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ECOLOGY OF AQUATIC MACROPHYTES IN BRAZIL: THE LEGACY OF FRANCISCO DE ASSIS ESTEVES

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Abstract: In this review, we evaluate the contribution of Brazilian limnologists to research outputs on aquatic macrophyte ecology. We found a strong "adviser effect" of Professor F.A. Esteves on the Brazilian scientific production focused on aquatic macrophytes. In general, articles focused on a variety of themes, including, *inter alia*, the role of aquatic macrophytes on the biodiversity of other groups, the interaction between macrophytes and the environment, the effects of environmental factors on aquatic macrophytes distribution and biodiversity, the effects of invasive species on aquatic biodiversity, aquatic macrophytes control and decomposition. Emerging topics (*e.g.*, metacommunity ecology, biodiversity-ecosystem functioning, and patterns of diversity and their determinants) are being embraced by Brazilian limnologists that use aquatic macrophytes as organism models. Despite the fact there is much to study, we think that directly (*e.g.*, via mentoring) or indirectly (via publications), our current knowledge about macrophytes ecology was inspired by Chico Esteves.

Keywords: tribute, aquatic plants, limnology, emerging topics.

INTRODUCTION

Currently, it is almost an aphorism to state that aquatic macrophytes are of pivotal importance to the structure and functioning of aquatic ecosystems. Also, this community has been widely used as a model to test a range of ecological hypotheses at different levels of the biological organization (from populations to ecosystems; *e.g.*, Menezes *et al.* 1983 and Barbieri *et al.* 1984) and spatial scales (from local to global; *e.g.*, da Silva & Esteves 1993 and Murphy *et al.* 2020). Paralleling the development of other areas in ecology, the contribution of Brazilian limnologists, focused on aquatic macrophytes, has been growing consistently (Figure 1). As we will discuss below, this contribution has been increasing in terms of diversity of approaches and has been embracing different emerging topics in ecology.

The very first article on aquatic macrophytes ecology, listed on the Web of Science (WoS) database and whose authors belonged to a Brazilian institution, was published in 1977 (Howard-Williams & Junk 1977). Five years later, the second oldest article retrieved by our search (see details below) already discussed the problems caused by the excessive growth of aquatic macrophytes in reservoirs (Junk 1982). Afterward, according to our survey in the WoS, Esteves & Barbieri (1983) were the first Brazilian authors who published an article on freshwater aquatic macrophytes in the specialized journal Aquatic Botany (see Table S1 in the Supplementary Material).

Here, we pay a tribute to Professor Francisco de Assis Esteves (hereafter Chico or Chico Esteves for the rest of the paper), a precursor of the modern studies of aquatic macrophytes in Brazil. We first demonstrated that a relevant part of the Brazilian scientific production on aquatic macrophytes ecology can be attributed directly and indirectly to Prof. Esteves's influence as a mentor. Then, we conducted a literature survey to describe the main themes that have been investigated by Brazilian limnologists working with aquatic macrophytes. Finally, we summarize how macrophytes have been used to test ecological questions and analyze other Limnology issues. We believe important researchers like Chico Esteves should be honored and this was the main inspiration to write this paper.

THE LEGACY OF CHICO ESTEVES

Chico's work goes far beyond the study of macrophytes. He worked with virtually all aquatic communities, from phytoplankton (*e.g.*, Melo *et al.* 2007) and zooplankton (*e.g.*, Sodré *et al.* 2017), to benthic invertebrates (Alves *et al.* 2010) and fish (Guariento *et al.* 2010). Chico also worked with different themes in Limnology,

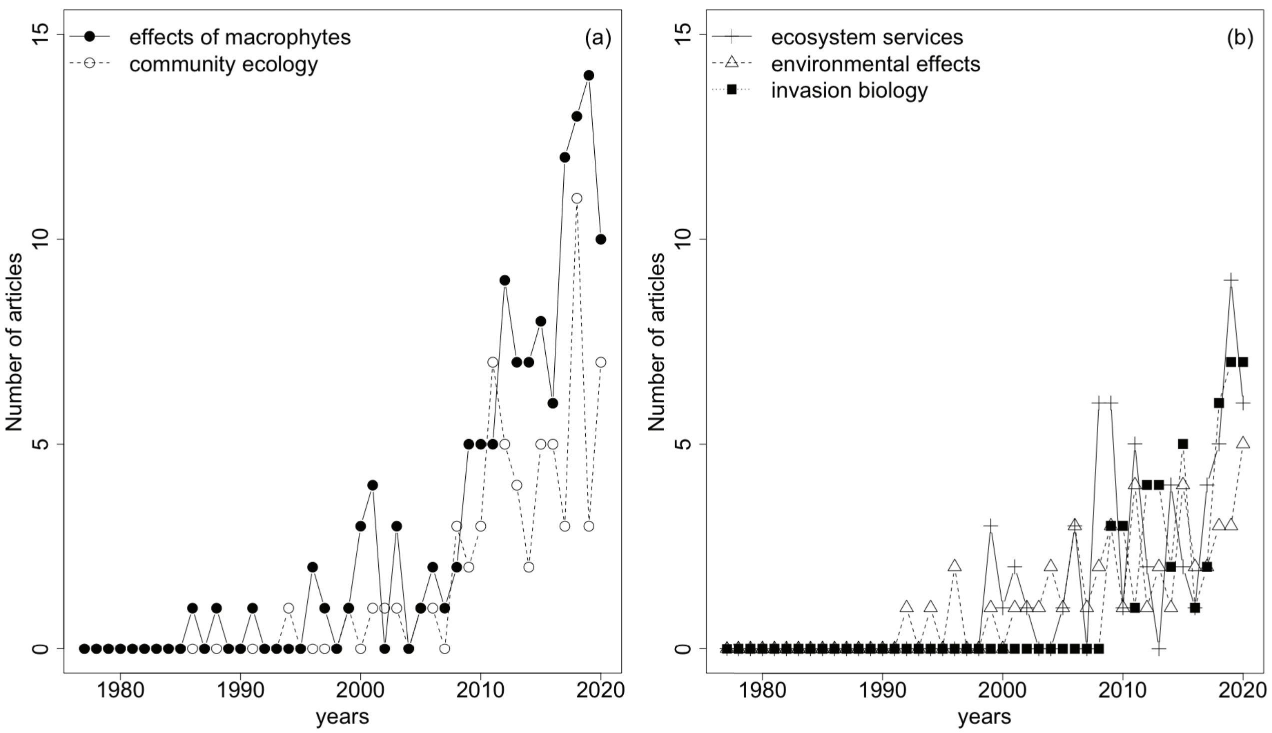

Figure 1. Temporal trends of the number of articles published (indexed in the Web of Science) in different subjects (a, b). Our survey identified a total of 459 articles about aquatic macrophytes published by Brazilian researchers between 1977 and 2020. Some articles were classified in more than one category. See Figure S1 for the temporal trends of other subjects.

considering all levels of the biological organization, from population (Palma-Silva *et al.* 2000), to community (Callisto *et al.* 2002) and ecosystem ecology (*e.g.*, Caliman *et al.* 2011). Modern approaches, like the biodiversity-ecosystem functioning, to cite one example, did not remain outside his attention (*e.g.*, Caliman *et al.* 2013). His list of publications includes one seminal book ("Fundamentos de Limnologia", 1988 with a reprint in 1998, see also Esteves, 2011) that has been used by generations of limnologists. The influence of "Fundamentos" is shown, for example, by the high number of citations it receives (4450 citations, checked in Google Scholar on 25 April 2022).

Early in his career, Chico studied macrophytes employing an ecosystem perspective, which was in accordance with the focus developed in Europe, and mainly in the Max Planck Institute für Limnologie in the 1970ths, when he finished his Ph.D. under the supervision of Dr. Harald Sioli. It is opportune to state that August Friedrich Thienemann, who pioneered studies using an ecosystem perspective, was the mentor of Harald Sioli. Thus, every student who was mentored by Chico or by Chico's students stands in the direct scientific genealogy of giants like A. Thienemann and H. Sioli. This is a great source of pride and responsibility for all of us!

The influence of the ecosystem approach is very clear in Chico's Ph.D. thesis, where he investigated the role of macrophytes in the biomass production and nutrient budget of Lake Schöh in Germany (Esteves 1979). After finishing his Ph.D. in the Max Planck Institute, Chico was hired as a Professor at the Universidade Federal de São Carlos (São Paulo, Brazil), in 1979. Right at the beginning, Chico started to work under the influence he received in Germany. For example, he supervised three master's students (Antonio Fernando Monteiro Camargo, Carlos Frederico Silveira Menezes and Ricardo Barbieri) who conducted studies on the role of aquatic macrophytes in the primary production and the nutrient cycling at the Lobo Reservoir (State of São Paulo).

In a search on Google Scholar (February 2021), we identified 68 papers and book chapters published by Chico where aquatic macrophytes were the main or the secondary focus. Most of these publications were authored or co-authored by Chico´s students and some by senior Brazilian and foreign researchers, showing his large network of scientific interactions. These publications about macrophytes focus on population ecology (*e.g.*, Nogueira & Esteves 1990), community ecology (*e.g.*, Henriques *et al.* 1988), ecosystem ecology (*e.g.*, Ferreira & Esteves 1992) and about their role in habitat structuring for other organisms, as invertebrates (Gonçalves Jr. *et al.* 2004). Macrophytes were studied using experimental and observational approaches, and the ecosystems investigated included lakes, reservoirs, rivers and river-floodplain ecosystems. Thus, his massive production using macrophytes as model organisms helps to understand typical and important aquatic ecosystems in tropical and sub-tropical areas.

Chico influenced generations of researchers who have studied and are still studying macrophytes all over Brazil. It is difficult to draw a "scientific genealogic tree" with all macrophyte scientists who are Chico's descendants. However, one can have a crude perspective about the importance of Chico as a mentor by analyzing the scientific contribution of the authors of this paper: S. M. Thomaz was Chico´s student. S. M. Thomaz supervised L. M. Bini (who was also supervised by A. F. M. Camargo, former Chico's student), P. Carvalho, A. A. Padial and R. P. Mormul. A. A. Padial supervised E. F. Galvanese and R. P. Mormul supervised R. Ruaro. Thus, only considering the authors of this paper, there are three generations of limnologists who study mainly (but not only) macrophytes. In addition, the senior authors of this paper (S. M. Thomaz and L. M. Bini) already supervised dozens of students at different levels, and several of their students also formed others. Thus, one can grasp the huge influence of Chico even considering the small group of authors of this paper.

Finally, it is important to mention that Chico's legacy is also reflected in his contribution to society through, for example, his outreach activities (*e.g.*, the creation of an environmental education program in the Macaé region; State of Rio de Janeiro, Brazil) and his contribution to biodiversity conservation (*e.g.*, creation of the National Park of Jurubatiba, Rio de Janeiro).

A SUMMARY OF THE STUDY OF AQUATIC MACROPHYTES IN BRAZIL

Literature survey

In this section, we used a literature survey to identify what are the trends used by Brazilians in studies about aquatic macrophytes. We think that this is another way to honor Chico, who is in great part responsible for the development of this field in Brazil (see Padial *et al.* 2008), as we stated in the previous section.

We conducted a survey in November 2020 using the following search string in Web of Science – Clarivate Analytics: TITLE: (macrophyte*) AND ADDRESS: (Brazil OR Brasil). This brief description, however, should not be taken as a definitive survey about macrophytes. Indeed, there are other important papers (*e.g.*, Arens 1946) and even books (*e.g.*, Hoehne 1948) not indexed in this database, published decades ago (see, for example, Thomaz & Bini 2003).

Our survey shows an increase in the number of studies focusing on macrophytes published by Brazilians, especially after the year 2000 (Figure 1 and Figure S1). This trend parallels other surveys showing that studies of Limnology in general, published by Brazilians, also increased over time (Melo *et al.* 2006). We highlight that the early 2000s was a period of increased investment in Brazilian science, which had a clear long-term impact on Brazil's potential to become inserted into the international scientific scenario. Unfortunately, science funding declined in the last years, which along with an anti-scientific movement may jeopardize the efforts made in the last two decades (*e.g.*, Thomaz *et al.* 2020).

We identified a variety of themes in our survey. The highest number of papers focused on the "effects of aquatic macrophytes on the environment and other communities" (Figure 1a). In the sequence, there are four other groups with a similar number of papers that focus on "community ecology", "effects of environmental factors on macrophytes", "effects of macrophytes on ecosystem functions and services" and invasion biology (Figure 1a, b). A smaller number of papers focused on "macrophyte decomposition", "methods", "surveys" and "interactions" (Figure S1). Few "review papers" were found. The group "others" refers to the studies about the chemical composition of plants and the influence of herbicides on aquatic macrophytes, among others. We discuss the main topics below, using mainly (but not only) our literature survey. Due to space limitation, the themes less often investigated according to our survey (decomposition, methods, macrophyte surveys and interactions) were described in the Supplementary Material (see also Figure S1).

Effects of macrophytes on the environment and other communities

Investigations belonging to this group include, for example, those on how macrophytes change the aquatic environment through their activities (*e.g.*, Bini *et al.* 2010, Ferreira *et al.* 2018). Other studies investigated the role of macrophytes to maintain other populations and communities of aquatic organisms (*e.g.*, Dias *et al.*, 2017).

Macrophytes are often the main primary producers of different types of ecosystems, especially in shallow lentic environments, and play an important role in nutrient cycling (Thomaz & Esteves 2011). For example, a large fraction of the nutrient pool can be stored in the biomass of these plants. However, they contribute nutrients and organic matter to the water during their decomposition (Bento *et al.* 2007, Ferreira *et al.* 2018), which can be used by microalgae and bacteria (Thomaz & Esteves 2011, Thomaz & Cunha 2010). As for Chico's contribution to studies on the influence of macrophytes on the dynamics of detritus and nutrients, we can cite Fonseca *et al.* (2015) and Marinho *et al.* (2010).

Submerged vegetation can increase water transparency by reducing sediment resuspension (Scheffer 1998). In addition, aquatic plants can affect pH (Thomaz & Esteves 2011), sunlight penetration (Bini *et al.* 2010) and dissolved oxygen concentration (Teixeira-de-Mello *et al.* 2016). The protection against the waves also promotes the stabilization of the margins and the reduction of erosion (Thomaz & Esteves 2011).

Aquatic macrophytes can strongly affect other aquatic organisms. For example, areas with intermediate and high levels of macrophyte complexity were more suitable for fish communities (Dias *et al.* 2017) and the habitat provided by macrophytes is a nursery for the early stages of fish (Agostinho *et al.* 2003).

The abovementioned effects on the environment linked to the complexity of the habitat provided by aquatic macrophytes are key factors in determining their relationships with other aquatic organisms (Thomaz *et al.* 2008). For example, Dias *et al.* (2017) evaluated the influence of macrophyte complexity on fish communities in the Upper Paraná River floodplain and found that areas with intermediate and high degrees of macrophyte complexity were more suitable for fish communities. In floodplain areas, macrophytes provide refuge for the reproduction and development of aquatic fauna, especially for younger fish (Agostinho *et al.* 2003).

Macrophytes provide food, refuge and reproductive sites for fish, zooplankton and macroinvertebrates (Sánchez-Botero *et al.* 2007, Thomaz & Esteves 2011, Oliveira *et al.* 2020). They also provide substrates for algae and invertebrates attachment (dos Santos *et al.* 2013, Cunha *et al.* 2012), but they attract predators, which further increase the diversity within macrophyte stands (Thomaz & Cunha 2010). Numerous studies retrieved by our search addressed the role of macrophytes as a refuge for zooplankton (*e.g.*, dos Santos *et al.* 2020, Quirino *et al.* 2021) and macroinvertebrates (*e.g.*, Padial *et al.* 2009), demonstrating how macrophytes can influence predator-prey interactions. Macrophytes provide an efficient physical and visual barrier against predators, decreasing predation rates and allowing different organisms to successfully explore these habitats (Pelicice *et al.* 2008, Dibble & Pelicice 2010, Oliveira *et al.* 2020). In addition, macrophytes can mediate trophic relationships through competition with phytoplankton, influencing the mechanisms of bottom-up and top-down control (Scheffer 1998).

In brief, macrophytes are key elements in aquatic ecosystems, and Chico's contribution to the study and advancement of this scientific field is evident. The expressive number of studies that addressed these issues reflects the importance of these plants for both the environment itself and other aquatic communities.

Community Ecology

The primary goal of papers about community ecology (the second most important theme) is to explain patterns in species distributions, a topic well described by Chico in his seminal books mentioned earlier. The substitution of life forms across a depth gradient is one of the first known patterns of aquatic macrophyte community organization (*e.g.*, Noleto *et al.* 2019). Eugene Warming, the so-called 'father of Plant Ecology', called attention to such macrophyte zonation pattern in 'Lagoa Santa' (a lake situated in Central Brazil) in his book published in 1892 ("Lagoa Santa. Et Bidragtil den biologiske Plante geografi", Thomaz & Bini 2003). Curiously, this well-established pattern relates to a modern goal: the functional responses of communities to environmental changes (*e.g.*, Schneider *et al.* 2018).

Macrophyte community structuring has been studied using different approaches. Earlier studies usually investigated how communities change in response to habitat filtering at different spatial scales (Bini *et al.* 1999, Rolon & Maltchick 2006, Rolon *et al.* 2008). After the development of the metacommunity framework, other structuring processes were also tested, including competition (Boschilia *et al.* 2008), connectivity, landscape features, human impacts (*e.g.*, Rolon *et al.* 2011, Rolon *et al.* 2012, Ribeiro *et al.* 2013), dispersal and neutral dynamics (Padial *et al.* 2014, Schneider *et al.* 2019, Trindade *et al.* 2018). There is now a consensus that a set of interacting mechanisms explains macrophyte community structure. However, it seems that the relative roles of these mechanisms may depend on the scale (Grimaldo *et al.* 2016), range of the environmental gradients, degree of isolation (Alahuhta *et al.* 2019) and on the different facets of community beta diversity (Boschilia *et al.* 2016, Pozzobom *et al.* 2020).

Numerous studies have described and tried to explain the temporal variation of macrophyte communities (Thomaz *et al.* 2009). In this context, the effects of flood pulses have been intensively studied given the importance of river-floodplain systems in Brazil (Sousa *et al.* 2011, Catian *et al.* 2018, Schneider *et al.* 2019).

In general, the excessive growth of macrophytes, as stated long ago by Cook (1993), is a symptom rather than the cause of problems and, therefore, aquatic macrophytes are reliable indicators of the effects of several anthropogenic activities (*e.g.*, eutrophication and river regulation). Accordingly, our review found, for example, several studies on macrophyte communities in reservoirs (Bini *et al.* 1999, Noleto *et al.* 2019), and focused on the effects of invasive species on native communities (Bora *et al.* 2020, Lolis *et al.* 2020).

Macrophyte communities have also been used as model organisms by Brazilian limnologists to study macroecological patterns, including large-scale patterns in species richness, species endemism, beta diversity and species geographic ranges (Chambers *et al.* 2008, Alahuhta *et al.* 2019, Murphy *et al.* 2019, García-Girón *et al.* 2020a, 2020b, Murphy *et al.* 2020).

Macrophytes and ecosystem functions and services

Ecosystem services (the third most important theme) studied by Brazilians largely (but not only) tested the use of macrophytes in bioremediation, mainly to reduce organic and inorganic pollutants (Demarco *et al.* 2020). The importance of aquatic macrophytes to ecosystem functions and services has been stated in some papers (*e.g.*, Moi *et al.* 2021a). The use of the term "ecosystem services" is related to ecosystem functioning; however, from an anthropocentric point of view, it emphasizes the benefits of biodiversity to humans (Millenium Ecosystem Assessment Panel 2005). We observed an increase in the number of studies focusing on aquatic plants and ecosystem services, for example, absorption of nutrients, herbicides and heavy metals from aquatic environments (Figure 1).

The worldwide increase in urbanization and industrialization resulted in the need for the development of alternative wastewater treatment technologies (*e.g.*, constructed wetlands systems; Colares *et al.* 2020; Bauer *et al.* 2021). Aquatic macrophytes are key components for the efficiency of these technologies given their high capacity to uptake nutrients and heavy metals (Vyamazal 2011; Afzal *et al.* 2019; Bauer *et al.* 2021).

According to our review, 42 species were used in the studies about phytoremediation by Brazilian limnologists. Most of the studies used free-floating species (*Salvinia*, *Eichhornia crassipes* and *Pistia stratiotes*). In addition, most of the studies were experimental (94.6%) and quantified the absorption of heavy metals (48.3%) and nutrients, mainly phosphorus and nitrogen (27.6%). For example, Henry-Silva & Camargo (2006) evaluated the efficiency of floating macrophytes in the treatment of Nile tilapia pond effluents. In 2017, Chico also published an article about the role of *Salvinia auriculata* and *Eichhornia azurea* in the methane cycle (Fonseca *et al.* 2017).

We found an increase in the number of researchers interested in the effect of aquatic macrophytes on ecosystem services. However, some gaps remain: i) most studies focused on a few species of macrophytes and ii) few studies analyzed the absorption of biocides (widely used in Brazil), antibiotics and other types of medication. There is still a lot of work to do in this field.

Effects of environmental factors on macrophytes

The influence of environmental factors was the fourth most frequent theme. Papers in this group (which has some overlap with the topic 'Community Ecology') showed that the temporal and spatial variation of macrophyte populations and communities were related to a variety of physical, chemical and biotic factors. Studies on macrophyte growth have helped to explain plant development in different types of aquatic habitats and their response to natural and anthropogenic disturbances (Bianchini Jr. *et al.* 2015).

The role of nutrients has been the focus of numerous investigations, probably because in addition to being one of the main factors explaining macrophytes growth, this topic is also associated with eutrophication (Silva *et al.* 2014). Studies showing positive effects of nutrients on macrophyte growth were conducted with species belonging to different life forms (Thomaz *et al.* 2007, Henry-Silva *et al.* 2008; Kobayashi *et al.* 2008, Mormul *et al.* 2020). There are also studies showing that in some ecosystems, spatial processes (*e.g.*, dispersal) are more important than limnological features as determinants of macrophyte composition (*e.g.*, Moura-Júnior *et al.* 2020).

Among the physical disturbances affecting macrophytes, we found numerous investigations addressing water level fluctuations. Macrophyte communities respond to disturbances related to the flood pulse (Camargo & Esteves 1996, Monção *et al.* 2012, Catian *et al.* 2018), bar-opening in coastal lagoons (dos Santos & Esteves 2004), drought-wet seasons in semi-arid ecosystems (Maltchik & Pedro 2001, Pedro *et al.* 2006) and water level drawdown in reservoirs (Thomaz *et al.* 2006, Moura-Júnior *et al.* 2019). These types of studies are important because aquatic ecosystems suffering from severe water level fluctuations are common in Brazil, and they include floodplains, reservoirs and ponds in Northeast and other regions. Although disturbances produced by water level oscillations influence macrophytes directly, these disturbances cause various other changes in water's physical and chemical features, like light and nutrients (*e.g.*, Camargo & Esteves 1996), which in turn also affect macrophytes.

Moreover, experimental studies focused on the effect of individual environmental factors on macrophyte growth. For instance, studies have addressed the response of submerged macrophytes to underwater light levels (Tavechio & Thomaz 2003, Pezzato & Camargo 2004) and inorganic carbon (Pierini & Thomaz 2004), and the response of free-floating macrophytes to inorganic carbon (Pontes *et al.* 2019). Studies evaluating the interaction of more than one environmental factor on macrophyte richness and composition are also very common in the Brazilian literature (Mormul *et al.* 2020, Nunes & Camargo 2020, Rolon *et al.* 2008, Rolon & Maltchik 2006).

While most of the studies commented earlier have shown the importance of bottom-up mechanisms to explain macrophyte growth, distribution or community attributes, others have studied top-down mechanisms. For example, Moi *et al.* (2021b) evidenced the importance of the top-down control via piscivorous fish to maintain the state dominated by submerged macrophytes.

The influence of human disturbances on macrophyte communities has also been increasingly studied in Brazil. For example, macrophytes communities responded to the impacts of agriculture (Ribeiro *et al.* 2019, Forini *et al.* 2020), mining (Mormul *et al.* 2015, Bottino *et al.* 2017) and the functioning of hydroelectric power plants (Thomaz *et al.* 2006).

The effects of environmental factors on macrophyte populations and communities have been studied in different regions and ecosystems in Brazil. These studies are of paramount importance to elaborate management strategies aiming at biodiversity conservation or at controlling plant biomass where macrophytes become nuisances.

Invasion Biology

The fifth most studied topic focused on invasion biology. Here we will approach only studies about non-native species, even though several species of macrophytes native to Brazil have also become invasive (*e.g.*, *Eichhornia crassipes* and *Egeria najas*; *e.g.*, Thomaz *et al.* 2006, Marcondes *et al.* 2003). Studies about these native invasive macrophytes usually do not employ the concepts developed by the Invasions Biology field and they were treated in all other sections of our paper. For these reasons, we preferred to discuss only the non-native invasive species in this topic.

Investigations of non-native invasive macrophytes employed a variety of experimental and observational approaches, trying to identify the main determinants of invasive success along with the impacts of invasive macrophytes on native communities and ecosystems. By studying the impacts of macrophytes on the diversity of native organisms, this theme has some overlap with the first one (role of macrophytes on environment and organisms).

The highest number of studies found in our survey investigated the impacts of non-native macrophytes on native populations and communities. These studies analyzed how invasive macrophytes influence aquatic organisms like other macrophytes, invertebrates and fish. For example, the African Poaceae *Urochloa arrecta*, which is invading several Brazilian ecosystems (Pott *et al.* 2011, Fernandes *et al.* 2013, Alves *et al.* 2017, Fares *et al.* 2020), seems to have strong negative impacts (through competition) on native macrophytes communities, decreasing their diversity and changing the community composition (Michelan *et al.* 2010, Fernandes *et al.* 2013, Amorim *et al.* 2015). Experiments also show negative impacts of the submerged macrophyte *Hydrilla verticillata* on the native *Egeria najas* (Silveira *et al.* 2018).

There are studies showing that non-native invasive macrophytes change food webs (Saulino *et al.* 2018), community composition (Mormul *et al.* 2010), beta diversity of invertebrate communities (Gentilin-Avanci *et al.* 2021) and detritus decomposition (de Castro *et al.* 2020).

The influence of non-native invasive macrophytes on fish has been found to depend on the species studied. For example, local fish communities are close to extinction in stands with high biomass of *U. arrecta* (Carniatto *et al.* 2013), but it seems that the submerged macrophyte *H. verticillata* does not affect fish behavior (Figueiredo *et al.* 2015), nor fish density and diversity (Cunha *et al.* 2011).

The second group of studies investigated the factors that explain the success of non-native invasive macrophytes (known as "invasibility" in the Invasion Biology field). Several abiotic and biotic filters related to invasive success were identified in these studies. For example, Mormul *et al.* (2012) showed that brownification may enhance the success of invasive submerged macrophytes in temperate regions. Abiotic filters related to sediment characteristics (*e.g.*, organic matter) also explain the successful invasion of *U. arrecta* (Fasoli *et al.* 2015) and *H. verticillata* in Brazilian ecosystems (Silveira & Thomaz 2015, Silveira *et al.* 2016, Pulzatto *et al.* 2019). Wave disturbance was also found to be an important factor in preventing colonization of *U. arrecta* in reservoirs (Thomaz *et al.* 2012).

The biotic resistance hypothesis (Elton 1958) has also been tested by Brazilian limnologists, and this hypothesis has been supported experimentally (Michelan *et al.* 2013). Field investigations support the interactive role of biotic resistance and abiotic filters to explain the success of the non-native macrophyte *H. verticillata* (Pulzatto *et al.* 2019), while an experiment showed that herbivory interacts with warming to determine the establishment of this same species (Calvo *et al.* 2019). Investigations like these last two ones highlight the importance of studying interacting, instead of isolated factors, on the fate of macrophytes invasion.

The third group of studies containing a small number of papers focused on the factors related to the invasive species biology that facilitates invasion (known as "invasiveness", in the invasion biology field). For example, Ribas *et al.* (2018) used niche models and showed that *H. verticillata* has a massive potential to invade freshwater ecosystems in South America. The successful invasion currently observed for this species can be explained, among other factors, by its high plasticity regarding CO_2 utilization (Fasoli *et al.* 2018). All these examples clearly show how different approaches help to explain the fate of invasive species.

Far fewer investigations approached the potential role of propagule pressure on non-native invasive macrophyte success. This has been a classical theme in the Invasion Biology field because invasive species can successfully invade an ecosystem with non-appropriate environmental conditions if propagules arrive at great numbers or high frequencies (Lockwood *et al.* 2005). Thus, studies filling this gap can help to understand the relative success of some invasive macrophytes in Brazilian waters. For example, *in situ* observations showed that small individuals of *U. arrecta* are dispersed on floating mats of native macrophytes (Michelan *et al.* 2018). Studies about *H. verticillata* showed that its fragments regenerate very fast (Umetsu *et al.* 2012) and resist droughts (Silveira *et al.* 2009), which help explain its fast spread in the Upper Paraná River basin. Indeed, the colonization success of this species was explained mainly by the number of propagules released instead of the biotic resistance provided by a native isoetid-like macrophyte (Louback-Franco *et al.* 2018). These findings indicate the important role of propagule pressure in the success of invasive macrophytes.

Our review identified a bias towards a small number of invasive species (*U. arrecta* and *H. verticillata*) that are studied in a particular region (Upper Paraná River floodplain), with fewer studies devoted to other species (*e.g.*, *Hedychium coronarium*; see de Castro *et al.* 2020, 2021). Thus, it remains to be clarified whether there are other relevant invasive non-native macrophytes in Brazilian freshwater ecosystems. This is a key gap that should be addressed in future studies.

CONCLUSION

Our survey reveals important aspects of the scientific literature produced by Brazilians who have worked with macrophytes in the last decades. More importantly, we found a large number of papers focusing on topical issues in Ecology and Limnology. Undoubtedly, this increasing number of scientists studying macrophytes, along with their contribution to the advancement of theoretical and applied Limnology, has its roots in the influence of a giant like Chico Esteves. He is recognized as not only an influential scientist but also as an influential communicator and consultant for environmental policies and environmental preservation. We are proud to have an inspiring person like him influencing generations of limnologists in Brazil!

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