J. Aquat. Plant Manage. 53: 191–196

Effects of a nonnative species of Poaceae on aquatic macrophyte community composition: A comparison with a native species

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ABSTRACT

Invader-dominated systems of exotic species frequently damage native communities, mainly because there is a shift in the competition–facilitation balance, and competition intensifies in communities structured by facilitation. We tested whether areas dominated by the exotic species African signalgrass [*Urochloa arrecta* (Hack. ex T. Dur. & Schinz) O. Morrone & F. Zuloaga] can affect the assemblage structure of aquatic plants in tropical freshwater ecosystems, compared with the native species, anchored waterhyacinth [*Eichhornia azurea* (Sw.) Kunth]. We predicted that the dominance of African signalgrass (expressed as an increase in biomass) would reduce species richness, diversity, and functional diversity of the macrophyte assemblages, when compared with anchored waterhyacinth. Species cover and the occurrence of associated species were assessed in quadrats (1 m^2), located in sites dominated by exotic species (African signalgrass), native species (anchored waterhyacinth), and without dominance. The effects of dominance on species richness and diversity of aquatic macrophytes were assessed through generalized linear model and composition with detrended correspondence analysis. African signalgrass negatively affected species richness and Shannon diversity, whereas anchored waterhyacinth showed no effects on species richness and Shannon diversity. However, native species positively affected functional diversity. Our study showed that invasive species reduced the presence of rooted-submerged species, whereas native species facilitated the occurrence of rooted-submerged and free-submerged species. Thus, African signalgrass was able to change the composition of the macrophyte assemblage and can represent a threat to native communities of tropical freshwater ecosystems.

Key words: dominance, *Eichhornia azurea*, exotic species, generalized linear models, tropical freshwater ecosystems, *Urochloa arrecta*.

INTRODUCTION

The introduction of exotic species is one of the most concerning consequences of human activities that have ecological and economic implications (Pimentel et al. 2001). Because of the increase in biological invasions, the effects of these species on natural ecosystems have become a focal area of ecological studies (Naeem et al. 2000, Battaglia et al. 2009, Quinn et al. 2011). Some exotic, invasive species have several detrimental impacts on native biota, such as negative effects on species richness, diversity, and community composition (Hedja et al. 2009), as well as the disassembly and alteration of community organization (Sanders et al. 2003).

Once established, exotic species can reproduce consistently and sustain dominant populations (Richardson et al. 2000). Systems dominated by exotic invader species suffer species loss primarily because there is a shift in the competition–facilitation balance, and competition intensifies in communities structured by facilitation (Richardson et al. 2012). The dominance of invasive species can lead to the exclusion of less-competitive species (Gurevitch and Padilla 2004). However, it is possible to find indicators that exotic species can facilitate native species (Rodriguez 2006) by providing a habitat, serving as functional substitutes for extinct taxa, and supplying desirable ecosystem functions (Schalaepfer et al. 2011). Thus, we compared an exotic Poaceae African signalgrass [*Urochloa arrecta* (Hack. ex. T. Dur. & Schinz) O. Morrone & Zuloaga], which is known to affect subtropical communities (Reinert et al. 2007, Pott et al. 2011), with a native species anchored waterhyacinth [*Eichhornia azurea* (Sw.) Kunth]. These two species have the same emergent/floating life form, i.e., rooted plants with vegetative parts emerging above the water's surface, as well as long floating steams. Recently, African signalgrass was recorded in the Itanhaém River basin (located in the south littoral of the São Paulo State, Brazil); this species is native to Africa and has infested tropical and subtropical zones worldwide. It is a perennial, aquatic grass with long, floating branches that can form thick mats or tussocks with dense, usually stoloniferous, root systems. This species, recently identified as tropical signalgrass [*Urochloa subquadripara* (L.) T.Q. Nguyen] (Michelan et al. 2010a; see Michelan et al. 2013) has high regeneration potential, and recent studies have shown that this species can compete with emergent species and has negative effects on species richness and functional diversity (Michelan et al. 2010b).

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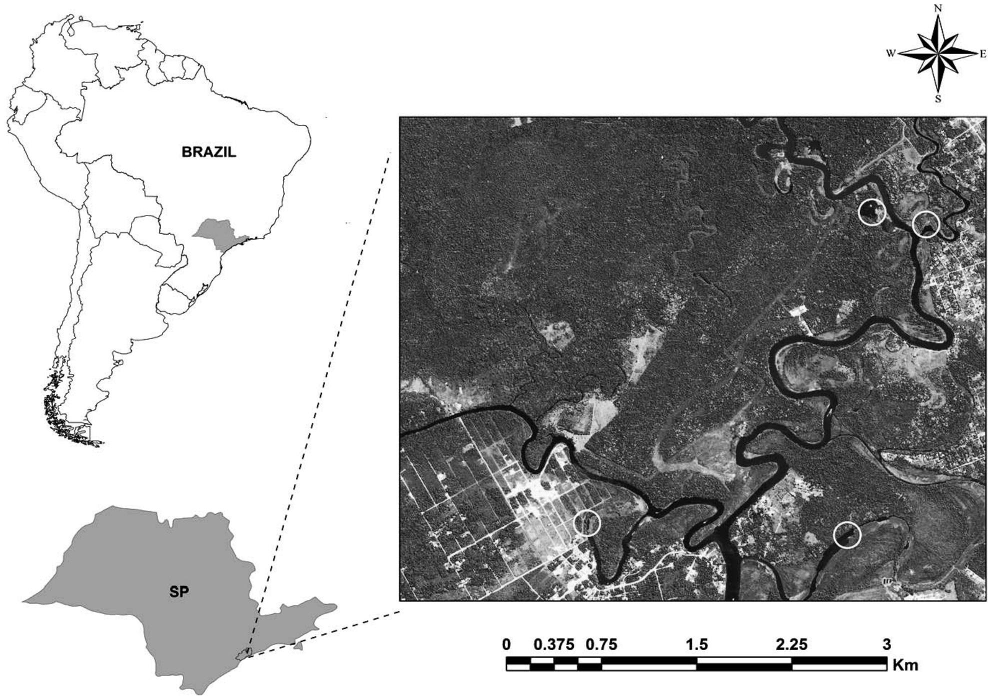

Figure 1. A map of the area studied in the Itanhaém River basin, Brazil. The circles indicate the patches that were sampled.

However, this last investigation did not compare its results with the effects of a similar native plant and, therefore, could not be generalized.

Anchored waterhyacinth is a native, rooted, aquatic macrophyte; its long, floating stems develop a few centimeters below the water's surface, forming dense stands and ensuring additional structural complexity in littoral regions (Agostinho et al. 2007). There is no record that this species is considered invasive, but it seems to increase structural complexity in aquatic ecosystems and provide habitats for both animal and plant assemblages (Boschilia et al. 2008, Padial et al. 2009, Cunha et al. 2012). Both African signalgrass and anchored waterhyacinth are dominant species in almost all habitats of the Itanhaém River basin, and that is the reason why we chose these two emergent species for this study. Thus, our study can provide an excellent opportunity to show how the dominance of exotic and native species, evaluated in a gradient of biomass, affects the community composition. Many studies test the effects of exotic species on the attributes of communities and rarely compare the effects of other species on community structure (Hulme et al. 2013). Moreover, there are several investigations showing the effects of exotic plants on terrestrial native plants (Hedja et al. 2009, Souza et al. 2011), but there are few investigations testing whether the same remains true for aquatic ecosystems (e.g., Madsen et al. 1991). We tested whether areas dominated by one exotic species of aquatic macrophytes can affect the structure of the assemblage of aquatic plants, compared with one native species. We evaluated the effect of increased biomass from the exotic African signalgrass and the native anchored waterhyacinth on community structure of aquatic macrophytes. We hypothesized that the increase in biomass from the exotic species would negatively affect the structure of the aquatic macrophyte assemblages. We predicted that the dominance of African signalgrass (expressed as an increase in biomass) would reduce species richness, diversity, and functional diversity of the macrophyte assemblages, when compared with anchored waterhyacinth.

MATERIALS AND METHODS

Data sampling

Our samples were made in the Itanhaém River basin, located in the south littoral of the São Paulo State, Brazil (Figure 1). Field samples were collected in the summer of 2012 in the littoral zone of the rivers in three visually different patches of aquatic macrophytes: patches dominated by exotic species African signalgrass (UA), patches dominated by the native anchored waterhyacinth (EA), and patches without dominance by either exotic or native species (WD). We defined dominant quadrats as those in which the exotic and native species had more than 50% of the total biomass, by visual inspection, confirmed later in the laboratory, and quadrats without dominance had less than 50% cover and 50% of total biomass. Samplings were carried out in all patches using a 1 m^2 quadrat (1 m × 1 m), totaling 90 samples. Each river sampled received approximately the equivalent number of quadrats (approximately 23), subdivided into UA, EA, and WD. In each quadrat, we identified aquatic macrophytes species and measured the frequency of occurrence (presence/absence) for all species. Species that could not be identified in the field were

Table 1. A list of aquatic macrophytes species present in patches dominated by African signalgrass (UA), anchored waterhyacinth (EA), and without dominance (WD), with their growth forms and codes used in an ordination analysis.

Family	Scientific Name	Common Name	Growth Form	Code	UA	EA	WD
Araceae	*Lemna minuta* Kunth	Minute duckweed	Free-floating	Lm	x	x	x
Araceae	*Pistia stratiotes* L.	Waterlettuce	Free-floating	Ps	x	x	x
Araliaceae	*Hydrocotyle bonariensis* Comm. ex Lam.	Coastal plain pennywort	Emergent	Hb	x	x	x
Asteraceae	*Enydra sessilis* (Sw.) DC.	Smallray swampwort	Epiphyte	Es			x
Azollaceae	*Azolla filiculoides* Lam.	Pacific mosquitofern	Free-floating	Af	x	x	x
Cabombaceae	*Cabomba furcata* Schult. & Schult. f.	Forked fanwort	Rooted submerged	Cf		x	x
Cyperaceae	*Oxycaryum cubense* (Poepp. & Kunth) Lye	Cuban club-rush	Epiphyte	Oc		x	x
Commelinaceae	*Commelina* L. sp.	Dayflower	Epiphyte	Co		x	
Haloragaceae	*Myriophyllum aquaticum* (Vell.) Verd.	Parrot feather watermilfoil	Emergent	Ma		x	x
Hydrocharitaceae	*Egeria densa* Planch.	Brazilian egeria	Rooted submerged	Ed		x	x
Hydrocharitaceae	*Limnobium laevigatum* (Humb. & Bonpl.) ex Willd.	Sponge plant	Free-floating	Ll	x	x	x
Lentibulariaceae	*Utricularia foliosa* L.	Leafy bladderwort	Free submerged	Uf	x	x	x
Nymphaeaceae	*Nymphaea rudgeana* G. Mey.	Rudge's waterlily	Rooted floating-leaved	Nr		x	
Poaceae	*Urochloa mutica* (Forsk.) T.Q. Nguyen	Paragrass	Emergent	Bm	x		
Poaceae	*Urochloa arrecta* (Hack. ex T. Dur. & Schinz) O. Morrone & F. Zuloaga	African signalgrass	Emergent	Ua		x	
Poaceae	*Echinochloa polystachya* (Kunth) Hitchc.	Creeping river grass	Emergent	Ep	x		x
Poaceae	*Panicum repens* L.	Torpedograss	Emergent	Pr		x	
Polygonaceae	*Polygonum acuminatum* Kunth	Tapertips smartweed	Emergent	Pa	x	x	x
Polygonaceae	*Polygonum ferrugineum* Wedd.	Caatay guazú	Emergent	Pf	x	x	x
Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth	Anchored waterhyacinth	Emergent	Ea	x		
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	Waterhyacinth	Free-floating	Ec		x	x
Ricciaceae	*Ricciocarpos natans* (L.) Corda	Purple fringed Riccia	Free-floating	Rn	x	x	x
Salviniaceae	*Salvinia molesta* Mitchell	Giant salvinia	Free-floating	Sm	x	x	x

collected and preserved for subsequent identification in the Herbarium Rioclarense (HRCB, http://www.rc.unesp.br/ib/herbario/). A rake was used to sample submerged macrophytes within deeper waters.

Biomass of aquatic macrophytes was quantified in supplementary samples with a 0.25-m^2 quadrat (0.5 m by 0.5 m), placed in the center of each 1-m^2 quadrat. The plants obtained from supplementary samples were manually collected and transported to the laboratory. For both African signalgrass and anchored waterhyacinth, we removed the above-water biomass (leaves and stems) and 20-cm underwater biomass (roots), i.e., 20 cm below the waterline. The plants were washed and oven-dried at 60 C until a constant mass was obtained.

We evaluated species richness, diversity (Shannon diversity index; Magurran 2004), and the number of functional groups, herein called *functional richness*. Functional groups, or sets of species that have similar life forms (Tilman 2001), can be an important measure to predict environmental changes because they are most likely similar in their responses to ecosystem functioning. We used the following six functional groups: free-floating (plants that float on the water's surface; e.g., salvinia [*Salvinia* spp.]), free-submerged (e.g., bladderwort [*Utricularia* spp.]), rooted-submerged (rooted in the bottom soil with the vegetative parts predominantly submerged; e.g., Brazilian egeria [*Egeria densa* Planch.]), rooted floating-leaved (rooted in the bottom soil but with leaves and flowers that float on the water's surface; e.g., waterlily [*Nymphaea* spp.]), emergent-plus-emergent/floating (rooted plants with vegetative parts emerging above the water's surface; e.g., anchored waterhyacinth and African signalgrass), and epiphytes (plants that rely on other plants for support; e.g., Cuban club-rush [*Oxycaryum cubense* (Poepp. & Kunth) Lye]).

Data analysis

We analyzed the effects of biomass on richness and diversity using generalized linear models (GLMs), which are extensions of standard linear models that can accommodate various nonnormal error distributions (Nelder and Wedderburn, 1972). Because the dependent variable species richness represented counts and diversity represented positive continuous data, we applied Poisson with a log-link function and γ errors with identity-link function, respectively. The goodness of fit was measured by deviance statistics (D^2).

We also applied a logistic regression to verify whether the likelihood of occurrence of free-floating, emergent, rooted submerged, free submerged, rooted floating-leaved species were affected by the biomass of anchored waterhyacinth and African signalgrass. For this analysis, we considered the presence or absence of each functional group.

We applied detrended correspondence analysis (DCA) to explore the spatial gradient of distribution for species of aquatic macrophytes and to visualize macrophyte community changes based on the dominance and absence of anchored waterhyacinth and African signalgrass. The differences in treatments were assessed using a one-way ANOVA applied to the axis scores of the DCA, considering dominance and absence of species as factors, and then by *a posteriori* multiple comparison among means using Tukey's test. The level of significance for the tests was set at 0.05.

All statistical calculations were performed using statistical package R version 3.1.2 (R Development Core Team, 2014).

RESULTS AND DISCUSSION

In total, we recorded 23 species of macrophytes, and the emergent functional group was the most representative

Table 2. Summary statistics of generalized linear models between African signalgrass and anchored waterhyacinth biomass and species richness and Shannon diversity index.

	African Signalgrass				Anchored Waterhyacinth			
	Richness		Shannon Index		Richness		Shannon Index	
Parameter	Intercept	Biomass	Intercept	Biomass	Intercept	Biomass	Intercept	Biomass
Estimation	1,670	−0.002	0.862	−0.001	1,515	3.E-04	0.757	−1.E-04
Standard error	0.061	5.E-04	0.051	2.E-04	0.056	2.E-04	0.043	1.E-04
Z statistic	27,390	−4,347	17,000	−5,830	26,830	1,340	17,413	−0.719
P value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.180	< 0.001	0.474

(nine species), followed by the free-floating group (seven species). The functional groups of epiphytes, rooted submerged, free-submerged, and rooted floating-leaved had the lowest number of species (3, 2, 1, and 1, respectively). The UA group contained 13 associated species, whereas the EA and WD categories contained 19 and 17 associated species, respectively (Table 1).

Generalized linear modeling of species richness and diversity showed that the biomass of UA patches was significant ($P < 0.01$; Table 2), indicating that the biomass of this species negatively influenced these attributes of macrophyte assemblage (Figures 2a and 2b), as confirmed by deviance of models: $D^2 = 72.56$, $P = 0.88$ and $D^2 = 89.44$, $P = 0.98$, respectively. Alternatively, the biomass of the EA patches showed no relationship with richness ($P = 0.18$) or diversity ($P = 0.47$) (Figures 2c and 2d; Table 2), and their deviance explained by GLM were $D^2 = 70.42$, $P = 0.91$ and $D^2 = 88.87$, $P = 0.45$, respectively. Thus, our results corroborate the hypothesis that an increase in biomass by the exotic species negatively affected the structure of the aquatic macrophyte assemblages. In fact, the dominance of African signalgrass seems to affect the attributes of macrophyte community by reducing the species richness and diversity, where it occurs locally, compared with where the native anchored waterhyacinth and other native species occur. The predominance of this exotic species appears to be related to the small numbers of associated species and restricts the occurrence of rooted-submerged species. Patches with anchored waterhyacinth and patches without dominance did not negatively interfere with the composition of the assemblage, but the native species was able to increase the occurrence of others aquatic macrophytes.

The attributes of macrophyte assemblage influenced by dominance of exotic species can be related to some inherent characteristics of the species. African signalgrass has many characteristics that are common to invasive species, such as rapid growth, which allows it to become a dominant species in a broad range of aquatic environments (Thomaz et al. 2009). A recent study showed that this species negatively affected emergent species, rooted species with floating stems, and rooted-submerged species, but free-floating species were positively affected (Michelan et al. 2010b). Our results showed the same pattern, with rooted-submerged species negatively affected because the dense banks by African signalgrass impeded the occurrence of this functional group. Thus, our results support the prediction that even this macrophyte life form may be threatened when African signalgrass attains high levels of biomass.

Logistic regression analysis revealed that the increase in African signalgrass biomass negatively and significantly affected the rooted-submerged species ($P < 0.01$). On the other hand, the increase in anchored waterhyacinth biomass positively and significantly influenced the occurrence of rooted-submerged ($P = 0.01$) and free-submerged species ($P = 0.02$). The specific architecture of each species can be responsible for the response of other species associated with them. Anchored waterhyacinth, for example, has floating stems that may reach several meters into the water, with roots and emergent leaves at each node (Milne et al. 2006). These structures provide favorable habitats and facilitate the occurrence of spiders (Cunha et al. 2012), invertebrates (Fulan and Henry 2006, Villabona-Gonzales et al. 2011), and fish (Bulla et al. 2011). A recent study showed that the physical structure of anchored waterhyacinth facilitated colonization by several other macrophyte species, resulting in an increase in richness and diversity (Sousa et al. 2011). In our case, results indicated that this species facilitated the occurrence of free-submerged and rooted-submerged species, such as leafy bladderwort (*Utricularia foliosa* L.) and Brazilian egeria, respectively. This result can also indicate that this species is important to facilitate the occurrence of other species, mainly in running waters. African signalgrass, in turn, develops floating stands that can extend for hundreds of meters toward the pelagic region. Its biological structure hinders the development of rooted-submerged species by decreasing light penetration and emergent species because of the competition for space and resources (Thomaz and Michelan 2011).

Two groups were defined according to DCA. The first group represented quadrats of UA and the second represented quadrats of EA and WD. The one-way ANOVA confirmed significant differences between groups related to the distribution of quadrats on axis 1 ($F = 23.39$; $P < 0.001$) and axis 2 ($F = 4.22$; $P = 0.018$) of DCA (Figure 3). The scores of first DCA axis showed that quadrats of UA differed significantly from EA and WD ($P < 0.001$), with no difference between EA and WD ($P = 0.99$). The scores of the second DCA axis showed a significant difference between UA and EA ($P = 0.013$). However, WD did not differ from the UA and EA ($P = 0.38$ and $P = 0.20$, respectively).

The principal species that positively contributed to Axis 1 were smallray swampwort [*Enydra sessilis* (Sw.) DC.], waterhyacinth [*Eichhornia crassipes* (Mart.) Solms], Brazilian egeria, Rudge's waterlily (*Nymphaea rudgeana* G. Mey.), parrot feather watermilfoil [*Myriophyllum aquaticum* (Vell.) Verdc.],

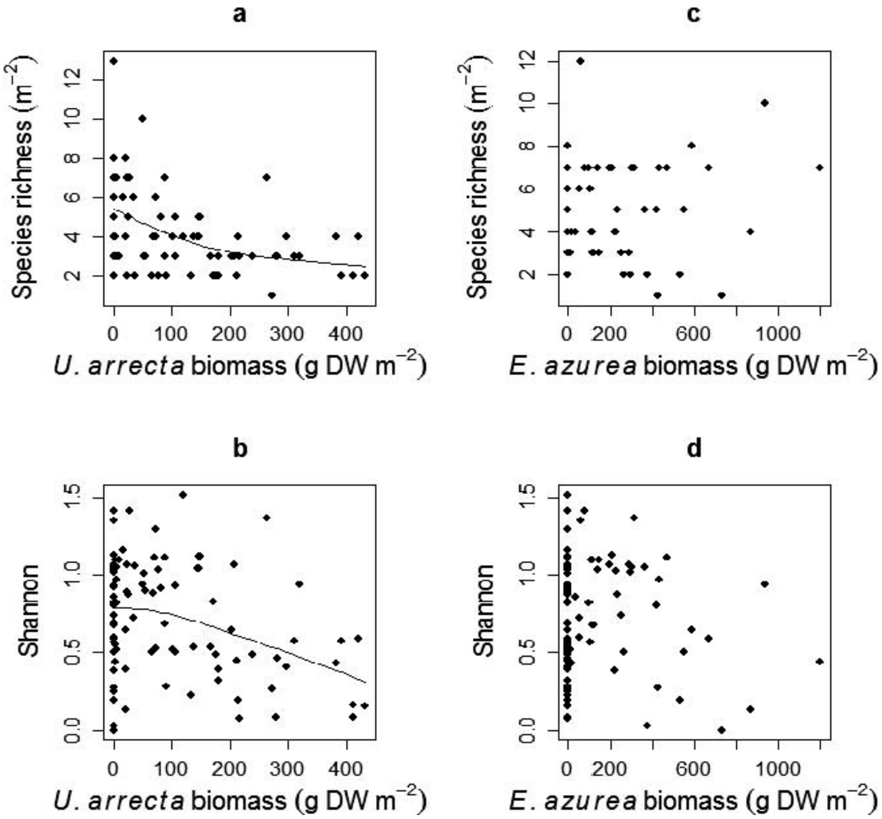

Figure 2. The relationship between the biomass of African signalgrass and the attributes of aquatic macrophytes: (a) species richness and (b) Shannon index; and (c) the biomass of anchored waterhyacinth and the macrophyte species richness and (d) Shannon index. Lines were fitted with generalized linear models.

and forked fanwort (*Cabomba furcata* Schult. & Schult. f.), and the species that positively contributed to Axis 2 were creeping river grass [*Echinochloa polystachya* (Kunth) Hitchc.] and tapertip smartweed (*Polygonum acuminatum* Kunth). Torpedograss (*Panicum repens* L.) sponge plant [*Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine], purple fringed Riccia [*Ricciocarpos natans* (L.) Corda], and caatay guazú (*Polygonum ferrugineum* Wedd.) contributed negatively for both Axes 1 and 2 (Figure 4). The emergent species paragrass [*Urochloa mutica* (Forsk.) T.Q. Nguyen], creeping river grass, and tapertip smartweed seem to be associated with the presence of African signalgrass. Anchored waterhyacinth seems to be associated with the presence of species

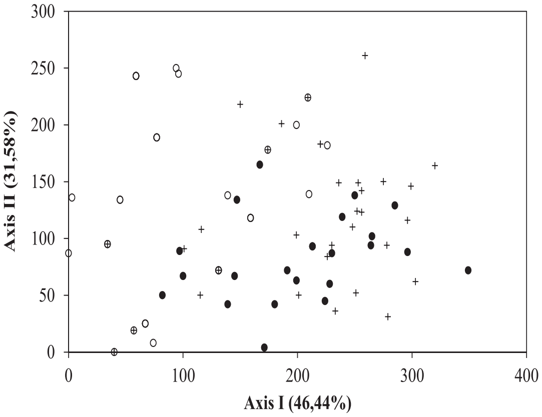

Figure 3. The ordination of the scores of samples. The first two axes show the scores of samples derived from detrended correspondence analysis. The symbols indicate the three dominant groups: hollow circle: African signalgrass; filled circle: anchored waterhyacinth; and cross: without dominance.

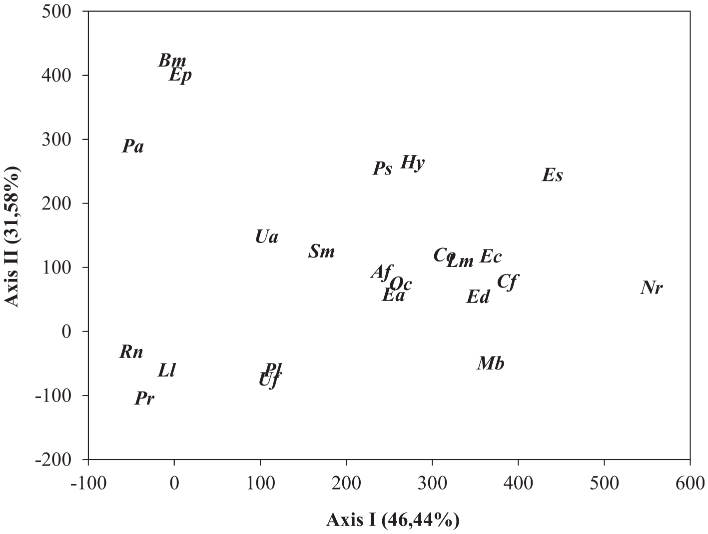

Figure 4. The species scores for ordination axes. Species codes are shown in Table 1.

Brazilian egeria, forked fanwort, waterhyacinth, and Rudge's waterlily. Our results show that the occurrence of this exotic species seems to be able to change the composition of the macrophyte assemblage when compared with native species. It is difficult to affirm that this invasive species is responsible for damage or alteration to ecosystem functioning. Many studies have tried to show that the introduction of an invasive species is always related with the decline of native species; however, many times, the results are anecdotal (Gurevitch and Padilla 2004). Moreover, our study focused on samples at a small scale (1 m^2), and this may have been the reason why we found a negative relationship between native and exotic species; perhaps, at courser scales, we would find a different pattern, i.e., positive co-occurrences between species, as suggested by Thomaz and Michelan (2011).

Our study highlights species differences that affect the composition of aquatic macrophytes. Although native species can allow for the presence of other species and even facilitate their occurrence, the exotic ones appear to prevent the development of other species, suggesting that exotic species can outcompete native ones. This conclusion is concerning, giving the widespread nature of African signalgrass in Neotropical aquatic ecosystems.

ACKNOWLEDGEMENTS

S.R.A. and A.F.M.C. are especially thankful to C. F. Sanches for field assistance. We also thank Sidinei Magela Thomaz for helping in the early version of this manuscript.

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