hydrocotyle ranunculoides; L. grandif.* = *Ludwigia grandiflora; L. peploid.* = *Ludwigia peploides; M. heteroph.* = *Myriophyllum heterophyllum; M. salicar.* = *Myriophyllum salicaria; P. arundi.* = *Phalaris arundinacea; T. ramosis.* = *Tamarix ramosissima*. Environmental conditions subtitles: H. temp. = High temperatures; Dessicat. = Desiccation; Low temp. = Low temperatures; Light lim. = light limitations; Eutrophic. = Eutrophication; Hydrol. Variat. = Hydrological variation; Light incr. = Light increases; Natives pre. = natives presence; Humic concen. = High humic concentrations; Water lv. Incr. = Water level increase; Precip. Incr. = Precipitation increase; Water vp. Incr. = Water vapor increase; Low N. Concen. = Low nitrogen concentrations.

usually show tolerance to stressful conditions (Bora et al., 2020; Michelan et al., 2010, etc), however, it is curious that *E. densa* and *E. canadensis* were the species most related to a wider range of environmental tolerances. This could be due to the number of articles working with these particular species. Still, within Hydrocharitaceae, there are other invasives with wide environmental tolerances, such as *Hydrilla verticillata* and *Thalassia testudinum* (Benzecry & Brack-Hanes, 2016), which may indicate a pattern inside the family.

The most studied invasive species group traits were morphological, response and biotic interaction traits. Morphological traits most often recorded were large leaves (n=6) and the formation of a canopy outside of the water surface (n=8). This group of traits is often measured and analyzed aiming to generate knowledge about the physiology and anatomy of the invasive species (Riis et al., 2012). When a given nuisance species is well studied the chances of a successful management action against it are higher. Response traits often are measured in ecological studies not only to study possible management actions but also to evaluate possible new environments where species could invade, therefore is a way to prevent invasion (Bora et al., 2020). Furthermore, biotic interaction traits often are measured in competition studies. Competition is the interaction and interference in performance between two or more individuals, affecting species abundance (Thouvenot et al., 2013). Therefore, it makes sense that there are many studies within this theme since it can measure invasive species' impacts in a given community (Carniatto et al., 2013) and also investigate native species that can act as a barrier against invasives establishment, preventing invasion from happening (Levine et al., 2004). It is interesting though, that biotic interaction traits were all very related to species invasiveness, and it raises the question of whether or not traits related to invasiveness are inherent in invasive species (Hussner et al., 2021). Even if traits related to invasiveness are a result of plastic phenotypic responses after an environmental selective pressure event, if phenotypic plasticity is considered a trait, then this hypothesis could be corroborated. Indeed, phenotypic plasticity is often recorded for invasive species, which could be responsible for their success in the colonization of new environments (Fleming & Dibble, 2015).

Overall, most invasive macrophyte traits were related to invasiveness as well, such as high seed persistence, high growth and reproductive rates, and vegetative reproduction. Vegetative reproduction was the trait most reported in the articles from the search and is very related to invasiveness since asexual clonal reproduction is very fast and aids aquatic plant species invasion (Fleming & Dibble, 2015). Within response traits, high temperature, desiccation, and shadow were the environmental conditions more studied. Simulations of higher temperatures within ecological studies are driven by the current climate change scenario. Niche modeling approaches are very useful for invasion studies since they can estimate possible new locations of invasive species occurrence in the future. Many studies claim that warmer temperatures can enhance macrophytes invasions (Calvo et al., 2019), however, in the articles found from the search, both invasive and native species possessed traits related to high-temperature tolerance, such as higher growth or biomass in this condition (Stephens et al., 2019). Macrophytes are by definition aquatic plants that need water for their survival or reproduction (Barrat-Segretain & Cellot, 2007; Silveira et al., 2009). However, there are many studies that recorded macrophytes relatively tolerant to this condition (Michelan et al., 2010). This is what we also observed, since most invasive macrophyte traits in desiccation regimes were related to invasiveness, that is, traits that indicated tolerance within this condition as well. Shadow conditions had not the same invasiveness trait rate recorded: invasives presented fewer traits related to shadow tolerance. Some studies have already demonstrated that shadow provided by native riparian vegetation could indeed prevent exotic macrophyte invasions (Evangelista et al., 2017).

Of all articles found and kept for analysis after the search, nearly half of them compared the traits of invasive and native species. This is probably due to studies aiming to find competition results between the species, which could be very useful for strategies in invasion management actions (Richter & Gross, 2013). Also, the biotic resistance hypothesis is very strong in invasion ecology, and some authors question the hypothesis's effectiveness (Fridley et al., 2007; Jeschke et al., 2012). It is well-established that biotic resistance (i.e., the high number of native species preventing invasive species establishment) is effective (Elton, 1958; Beaury et al., 2020). Other than preventing species invasion, studies that confirm cases of biotic resistance are very good for conservation strategies since native biodiversity conservation is encouraged.

In the 31 articles that compared invasive and native macrophyte traits, the most interesting differences between native and invasive traits can be seen in morphological, biotic interaction, and response traits. Morphological traits and biotic interaction traits of invasives were more related to invasiveness (57.89 and 88.23%, respectively), however, response traits of natives were more often related to invasiveness than invasive traits. This is curious since it is often reported that invasives are tolerant to a wide range of environmental factors, which indeed is the case when we look at all the articles from the search, where biotic interaction traits are related to invasiveness. This could be due to the fact that articles comparing invasives and native macrophyte traits in a given condition could be made aiming to find some biological control or environmental filter for invasives (Mouton et al., 2019). Also, competition studies often use phylogenetically similar species and this could also be responsible for the similar traits with invasive and native species. Overall, almost all groups of traits of invasives were more related to invasiveness, with the exception of response and growth traits. However, the growth traits of natives had a low number of reports, which makes this comparison more difficult.

Here, we reported all functional traits of invasive macrophytes found in a global search and related them with species invasiveness. All group traits of invasive species found in the article's search were related to a high invasiveness rate, with the exception of group trait "ecosystems effects". Ecosystem effects traits were related to invasiveness when species' presence modified the environment in a way that could facilitate their establishment in the new environment. However, only 3 traits were registered in this group category, and therefore it is difficult to state that this group was indeed not related to invasive species invasiveness. In the articles comparing invasive and native macrophyte traits, almost all trait groups of invasives were more related to invasiveness than natives' traits, with the exception of response traits.

We do believe that our work complements the recent work of Hussner et al. (2021), as well as their work complements ours. After all, they related invasiveness traits with macrophytes' life form, which we did not here. On the other hand, our work considered another perspective, with the analysis of a wider range and a different set of traits of macrophyte species. We also performed a quantitative register of species traits as well as their percentage of relation with invasiveness. Furthermore, we also compared all traits of native and invasive species reported in the articles found in the search, aiming to find if invasive traits were more related to their probability of establishment in new environments. Finally, we show species with a higher range of environmental tolerances, as well as the conditions more related to macrophytes invasion success.

Since there was a very high rate of invasive macrophyte traits that were related to their probability of succeeding in new environments, and also invasive traits were more related to invasiveness than native traits, we can say that our review is useful to understand macrophyte invasiveness. That can mean that, although it is difficult to say that there are traits exclusive to invasive macrophytes (likely due to context dependencies), they indeed possess a higher number of invasiveness-related traits in general that aid their establishment in new locations. Although no specific traits can be generalized to all environments, a higher proportion of traits of invasive species related to invasiveness indicate that invasive species present 'novel weapons' (see Callaway & Ridenour, 2004) to deal with ecological trade-offs, explaining their invasion successes. Also, we found that of all the groups of traits analyzed, the traits related to growth and reproduction are more associated with invasive success. In that matter, we hope that our review can be used as a baseline for aquatic management strategies since it can be used to elucidate how macrophyte traits can predict invasiveness.

Acknowledgements

A. A. Padial acknowledges CNPq for continuous financial support (Process Numbers: 307984/2015-0, 402828/2016-0, 301867/2018-6, 308648/2021-8). L. S. Bora also acknowledges CAPES for her student scholarship. The authors acknowledge the anonymous reviewers and the associate editor for valuable suggestions in previous drafts of this manuscript.

References

Alpert, P., Bone, E., & Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. Syst. 3(1), 52-66. http://dx.doi.org/10.1078/1433-8319-00004.

Azzurro, E., Tuset, V.M., Lombarte, A., Maynou, F., Simberloff, D., Rodríguez-Pérez, A., & Solé, R.V., 2014. External morphology explains the success of biological invasions. Ecol. Lett. 17(11), 1455-1463. PMid:25227153. http://dx.doi.org/10.1111/ele.12351.

Barrat-Segretain, M.H., & Cellot, B., 2007. Response of invasive macrophyte species to drawdown: the case of *Elodea* sp. Aquat. Bot. 87(4), 255-261. http://dx.doi.org/10.1016/j.aquabot.2007.06.009.

Beaury, E.M., Finn, J.T., Corbin, J.D., Barr, V., & Bradley, B.A., 2020. Biotic resistance to invasion is ubiquitous across ecosystems of the United States. Ecol. Lett. 23(3), 476-482. PMid:31875651. http://dx.doi.org/10.1111/ele.13446.

Benzecry, A., & Brack-Hanes, S., 2016. Evolutionary trends in hydrocharitaceae seagrasses. Annu. Res. Rev. Biol. 9(6), 1-8. http://dx.doi.org/10.9734/ARRB/2016/24354.

Bora, L.S., Thomaz, S.M., & Padial, A.A., 2020. Evidence of rapid evolution of an invasive poaceae in response to salinity. Aquat. Sci. Online 82(4), 76e. http://dx.doi.org/10.1007/s00027-020-00750-y.

Callaway, R.M., & Ridenour, W.M., 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Front. Ecol. Environ. 2(8), 436-443. http://dx.doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2.

Calvo, C., Mormul, R.P., Figueiredo, B.R.S., Cunha, E.R., Thomaz, S.M., & Meerhoff, M., 2019. Herbivory can mitigate, but not counteract, the positive effects of warming on the establishment of the invasive macrophyte *Hydrilla verticillata.* Biol. Invas. 21(1), 59-66. http://dx.doi.org/10.1007/s10530-018-1803-3.

Capers, R.S., Selsky, R., & Bugbee, G.J., 2010. The relative importance of local conditions and regional process in structuring aquatic plant communities. Freshw. Biol. 55(5), 952-966. http://dx.doi.org/10.1111/j.1365-2427.2009.02328.x.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kingiz, A.P., Daily, G.C., Loeau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., & Naeem, S., 2012. Biodiversity loss and the impact on humanity. Nature 486(7401), 59-67. PMid:22678280. http://dx.doi.org/10.1038/nature11148.

Carniatto, N., Thomaz, S.M., Cunha, E.R., Fugi, R., & Ota, R.R., 2013. Effects of an invasive alien poaceae on aquatic macrophytes and fish communities in a neotropical reservoir. Biotropica 45(6), 747-754. http://dx.doi.org/10.1111/btp.12062.

Centre d'Ecologie Fonctionnelle et Evolutive - CEFE, 2023, UMR 5175 du CNRS. [online]. Retrieved in 2023, July 18, from https://www.cefe.cnrs.fr/en/.

Elton, C.S., 1958. The ecology of invasions by animals and plants. The University of Chicago Press, Chicago. http://dx.doi.org/10.1007/978-1-4899-7214-9.

Erhard, D., & Gross, E., 2005. Do environmental factors influence composition of potential allelochemicals in the submersed freshwater macrophyte *Elodea nuttallii* (Hydrocharitaceae)? Verh. Internationalen Vereinigung Limnol. 29(1), 287-291. http://dx.doi.org/10.1080/03680770.2005.11902015.

Evangelista, H.B., Michelan, T.S., Gomes, L.C., & Thomaz, S.M., 2017. Shade provided by riparian plants and biotic resistance by macrophytes reduce the establishment of an invasive Poaceae. J. Appl. Ecol.

54(2), 648-656. http://dx.doi.org/10.1111/1365-2664.12791.

Fleming, J.P., & Dibble, E.D., 2015. Ecological mechanisms of invasion success in aquatic macrophytes. Hydrobiologia 746(1), 23-37. http://dx.doi.org/10.1007/s10750-014-2026-y.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., & Von Holle, B., 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88(1), 3-17. PMid:17489447. http://dx.doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2.

Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J., & Licari, D., 2005. Life-history correlates of plant invasiveness at regional and continental scales. Ecol. Lett. 8(10), 1066-1074. http://dx.doi.org/10.1111/j.1461-0248.2005.00809.x.

Hussner, A., Heidbüchel, O., Coetzee, J., & Gross, E.M., 2021. From introduction to nuisance growth: a review of traits of alien aquatic plants which contribute to their invasiveness. Hydrobiologia 848(9), 2119-2151. http://dx.doi.org/10.1007/s10750-020-04463-z.

Jeschke, J.M., Gómez Aparicio, L., Haider, S., Heger, T., Lortie, C.J., Pysek, P., & Strayer, D.L., 2012. Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14, 1-20. http://dx.doi.org/10.3897/neobiota.14.3435.

Lavorel, S., & Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16(5), 545-556. http://dx.doi.org/10.1046/j.1365-2435.2002.00664.x.

Levine, J.M., Adler, P.B., & Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7(10), 975-989. http://dx.doi.org/10.1111/j.1461-0248.2004.00657.x.

Michelan, T.S., Thomaz, S.M., Carvalho, P., Rodrigues, R.B., & Silveira, M.J., 2010. Regeneration and colonization of an invasive macrophyte grass in response to desiccation. Nat. Conserv. 8(02), 133-139. http://dx.doi.org/10.4322/natcon.00802005.

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. PMid:31096347. http://dx.doi.org/10.1016/j.scitotenv.2018.12.277.

Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., & Whiting, P., Moher, D., 2020. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews [online]. Retrieved in 2023, July 18, from http://prisma-statement.org

Pyšek, P., & Richardson, D.M., 2008. Traits Associated with Invasiveness in Alien Plants: Where Do we Stand? In: Nentwig, W. ed. Biological Invasions. Berlin, Heidelberg: Springer, Ecological studies: analysis and synthesis, vol. 193. https://doi.org/10.1007/978-3-540-36920-2_7

Richter, D., & Gross, E.M., 2013. *Chara* can outcompete *Myriophyllum* under low phosphorus supply. Aquat. Sci. 75(3), 457-467. http://dx.doi.org/10.1007/s00027-013-0292-9.

Riis, T., Olesen, B., Clayton, J.S., Lambertini, C., Brix, H., & Sorrell, B.K., 2012. Growth and morphology in relation to temperature and light availability during the establishment of three invasive aquatic plant species. Aquat. Bot. 102, 56-64. http://dx.doi.org/10.1016/j.aquabot.2012.05.002.

Silveira, M.J., Thomaz, S.M., Mormul, R.P., & Camacho, F.P., 2009. Effects of desiccation and sediment type on early regeneration of plant fragments of three species of aquatic macrophytes. Int. Rev. Hydrobiol. 94(2), 169-178. http://dx.doi.org/10.1002/iroh.200811086.

Skóra, F., Abilhoa, V., Padial, A.A., & Vitule, J.R.S., 2015. Darwin's hypotheses to explain colonization trends: evidence from a quasi-natural experiment and a new conceptual model. Divers. Distrib. 21(5), 583-594. http://dx.doi.org/10.1111/ddi.12308.

Stephens, K.L., Dantzler-Kyer, M.E., Patten, M.A., & Souza, L., 2019. Differential responses to global change of aquatic and terrestrial invasive species: evidences from a meta-analysis. Ecosphere Online 10(4), e4. http://dx.doi.org/10.1002/ecs2.2680.

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. PMid:30631329. http://dx.doi.org/10.3389/fpls.2018.01835.

Thouvenot, L., Puech, C., Martinez, L., Haury, J., & Thiébaut, G., 2013. 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. http://dx.doi.org/10.1016/j.aquabot.2013.01.003.

Tilman, D., 2001 Functional diversity. In: Levin, S.A., ed. Encyclopedia of biodiversity. San Diego: Academic Press, 109-120. http://dx.doi.org/10.1016/B0-12-226865-2/00132-2.

Received: 24 June 2022
Accepted: 27 June 2023

Associate Editor: Thaisa Sala Michelan.