

Associations between a highly invasive species and native macrophytes differ across spatial scales

Sidinei Magela Thomaz · Thaisa Sala Michelan

Received: 11 November 2010 / Accepted: 21 April 2011 / Published online: 8 May 2011
© Springer Science+Business Media B.V. 2011

Abstract The association between invasive and native species varies across spatial scales and is affected by phylogenetic relatedness, but these issues have rarely been addressed in aquatic ecosystems. In this study, we used a non-native, highly invasive species of Poaceae (tropical signalgrass) to test the hypotheses that (i) tropical signalgrass success correlates negatively with success of most native species of macrophytes at fine spatial scales, but its success correlates positively or at random with natives at coarse spatial scales, and that (ii) tropical signalgrass is less associated with native species belonging to the family Poaceae than with species belonging to other families (Darwin's naturalization hypothesis). We used a dataset obtained at fine (0.25 m²) and coarse (ca. 1,000 m²) scales. The presence/absence of all species was recorded at both scales, and their biomass was also measured at the fine scale. We tested the association between tropical signalgrass biomass and individual native species with logistic regressions at the fine scale, and using the T-score index between tropical signalgrass and each native species at both scales. The likelihood of the occurrence of six species

(submersed and free-floating) was negatively affected by tropical signalgrass biomass at the fine scale. T-scores showed that three species were less associated with tropical signalgrass than expected by chance, but 22 species co-occurred more than expected by chance at the coarse scale. Associations between species of Poaceae and tropical signalgrass were null at the fine scale, but were positive or null at the coarse scale. In addition to showing that spatial scale affects the patterns of association among the non-native and individual native species, our results indicate that phylogeny did not explain associations between the invasive and native macrophytes, at both scales.

Keywords Co-occurrence · Darwin's naturalization hypothesis · Diversity · Exotic species · *Urochloa subquadriflora*

Introduction

The conservation of biodiversity has become a central issue in ecology, especially in the last 3 decades, when mass extinctions have started to be recognized as one of the most severe global changes. The introduction of non-native species is considered to be one of the main causes of species loss (Clavero and García-Berthou 2005), although plant invasions

S. M. Thomaz (✉)
DBI/Nupélia/PEA, Universidade Estadual de Maringá,
Maringá 87020-900, Brazil
e-mail: smthomaz@nupelia.uem.br

T. S. Michelan
ICB, DE, Universidade Federal de Goiás, Goiânia,
GO 74001-970, Brazil

may impact native communities without causing extinctions (e.g., Jäger et al. 2009). In view of this scenario, the factors that make a non-native species more or less harmful to native assemblages and the ability of natives to co-exist with non-native invaders have attained the attention of researchers and decision-makers.

Investigations in aquatic ecosystems have shown that relationships between non-native and native species richness can be negative (e.g., Michelan et al. 2010), positive or neutral (e.g., Capers et al. 2007). However, the relationships between invasive and native species are highly dependent on spatial scale (Fridley et al. 2007). For example, negative relationships between native plant diversity and indicators of non-native species success are found at fine spatial scales (Kennedy et al. 2002; Michelan et al. 2010), whereas positive relationships are found at coarse spatial scales (Capers et al. 2007; Thomaz et al. 2009). The latter class of observations is explained by increases in resource and habitat heterogeneity (e.g., Byers and Noonburg 2003; Melbourne et al. 2007; Capers et al. 2007); a higher diversity of habitats and more resources facilitate the presence of both native and non-native species, increasing the richness of both groups.

Several abiotic and biotic factors have been considered to explain invasions success. Among the biotic ones, the degree of phylogenetic relatedness of a species with the others in the community to be invaded is an important predictor of alien species invasiveness ability (Darwin 1859). According to the Darwin's naturalization hypothesis (DNH), non-native species distantly related to natives will be more successful than closely related ones, largely because of the overlap in resource use among close relatives (Darwin 1859; Daehler 2001; Strauss et al. 2006). This hypothesis has received more attention in terrestrial organisms (e.g., Strauss et al. 2006; Dawson et al. 2009), but it has been tested little in aquatic ecosystems (but see Jiang et al. 2010). Phylogenetic relationships between non-native and native species also vary with stage of invasion, abundance of natives and with spatial scales (Diez et al. 2008). Closely related species are expected to occur in mutually exclusive patterns due to competition at small spatial scales, but would be more likely to co-occur at larger spatial scale because they have similar broad environmental preferences

and competitive exclusion is less likely to occur in large regions (Procheş et al. 2008; Cadotte et al. 2010). In fact, not only the evolutionary, but also the phenotypic relatedness affect invasion, and an increase in niche differences independent of phylogeny may permit coexistence between non-native and native species (MacDougall et al. 2009).

Macrophytes are key components in aquatic ecosystems because they influence nutrient cycling, fuel aquatic food webs and, in particular, increase habitat complexity in waterscapes (Wetzel 2001). However, some species of macrophytes have become a matter of concern because they have several attributes that make them excellent invaders (Michelan et al. 2010; Bianchini et al. 2010). The African Poaceae *U. subquadriflora* (Trin.) R.D. Webster (tropical signalgrass) has invaded a variety of aquatic ecosystems in the Neotropics, including lakes, reservoirs, wetlands and rivers (Thomaz et al. 2009). At fine spatial scales, this grass reduces the species and functional diversity of macrophytes and changes the composition of plant assemblages (Michelan et al. 2010), but at coarse spatial scales, its probability of occurrence increases with macrophyte richness (Thomaz et al. 2009). Despite these analyses emphasizing correlations of this invasive species with community attributes, its relationships with individual species of macrophytes is an open question. In view of the ecological importance of macrophytes, there is considerable interest in knowing which (if any) native species are more or less correlated with tropical signalgrass.

In this study, we combined two datasets obtained at fine and coarse spatial scales to answer the following questions: (1) do patterns of co-occurrences of native species and tropical signalgrass differ at different spatial scales and (2) is phylogenetic relatedness to native species an important determinant of tropical signalgrass invasibility? Given that grasses are usually dominant taxa which compete both above and below ground with other natives (Procheş et al. 2008), our main hypothesis linked to question (1) is that tropical signalgrass success correlates negatively with success of most native species of macrophytes at fine spatial scales, but its success correlates positively or at random with natives at coarse spatial scales. Following this hypothesis, we predict that (i) the probability of the occurrence of individual species of macrophytes decreases significantly with increasing tropical

signalgrass biomass; (ii) most species of macrophytes co-occur less than expected by chance with tropical signalgrass at fine spatial scales; and (iii) most species of macrophytes co-occur at random or more than expected by chance with tropical signalgrass at coarse spatial scales. Our hypothesis linked to question (2) is that tropical signalgrass is less associated with native species belonging to the family Poaceae than with species belonging to other families. Following this hypothesis, we predict that species of the family Poaceae are more affected by tropical signalgrass biomass and co-occur less than expected by chance with tropical signalgrass compared to species belonging to other families. These predictions are based on DNH, in which an invasion is less successful when two species are closely related due to high competition between them.

Materials and methods

Study area

We analyzed the same dataset used by Thomaz et al. (2009) and Michelan et al. (2010), who studied the response of tropical signalgrass to macrophyte diversity and its effects on macrophyte communities at coarse and fine spatial scales, respectively. We investigated four Brazilian freshwater ecosystems, including two natural lakes and two reservoirs (see details about these ecosystems in Thomaz et al. 2009 and Michelan et al. 2010).

Sampling

For fine spatial scale investigations, samplings were carried out between March and September 2008 within 0.25 m² (0.5 m × 0.5 m) quadrats, totaling 86 quadrats in 16 patches of macrophytes in the lakes and 27 patches in the reservoirs (Michelan et al. 2010). In each patch, we recorded the incidence data (presence/absence) of all species of macrophytes occurring in two quadrats, one dominated by tropical signalgrass and another where this species was not dominant or was absent. By using this procedure we obtained a gradient of tropical signalgrass biomass values, necessary to apply Logistic Regression (see below). The tropical signalgrass biomass was collected to be measured later in the laboratory

(dried in an oven at ca. 80°C until constant weight was achieved).

Because depth affects macrophyte zonation in the littoral zone (Sculthorpe 1967), quadrats were positioned at similar depths in each patch (depths varying from 0.3 to 2.4 m; mean = 0.96; SD = 0.46). This depth range was chosen because it is where tropical signalgrass occurs, and it is also the range of occurrence of most species of native macrophytes in these lakes/reservoirs.

For coarse spatial scale observations, we surveyed 251 points distributed in the eight arms of the Itaipu Reservoir on four different dates, September 2008 and 2009 and March 2009 and 2010. These sites have been monitored since 1999 (Thomaz et al. 2009), and the geographic position of each sampling point (latitude and longitude) was obtained using a GPS (global positioning system). At each sampling site, the presence/absence of all species was recorded by three persons from a boat moving at a constant slow velocity along the entire shoreline, covering ca. 80–100 m of shore (area of ca 800–1,000 m²). We also made observations from the banks of the reservoir on three occasions for the better verification of small species (e.g. *Lemna* sp., *Salvinia* spp.).

For submersed species, we used a rake attached to a 4 m long pipe for both fine and coarse spatial scale observations. Macrophytes that could not be identified in the field were collected for herborization and later identification (Cook 1990; Pott and Pott 2000; Lorenzi 2000) and maintained in the Herbarium of the University of Maringá (HUEM).

Data analyses

We first applied a logistic regression (Ter Braak and Looman 1986) to test whether the likelihood of occurrence of the native species were affected by tropical signalgrass at the fine spatial scale. We used logistic regression in addition to co-occurrence statistics (see below) because the former is based on a continuous predictor variable (tropical signalgrass biomass) and thus it shows more clearly how the presence of natives is correlated with the invasive species. We contend that because we collected two quadrats in each patch of macrophyte, there could be a certain degree of spatial dependence within patches, which could be of concern for our statistical analyses. However, this shortcoming is minor because (i) the

two quadrats had quite different tropical signalgrass biomass (indicating different colonization histories), (ii) patches were clearly separated from each other by uncolonized shore in each ecosystem and (iii) ecosystems are >100 km distant from each other, increasing even more the distance of patches among them.

It was not possible to analyze all species present due to the low number of occurrences of some species in our samples, so we only used species that were recorded at least nine times in our analyses. According to Vittinghoff and McCulloch (2006), the probability of type I error and the relative bias that is found in 10–16 events are almost the same as found in 5–9 events, and the coverage and bias will fall within acceptable levels. We recorded a total of 65 species of macrophytes at fine spatial scales, but by using the above criterion, we only retained 15 species for further analyses (see Table 1).

Logistic regression is the best choice for analyzing our dataset due to the characteristics of the dependent variables (binary, or presence–absence) that were regressed on an explanatory (quantitative) variable (tropical signalgrass biomass). For this analysis, we considered the presence (1) or absence (0) of each native species. The total dataset was used, but one lake was excluded from analyses for 10 species because they were absent from this lake and, thus, their absences might be explained for example by lack of dispersion which would prevent conclusions being drawn about patterns of co-occurrences. We used the SAM program, Version 3.1 (Rangel et al. 2006) for logistic regression models.

To determine whether the probability of co-occurrence of each native species with tropical signalgrass was higher or lower than expected by chance, we first made a correction. We used a binary matrix (presence/absence) at both fine and coarse scales to estimate the corrected proportion of occurrences of species i with tropical signalgrass (CPO_{it}):

$$CPO_{it} = \frac{n_{it}}{n_i \times \frac{n_t}{N}}$$

where n_{it} is the number of sites where ‘species i co-occurred with tropical signalgrass’; n_i is the total number of points where species i occurred; n_t is the number of points where tropical signalgrass occurred; and N is the total number of points. The CPO_{it} indicates whether tropical signalgrass co-occurred

more ($CPO_{it} > 1$) or less ($CPO_{it} < 1$) than expected by chance ($CPO_{it} = 1$) with each species of macrophyte.

Although the CPO_{it} values indicate whether each species co-occurs with tropical signalgrass more or less than expected by chance, they are not statistically testable. Thus, to test the degree of association between tropical signalgrass and each native species, we calculated the togetherness score (T-score; Stone and Roberts 1992) for pairs of species (species i and tropical signalgrass) and then tested each value using randomizations. The T-score test was originally proposed for entire communities; this statistic tests how often a group of species are aggregated or co-occur, but in this study, we used it to test patterns of co-occurrences only between pairs of species, as already employed by Sanderson (2000) and Sanderson et al. (2009). The presence/absence matrix was used again with a value of 1 when a species was present in a given sampling unit and 0 when it was absent.

The T-score values and their significances were calculated using R environment (R development Core Team 2008) with 30,000 randomizations (Lehsten and Harmand 2006). T-score values higher than those obtained at random ($P < 0.05$) indicate that a given species and tropical signalgrass co-occurred more than expected by chance, whereas T-score values lower than those obtained at random ($P < 0.05$) indicate that a given species and tropical signalgrass co-occurred less than expected by chance.

For the coarse spatial scale, we found a total of 83 species at the 251 sites, but we only selected 41 species and the exotic tropical signalgrass for our analysis because their occurrences were ≥ 10 and the presence of each species appeared on two or more sampling dates. Six species among these were also Poaceae, which allowed testing the DNH (see Table 2).

Results

There was a wide variation of the tropical signalgrass biomass, which was <20 g DW m^{-2} in 41 quadrats, 21–80 g DW m^{-2} in 27 quadrats and 81–160 g DW m^{-2} in 18 quadrats. At this fine spatial scale, the logistic regression analyses showed that the likelihood of the occurrence of native species in

relation to tropical signalgrass biomass differed among macrophyte species. Six taxa, *Egeria* spp., *E. azurea*, *E. crassipes*, *L. laevigatum*, *O. cubense* and *S. auriculata*, were negatively and significantly affected by tropical signalgrass biomass ($\chi^2 = 10.65$, 17.41, 4.12, 10.53, 7.8, 6.52, respectively, and $P < 0.05$; Fig. 1a). The likelihood of the occurrence of another nine species (including *H. amplexicaule*, *E. punctata* and *P. pedersenii*, other species of Poaceae) was unaffected by tropical signalgrass biomass ($P > 0.05$; Fig. 1b).

The CPO_{it} measured at the fine spatial scale showed that tropical signalgrass co-occurred less than expected by chance with all species of macrophytes (all values lower than 1; Fig. 2). The use of the T-score to test the significance of the co-occurrences showed that five species co-occurred significantly with tropical signalgrass less than expected by chance (i.e., the estimated T-score values were lower than those obtained in the random distribution at $P < 0.05$; Table 1; Fig. 2). However, co-occurrences

between each of the 3 species of Poaceae and tropical signalgrass were within those expected by chance.

At the coarse spatial scale, the CPO_{it} results varied conspicuously, indicating that both positive and negative associations between tropical signalgrass and native macrophytes existed. The species that co-occurred more often with tropical signalgrass were *S. minima* and *H. pusilla*, whereas those that co-occurred less often were two submersed species, *H. verticillata* and *Chara* sp. (Fig. 3). The T-score values showed a clear predominance of significant positive associations (more co-occurrences than expected by chance) at the coarse scale, i.e., the estimated T-score values were higher than those obtained in the random distribution at $P < 0.05$. Nine out of 41 species co-occurred more with tropical signalgrass than expected by chance on all occasions. Another 13 species co-occurred more with tropical signalgrass than expected by chance in 1, 2 or 3 samplings (Table 2; Fig. 3). For another 16 species, the associations were not significant, and only three species (all rooted submersed) co-occurred with tropical signalgrass less than expected by chance (Table 2; Fig. 3).

Two species of Poaceae (*A. bicornis* and *P. repens*) co-occurred with tropical signalgrass more than expected by chance in two samplings, as indicated by CPO_{it} values higher than 1 and significant T-score values at the coarse spatial scale (Table 2; Fig. 3). Four other species (*H. amplexicaule*, *L. hexandra*, *P. aquaticum* and *P. pernambucense*) were not significantly associated with tropical signalgrass at this scale (Table 2; Fig. 3).

Discussion

Our analyses encompassing fine (0.25 m²) and a coarse (ca. 1,000 m²) spatial scales showed that the patterns of co-occurrence between invasive tropical signalgrass and native macrophytes varied across these different scales. Negative associations between tropical signalgrass and native species predominated at the fine spatial scale, but there were more positive associations at the coarse spatial scale. Thus, our results obtained for pairs of species were similar to those that have been obtained for community attributes, for which invasive species have been found to

Table 1 Results of T-score (significant values are in bold) and significance levels measured for single pairs of species formed by tropical signalgrass and each of the other species at the fine spatial scale

Species	T-score	P
<i>Egeria</i> spp.*	0.063	0.001
<i>Eichhornia azurea</i> (Sw.) Kunth*	0.083	0.001
<i>Eichhornia crassipes</i> (Mart.) Solms	0.150	0.141
<i>Eleocharis</i> sp.	0.111	0.055
<i>Eriochloa punctata</i> (L.) Desv. ex Ham. ^a	0.128	0.170
<i>Hymenachne amplexicaulis</i> (Rudge) Nees ^a	0.171	0.431
<i>Limnobium laevigatum</i> (Humb. and Bonpl. ex Willd.) Heine*	0.112	0.031
<i>Oxycaryum cubense</i> (Poepp. and Kunth) Palla*	0.162	0.043
<i>Panicum pedersenii</i> Zuloaga ^a	0.123	0.131
<i>Polygonum acuminatum</i> Kunth	0.111	0.072
<i>Polygonum ferrugineum</i> Wedd	0.185	0.272
<i>Salvinia auriculata</i> Aubl	0.206	0.203
<i>Salvinia herzogii</i> de la Sota	0.183	0.475
<i>Salvinia minima</i> Baker	0.261	0.418
<i>Utricularia</i> sp.*	0.132	0.048

* Species for which the T-score values were lower than expected by chance

^a Species of the family Poaceae, which includes *U. subquadriflora*

Table 2 Results of T-scores (significant values are in bold) and significance levels measured for several single pairs of species formed by tropical signalgrass and each of the other species measured at the coarse spatial scale

Species	September/2008		March/2009		September/2009		March/2010	
	T-score	P	T-score	P	T-score	P	T-score	P
<i>Aeschynomene</i> sp.	–	–	0.295	0.043	0.234	0.296	0.150	0.073
<i>Alternanthera tenella</i> Colla	0.248	0.293	–	–	0.218	0.474	0.177	0.360
<i>Andropogon bicornis</i> L. ^a	0.262	0.204	0.262	0.246	0.279	0.019	0.231	0.034
<i>Caperonia castaneifolia</i> (L.) A. St.-Hil	0.242	0.311	0.236	0.4699	0.192	0.198	0.199	0.313
<i>Chara</i> sp.*	0.267	0.104	0.181	0.044	0.149	0.040	–	–
<i>Commelina nudiflora</i> L.	0.214	0.364	0.247	0.471	0.248	0.170	0.204	0.221
<i>Cyperus</i> sp.	–	–	0.192	0.138	–	–	0.163	0.192
<i>Eichhornia azurea</i> (Sw.) Kunth	0.264	0.103	0.296	0.047	0.215	0.413	0.175	0.326
<i>Eichhornia crassipes</i> (Mart.) Solms	0.323	<0.001	0.367	<0.001	0.280	0.021	0.253	0.002
<i>Egeria densa</i> Planch*	0.344	0.006	0.260	0.341	0.276	0.042	0.263	0.166
<i>Egeria najas</i> Planch	0.264	0.158	0.252	0.393	0.189	0.147	0.249	0.030
<i>Eleocharis filiculmis</i> Kunth	–	–	–	–	0.280	0.050	0.190	0.485
<i>Eleocharis interstincta</i> (Vahl) Roem. and Schult	–	–	0.232	0.586	0.183	0.161	0.172	0.275
<i>Eleocharis minima</i> Kunth	–	–	0.280	0.300	0.224	0.501	0.186	0.433
<i>Eleocharis</i> sp.	0.281	0.044	0.214	0.252	–	–	–	–
<i>Hydrilla verticillata</i> (L. f.) Royle*	0.164	0.012	0.101	<0.001	–	–	–	–
<i>Hydrocotyle pusilla</i> A. Rich	0.336	0.019	–	–	0.296	0.041	–	–
<i>Hymenachne amplexicaulis</i> (Rudge) Nees ^a	0.206	0.308	0.196	0.068	0.221	0.256	0.271	0.254
<i>Ipomoea carnea</i> Jacq	–	–	0.282	0.236	–	–	0.169	0.251
<i>Leersia hexandra</i> Sw ^a	0.196	0.164	0.269	0.170	0.176	0.064	0.201	0.217
<i>Lemna valdiviana</i> Phil	0.297	0.007	–	–	0.198	0.233	–	–
<i>Limnobium laevigatum</i> (Humb. and Bonpl. ex Willd.) Heine	0.338	<0.001	0.354	0.020	–	–	0.217	0.027
<i>Ludwigia lagunae</i> (Morong) H. Hara	0.285	0.022	0.217	0.274	0.277	0.104	0.192	0.405
<i>Ludwigia leptocarpa</i> (Nutt.) H. Hara	–	–	0.314	0.009	–	–	0.287	0.003
<i>Ludwigia</i> sp.	0.198	0.185	–	–	0.285	0.129	0.170	0.244
<i>Myriophyllum brasiliense</i> Cambess	0.245	0.419	–	–	–	–	0.217	0.274
<i>Nymphaea caerulea</i> Savigny	0.215	0.335	0.341	0.044	0.216	0.378	0.226	0.143
<i>Nymphoides indica</i> (L.) Kuntze	0.301	0.004	0.240	0.457	0.292	0.007	0.287	0.004
<i>Oxycaryum cubense</i> (Poepp. and Kunth) Palla	0.340	<0.001	0.337	0.012	0.244	0.025	0.233	0.028
<i>Panicum aquaticum</i> Poir ^a	–	–	0.248	0.463	0.263	0.228	–	–
<i>Panicum pernambucense</i> (Spreng.) Mez ex Pilg ^a	0.194	0.186	0.215	0.110	0.196	0.211	0.222	0.244
<i>Paspalum repens</i> P. J. Bergius ^a	0.280	0.039	0.383	<0.001	0.228	0.482	0.225	0.066
<i>Phyllanthus</i> sp.	–	–	–	–	0.263	0.100	0.194	0.364
<i>Pistia stratiotes</i> L.	0.285	0.033	–	–	0.183	0.102	0.218	0.016
<i>Polygonum acuminatum</i> Kunth	0.269	0.250	0.259	0.324	0.292	0.017	0.214	0.112
<i>Polygonum ferrugineum</i> Wedd	0.268	0.056	0.303	0.019	0.239	0.253	0.213	0.133
<i>Polygonum hydropiperoides</i> Michx	0.2512	0.273	–	–	0.237	0.253	0.163	0.184
<i>Rhynchospora corymbosa</i> (L.) Britton	0.259	0.284	–	–	0.268	0.182	–	–
<i>Salvinia auriculata</i> Aubl	0.326	<0.001	0.345	0.007	0.238	0.027	0.222	0.047
<i>Salvinia herzogii</i> de la Sota	0.356	<0.001	0.356	0.005	0.287	0.015	0.234	0.020
<i>Salvinia minima</i> Baker	0.362	<0.001	0.374	0.001	0.307	0.006	0.225	0.047

* Species for which the T-score values were lower than expected by chance

^a Species of the family Poaceae, which includes *U. subquadriflora*

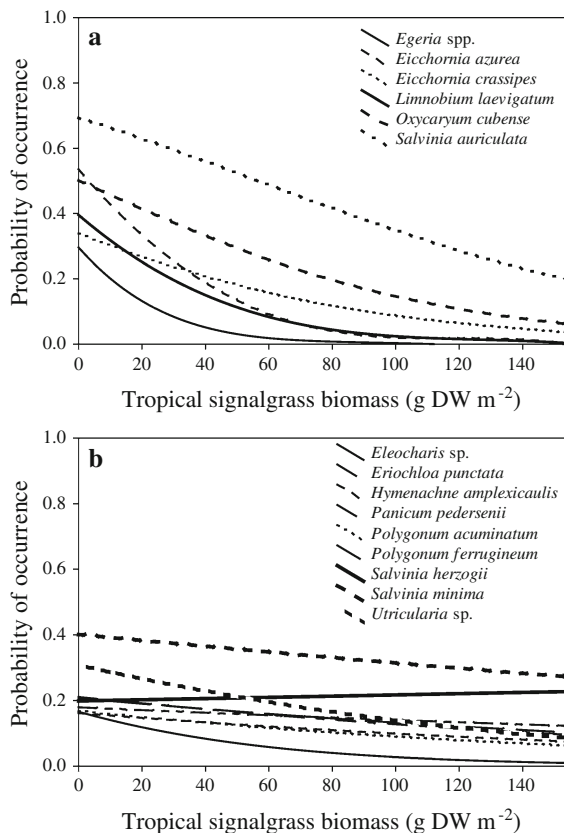


Fig. 1 The probability of occurrence of native macrophytes in response to tropical signalgrass biomass. (a) Species significantly affected and (b) species not affected by tropical signalgrass biomass

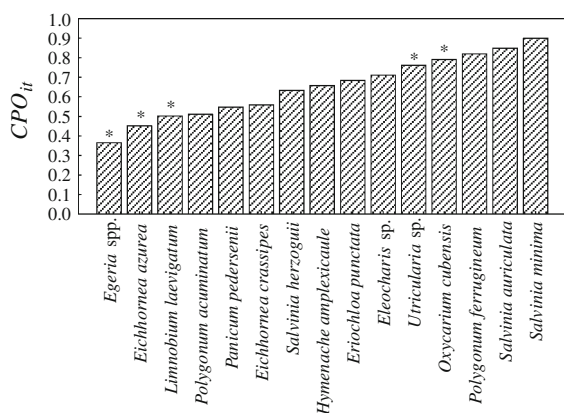


Fig. 2 The corrected proportion of occurrences of species *i* with tropical signalgrass (CPO_{it}) obtained at the fine spatial scale. Significant T-score values between species *i* and tropical signalgrass are indicated with asterisk

be negatively associated with richness at fine spatial scales but positively associated with richness at coarse spatial scales (Melborne et al. 2007; Capers et al. 2007; Thomaz et al. 2009; Michelan et al. 2010).

The patterns of co-occurrences that we measured through T-scores together with logistic regressions indicated that the responses of native species depend on tropical signalgrass abundance and native species identity on a fine scale. In fact, five native species co-occurred less than expected by chance, and no species co-occurred more than expected by chance with tropical signalgrass in our 0.25 m² quadrats. Accordingly, the probability of occurrence of 6 out of 15 species decreased with increasing invasive grass biomass on this scale. Three of these species (*E. crassipes*, *L. laevigatum* and *S. auriculata*) are free-floating, while one is rooted with floating stems (*E. azurea*), one is the epiphyte *O. cubense* which grows on these floating species and another one is rooted submersed (*Egeria* spp). It is difficult to draw conclusions about mechanisms, or whether direct interactions between species play any role in shaping the patterns we found. However, we infer that competition for space and limitation by light, as indicated by others in aquatic and terrestrial ecosystems (e.g., Hautier et al. 2009; Jäger et al. 2009), might be possible causes of decreasing probability of occurrence of these six species with increasing tropical signalgrass biomass, and of negative co-occurrences between each species and tropical signalgrass. In fact, the rooted submersed *Egeria* spp. suffered the steepest decrease with tropical signalgrass biomass (see Fig. 1a) probably because dense stands of tropical signalgrass reduce underwater light. However, habitat constraints cannot be discarded because they lead to nonrandom patterns of species co-occurrences like ours (Peres-Neto et al. 2001; Gotelli and Ellison 2002) and thus, species segregation may also be attributed to different responses to depth and other habitat characteristics (Boschilia et al. 2008).

In contrast to what we found at the fine spatial scale, there was a predominance of positive associations between tropical signalgrass and native species at the coarse spatial scale (22 species out of 41 co-occurred more than expected by chance with tropical signalgrass). Thus, for areas of ca. 1,000 m², tropical signalgrass co-occurs more than expected by

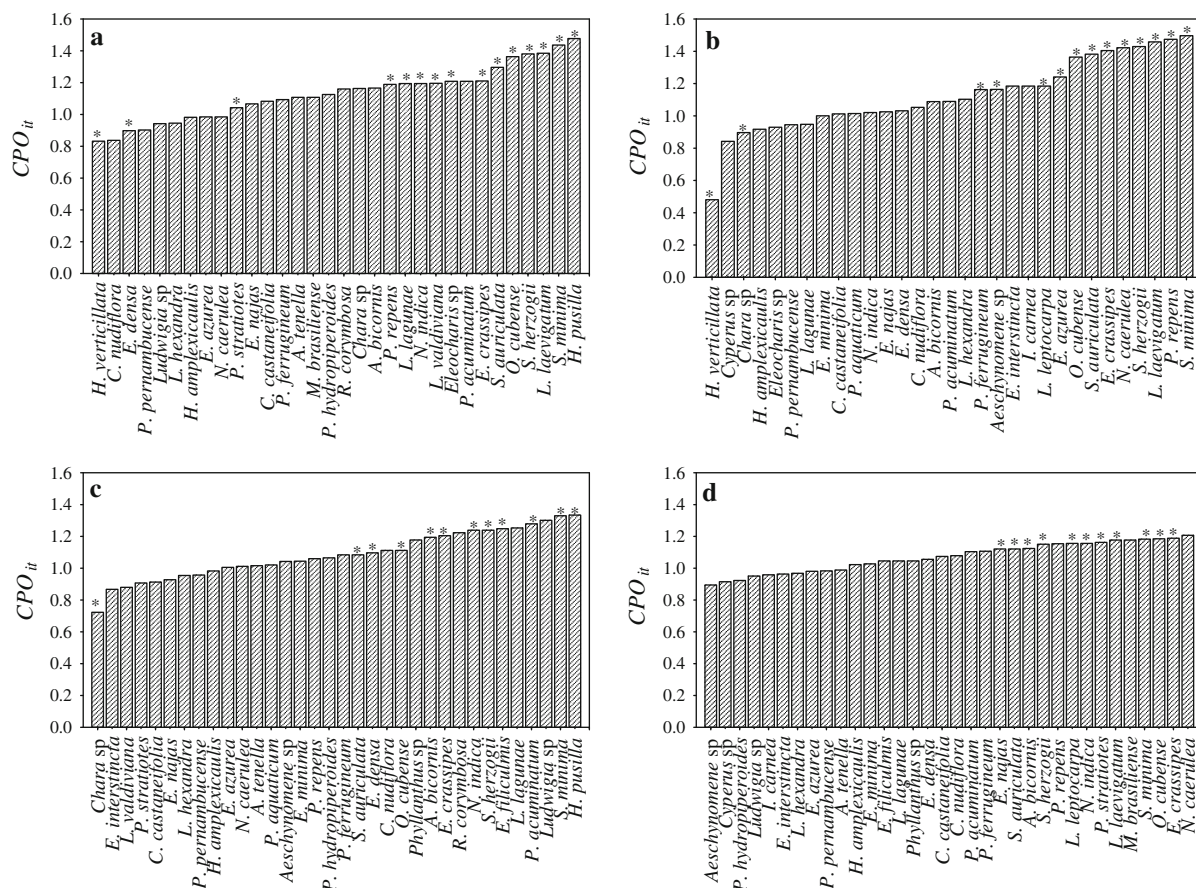


Fig. 3 The corrected proportion of occurrences of species i with tropical signalgrass (CPO_{it}) obtained at the coarse spatial scale in September 2008 (a), March 2009 (b), September 2009

(c) and March 2010 (d). Significant T-score values between species i and tropical signalgrass are indicated with asterisk

chance with several other native species. These positive associations can be explained by the fact that almost all native species colonize the most suitable habitats in the Itaipu Reservoir, which are also preferred by tropical signalgrass. However, tropical signalgrass also colonizes several unsuitable habitats (e.g., more eutrophic and wave disturbed sites) where it is found alone or with few other species (SM Thomaz, unpublished). In fact, the importance of disturbance for native macrophytes in Itaipu has been suggested by community analysis which show that fetch (a surrogate of wave disturbances) affects macrophyte diversity (Thomaz et al. 2003). In addition, at the coarse scale, habitats are more physically heterogeneous than at the fine spatial scale investigated in terms of depths, shading from riparian vegetation and sediment composition, allowing co-existence of several species. Habitat

heterogeneity, used here to explain individual positive associations, also operates at the community level, and it has been considered an important factor explaining macrophyte richness (Rolon et al. 2008) and positive relationships between invasives and natives (Capers et al. 2007; Melbourne et al. 2007; Thomaz et al. 2009).

Despite the predominance of positive co-occurrences, there were also three species that co-occurred less than expected by chance with tropical signalgrass at the coarse spatial scale. These are rooted, submersed species, and the same factor that likely explains this relationship at the fine spatial scale (underwater light limitation) may also explain it at the coarse spatial scale. Thus, the results we obtained at both fine and coarse spatial scales show that niche differences between tropical signalgrass (which grows extensively above water) and rooted

submersed plants (which grow completely under the water surface) are not enough to allow coexistence among these species.

Phylogeny has been considered to be an important predictor of plant invasiveness ability (Lambdon and Hulme 2006; Dawson et al. 2009; Ricotta et al. 2010), and also explains patterns of co-occurrences between native pairs of species (Sanderson et al. 2009). Phylogenetic dispersion may occur in response to competitive exclusion which limits the coexistence of closely related species, while phylogenetic clustering may occur if closely related species have similar physiological limitations and niche conservatism (Cavender-Bares et al. 2006). These different ecological processes operate simultaneously and may create opposing patterns in different scales (Cavender-Bares et al. 2006). At fine spatial scales, high similarity between closely related species results in repulsion of invasive species (DNH), but at coarse scales, competition becomes less important, and therefore, alien species more closely related to native species tend to share the same pre-adaptations and broad environmental preferences, which increase their co-occurrences (Procheş et al. 2008; Ricotta et al. 2010). Our results contradict this general hypothesis, because all three grasses that were recorded at the fine spatial scale were not affected by tropical signalgrass biomass, and their patterns of co-occurrence were within what was expected by chance (i.e., no negative effects were detected). Differently, at the coarse scale, two species co-occurred with tropical signalgrass more than expected by chance: *P. repens* (which belongs to the same tribe of *U. subquadriflora*) and *A. bicornis* (which belongs to the same sub-family of *U. subquadriflora*). The large number of terrestrial species in each of these genera indicates that they did not share an aquatic ancestor. However, pre-adaptation to environmental conditions is important in explaining alien success (Ricotta et al. 2010). Because tropical signalgrass is an African plant inhabiting warm, shallow aquatic and wet habitats, pre-adaptations to these conditions allow it to colonize similar habitats in Neotropical ecosystems, which are highly colonized by other species of Poaceae. For another four species of Poaceae (*P. aquaticum*, *P. pernambucense* and *H. amplexicaulis*, which belong to the same tribe of *U. subquadriflora*, and *L. hexandra*, which belongs to the same family but to a different sub-family), their co-occurrences

with tropical signalgrass were within what was expected by chance at the coarse scale. Thus, for these species the expected phylogenetic clustering at coarse scale did not occur. Analyses using more refined data about phylogenetic relatedness have to be carried before reaching a firmer conclusion regarding the effects of phylogeny at a coarse spatial scale.

In summary, our results indicate that macrophyte species respond differently to invasions across spatial scales, similar to results obtained in terrestrial ecosystems. Although it is difficult to find the mechanisms that explain our results, we suggest that competition and/or habitat constraints may be important for negative co-occurrences at fine spatial scale, while habitat heterogeneity and the presence suitable habitats for both natives and invasive species seem to be important for the positive co-occurrences at coarse spatial scales. Finally, the results of logistic regression and the patterns the co-occurrence between tropical signalgrass and other Poaceae did not corroborate the DNH at either the fine or coarse spatial scale. Thus, it seems at least for tropical signalgrass, that invasion and patterns of co-occurrences with natives are more related to functional characteristics of native species (different uses of habitats by distinct macrophyte life forms) than to phylogeny.

Acknowledgments T. S. M. acknowledges the Brazilian Council of Research (CNPq) for providing a scholarship, and S. M. T. is especially thankful to the CNPq for continuous funding through a Research Productivity Grant. We thank Thiago Santos (Universidade Federal de Goiás) for statistic assistance, Dr. Kevin J. Murphy (University of Glasgow, UK) for polishing the language of the second version of this paper, two anonymous reviewers and Dr. Marc Cadotte for suggestions that improved the quality of our work. This research was partially funded by Itaipu Binacional.

References

- Bianchini Jr I, Cunha-Santino MB, Milan JAM, Rodrigues CJ, Dias JHP (2010) Growth of *H. verticillata* (L.f.) royle under controlled conditions. *Hydrobiologia* 644:301–312. doi:10.1007/s10750-010-0191-1
- Boschilia SM, Oliveira EF, Thomaz SM (2008) Do aquatic macrophytes co-occur randomly? An analysis of null models in a tropical floodplain. *Oecologia* 156:203–214. doi:10.1007/s00442-008-0983-4
- Byers JE, Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84: 1428–1433

- Cadotte MW, Borer ET, Seabloom EW, Cavender-Bares J, Harpole WS, Cleland E, Davies KF (2010) Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in northern California. *Divers Distrib* 16:892–901. doi:[10.1111/j.1472-4642.2010.00700.x](https://doi.org/10.1111/j.1472-4642.2010.00700.x)
- Capers RS, Selsky R, Bugbee GJ, White JC (2007) Aquatic plant community invisibility and scale-dependent patterns in native and invasive species richness. *Ecology* 88: 3135–3143
- Cavender-Bares J, Keen A, Miles B (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:109–122
- Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110. doi:[10.1016/j.tree.2005.01.003](https://doi.org/10.1016/j.tree.2005.01.003)
- Cook CDK (1990) Origin, autecology, and spread of some of the world's most troublesome aquatic weeds. In: Pieterse AH, Murphy KJ (eds) *Aquatic weeds: the ecology and management of nuisance aquatic vegetation*. Oxford Science Publications, Oxford, pp 31–38
- Daehler CC (2001) Darwin's naturalization hypothesis revisited. *Am Nat* 158:324–330
- Darwin C (1859) *On the origin of species by means of natural selection*. Murray, London
- Dawson W, Burslem DFRP, Hulme PE (2009) Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. *J Ecol* 97: 657–665. doi:[10.1111/j.1365-2745.2009.01519.x](https://doi.org/10.1111/j.1365-2745.2009.01519.x)
- Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. *Ecol Lett* 11: 674–681. doi:[10.1111/j.1461-0248.2008.01178.x](https://doi.org/10.1111/j.1461-0248.2008.01178.x)
- Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88:3–17
- Gotelli NJ, Ellison AM (2002) Assembly rules for New England ant assemblages. *Oikos* 99:591–599
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638. doi:[10.1126/science.1169640](https://doi.org/10.1126/science.1169640)
- Jäger H, Kowarik I, Tye A (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galápagos highland vegetation. *J Ecol* 97:1252–1263. doi:[10.1111/j.1365-2745.2009.01578.x](https://doi.org/10.1111/j.1365-2745.2009.01578.x)
- Jiang L, Tan J, Pu Z (2010) An experimental test of Darwin's naturalization hypothesis. *Am Nat* 175:415–423. doi:[10.1086/650720](https://doi.org/10.1086/650720)
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638
- Lambdon PW, Hulme PE (2006) How strongly do interactions with close-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. *J Biogeogr* 33:1116–1125. doi:[10.1111/j.1365-2699.2006.01486.x](https://doi.org/10.1111/j.1365-2699.2006.01486.x)
- Lehsten V, Harmand P (2006) Null models for species co-occurrence patterns: assessing bias and minimum iteration number for the sequential swap. *Ecography* 29:786–792
- Lorenzi H (2000) *Plantas daninhas do Brasil: terrestres, aquáticas, parasitas e tóxicas*. Nova Odessa, São Paulo
- MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. *J Ecol* 97:609–615. doi:[10.1111/j.1365-2745.2009.01514.x](https://doi.org/10.1111/j.1365-2745.2009.01514.x)
- Melborne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol Lett* 10:77–94. doi:[10.1111/j.1461-0248.2006.00987.x](https://doi.org/10.1111/j.1461-0248.2006.00987.x)
- Michelan TS, Thomaz SM, Carvalho P, Mormul RP (2010) Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity. *Freshw Biol* 55: 1315–1326. doi:[10.1111/j.1365-2427.2009.02355.x](https://doi.org/10.1111/j.1365-2427.2009.02355.x)
- Peres-Neto PR, Olden JD, Jackson DA (2001) Environmentally constrained null models: site suitability as occupancy criterion. *Oikos* 93:110–120
- Pott VJ, Pott A (2000) *Plantas aquáticas do Pantanal*. EMB-RAPA, Brasília
- Procheş Ş, Wilson JR, Richardson DM, Rejmánek M (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecol Biogeogr* 17:5–10
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN: 3-900051-07-0. <http://www.R-project.org>. Accessed 05 Nov 2010
- Rangel TFLVB, Diniz-Filho JAF, Bini LM (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Glob Ecol Biogeogr* 15:321–327. doi:[10.1111/j.1466-822x.2006.00237.x](https://doi.org/10.1111/j.1466-822x.2006.00237.x)
- Ricotta C, Godefroid S, Rocchini D (2010) Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species. *Divers Distrib* 16:655–662. doi:[10.1111/j.1472-4642.2010.00676.x](https://doi.org/10.1111/j.1472-4642.2010.00676.x)
- Rolon AS, Lacerda T, Maltchik L, Guadagnin DL (2008) Influence of area, habitat and water chemistry on richness of macrophyte assemblages in southern Brazilian wetlands. *J Veg Sci* 19:221–228. doi:[10.3170/2008-8-18359](https://doi.org/10.3170/2008-8-18359)
- Sanderson JG (2000) Testing ecological patterns. *Am Sci* 88:332–339
- Sanderson JG, Diamond JM, Pimm SL (2009) Pairwise co-existence of Bismarck and Solomon landbird species. *Evol Ecol Res* 11:1–16
- Sculthorpe CD (1967) *The biology of vascular plants*. Edward Arnold, London
- Stone L, Roberts A (1992) Competition exclusion, or species aggregation? An aid in deciding. *Oecologia* 91:419–424
- Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. *Proc National Acad Sci USA* 103:5841–5845. doi:[10.1073/pnas.0508073103](https://doi.org/10.1073/pnas.0508073103)
- Ter Braak CJF, Looman CWN (1986) Weighted averaging, logistic regression and the Gaussian response model. *Vegetation* 65:3–11
- Thomaz SM, Souza DC, Bini LM (2003) Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu reservoir, Brazil): the influence of limnology and morphometry. *Hydrobiologia* 505: 119–128
- Thomaz SM, Carvalho P, Mormul RP, Ferreira FA, Silveira MJ, Michelan TS (2009) Temporal trends and effects of

- diversity on occurrence of exotic macrophytes in a large reservoir. *Acta Oecol* 35:614–620. doi:[10.1016/j.actao.2009.05.008](https://doi.org/10.1016/j.actao.2009.05.008)
- Vittinghoff E, McCulloch CE (2006) Relaxing the rule of 10 events per variable in logistic and cox regression. *Am J Epidemiol* 20:1–9. doi:[10.1093/aje/kwk052](https://doi.org/10.1093/aje/kwk052)
- Wetzel RG (2001) *Limnology: lake and river ecosystems*. Academic, San Diego