# Biotic resistance at different spatial scales did not inhibit the colonization success of an exotic submerged aquatic plant.

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# Abstract

The success of exotic species in different environments is affected by biotic and abiotic filters, whose effects depend on the spatial scale employed. This study tested the hypotheses that (i) native species richness and abiotic conditions explain the sucess of exotic species *Hydrilla verticillata* and (ii) that biological resistance to invasion provided by diversity varies at different scales. The samples were collected at 176 georeferenced points in Rosana Reservoir. In each sampling site, measurements of *fetch*, distance between shores, organic matter concentration and grain size at sediment, depth, Secchi disk depth, conductivity, pH, and species richness of submerged macrophytes in three different scales (small, medium and large) were taken. Our results demonstrated that the occurrence of *H. verticillata* was positively correlated with increase in native species richness at three scales, with no difference between scales, as well as between *fetch* and distance between reservoir shores. However, it responded negatively to the concentration of organic matter in the sediment and depth. The results allowed the following conclusions: (i) biotic resistance did not reduce the success of exotic invasive *H. verticillata*, (ii) contrary to expectations, the competition mechanism did not influence the occurrence of this species at a small scale, (iii) at the moment, abiotic factors may be more important than biotic resistance in determining the success of this species at reservoir, but this relationship may change in the future and (iv) possibly, the dominant general pattern in invasion ecology at multiple spatial scales may be one of "biotic acceptance" in certain environments.


# Introduction

Exotic species have attracted the attention of various researchers, both due to their negative impacts on communities and ecosystems (Mack et al. 2000) and their relevance for testing general ecological theories (Tilman 1993, 1997; Levine 2000, 2001; Davis et al. 2001; Moore et al. 2001). Currently, few ecosystems remain free from the introduction of exotic species (Vitousek et al. 1997).

Most research on biological invasions is conducted in terrestrial ecosystems (e.g., Hector 2001; Thomaz et al. 2015), with a significant bias towards temperate regions that receive more attention than tropical and subtropical ones (Petenon and Pivello 2008). However, there is a special interest in understanding and possibly preventing the introduction of exotic species in aquatic environments, as these ecosystems exhibit high biodiversity, explained, among other factors, by the presence of aquatic macrophytes that increase habitat complexity at different spatial scales (Dibble et al. 2006).

Some studies indicate that at larger spatial scales, the success of exotic species increases with increasing species richness (Levine and D'Antonio 1999), suggesting that exotic species and native species respond similarly to environmental conditions. However, at smaller spatial scales (e.g., plots of a few square meters), where environmental conditions are similar, most studies demonstrate that the success of exotic species declines with the richness of the native community. This can be explained by niche overlap and competitive exclusion, which drive the relationship between exotic species and native species at these smaller scales (Shea and Chesson 2002; Michelan et al. 2010). Although these

hypotheses are plausible, they are rarely tested simultaneously, especially in situ in aquatic environments.

The susceptibility of the environment to invasion by new organisms (invasibility) is a factor that can determine the establishment of species in different habitats (Lonsdale 1999). Reservoirs are considerably different environments from natural ecosystems, and their characteristics (e.g., increased inundation area and disturbance intensity) facilitate introductions and dispersal of species to other aquatic ecosystems (Havel et al. 2005).

The relationship between ecosystem invasibility by exotic species and the diversity of native species has long concerned naturalists. Darwin (1859) formally proposed that communities with higher species richness were less susceptible to invasions, especially aquatic communities. The relationship between species diversity and invasibility ("biotic resistance") was further addressed by Elton (1958), whose ideas have since underpinned discussions on invasions over the past 50 years, making it one of the most cited topics in invasion-related scientific literature (Levine and D'Antonio 1999). Biotic resistance against invasion is caused by mechanisms associated with allelopathy, predation, herbivory, parasitism (Gurevitch, 2011) and competition regarding use of space and nutrient uptake, which are most inflfluential biotic resistance mechanisms in plants (Levine and Antonio 1999; Levine et al. 2004; Gurevitch et al. 2011; Byun et al. 2014). Within this context, the use of resources by native species might reduce the invasive performance of exotic species as long as these species use similar resources to the native ones (Levine and Antonio 1999; Levine et al. 2004). Despite, other studies have demonstrated that even communities with higher species richness can be as vulnerable to introductions as poorer communities (Dunstan and Johnson 2004; Capers et al. 2007), thus, the introduction of exotic species can also occur in areas with lower species richness.

Studies have shown that abiotic factors also have a significant effect on plant growth and reproduction, and thus these factors can determine the success or failure of exotic plant species introductions (Spence, 1982; Barrett et al. 1993; Van den Berg et al. 2003). Sediment characteristics, along with other physicochemical features such as water transparency and nutrient availability (Sousa et al. 2010), act as abiotic filters to plant species introductions in aquatic ecosystems and play an important long-term role in the establishment and survival of rooted submerged macrophytes (Harwell and Havens 2003).

In this study, was analyzed the relationship between native species richness and the probability of occurrence of the exotic species *Hydrilla verticillata* at three different spatial scales. Additionally, we evaluated the probability of exotic species occurrence in relation to morphometric characteristics and sediment composition. Were tested the following hypotheses: (i) the invasion success of *Hydrilla verticillata* is positively related to native species richness at large and medium spatial scales but negatively related to native species richness at small spatial scales, and (ii) abiotic factors such as light penetration in the water, fetch (an indicator of wave disturbance), and sediment organic matter are important predictors of *H. verticillata* success. Hypothesis (i) was based on biotic resistance (Elton

1958), while hypothesis (ii) is based on the fact that abiotic environmental filters can be determinants of exotic species invasion success.

## Materials and Methods

# Study Area

# Rosana Reservoir

The Rosana reservoir is located in the lower Paranapanema River section (22°36'S 52°50'W). The reservoir was flooded in November 1986 and covers an area of 350 km², operating as a run-of-the-river type, with a residence time of 18.6 days and shallow depth (CESP, 1998) (Fig. 1). Aquatic plants are commonly found in the reservoir, with the submerged species *Egeria densa* being among the most abundant and with the highest vegetative cover. Other species are also found, such as *E. najas*, *Eichhornia azurea*, *Eichhornia crassipes, Salvinia herzogii*, *Echinodorus tenellus*, *Nymphaea amazonum*, *Typha domingensis*, and several species of grasses (Thomaz et al. 2005).

# >>> Fig. 1

# Data Collection

Data collection was conducted in the Rosana Reservoir in October 2010. Sampling involved recording the presence (1) or absence (0) of submerged macrophyte species at 176 previously demarcated and georeferenced points. Species sampling was performed using a long-handled rake (approximately 4 m), which was dragged along the sediment to the maximum depth limit colonized by macrophytes. However, 89 points located upstream of the reservoir were excluded from the analyses because the absence of *Hydrilla verticillata* in these locations may be due to dispersal limitations (see Fig. 1, points demarcated by the rectangle on the map).

# Sampling at Different Spatial Scales

At each sampling point, an area of approximately 1200m² was selected and subdivided into three scales: (i) small scale (rake area of 0.02m², with 10 sampling units for each collection point, n = 870 sampling units; for analysis, the species found in each rake were considered); (ii) medium scale (transects of ~ 60x4, equivalent to 240 m², with one transect at each sampling point, n = 87 sampling units; for analysis at this scale, only the species found in the transect were considered); and (iii) large scale, an area of ~ 60x20, equivalent to 1200 m², where the species composed of the aggregate of 10 sampling units of 0.02m², along with the species found at the medium scale were considered (n = 87 sampling units). Samples at different scales were used to test hypothesis (i).

# Sampling of Abiotic Variables

At all sampled points, the minimum ($Z_{min}$) and maximum ($Z_{max}$) depth of occurrence of submerged macrophytes were determined, with $Z_{min}$ and $Z_{max}$ being determined perpendicular to each transect using the metric scale of the rake handle. Additionally, at each sampling point, the straight-line distance (in meters) from the shoreline ahead of the point was determined to assess the influence of reservoir width on submerged macrophyte colonization. Furthermore, the following abiotic variables: electrical conductivity (μS cm^$^{-1}$), pH, Secchi disk transparency (m), and fetch (distance free for wind action; km), were measured to assess the influence of these abiotic variables on submerged macrophyte colonization in the Rosana Reservoir. *Fetch* can be considered as a variable indicating wave disturbance caused by wind. The fetch calculation used the following equation proposed by Håkanson and Jansson (1983) and modified by Azza et al. (2007).

where *Ef* (km) is the effective *fetch* (i.e., the distance in open water where waves are induced by the wind), xi (km) is the straight-line distance or length from the point towards land or an island, and ai (degrees) is the angle of inclination in the direction of the wind, starting from 0° with increments every 6° up to + 42° and − 42°. However, unlike the referenced authors above, who considered the central line as the one corresponding to the azimuth of the most prevalent winds, we applied as the central line the one that formed an angle of 90° in relation to the shoreline. We opted for this change because the wind originates from various directions in the reservoir, and because wave disturbances are apparently greater when the winds reach the macrophytes coming from the frontal direction (i.e., at 90° in relation to the shoreline).

A sediment sample was collected at each sampling point to determine the grain size distribution and organic matter content (% $OM_{sed}$ g DW). The grain size distribution was determined using the Wentworth scale (Wentworth 1922; Suguto 1973). Additionally, the estimate of organic matter present in the sediment was obtained by the ratio of the initial and final masses after burning 20g of sediment in a muffle furnace at 560°C for about four hours. The collection of data on abiotic variables at all sampling points was used to test hypothesis (ii).

# Statistical Analyses

Logistic regressions were applied to test the probability of occurrence of *H. verticillata* in response to the richness of native species recorded at the three sampled scales. Logistic regression was also applied to the abiotic variables: electrical conductivity, pH, Secchi depth, *fetch*, distance between shores, sediment organic matter, and depth of the reservoir where the plants were sampled. The positive effect of any of these variables would be confirmed if the probability of occurrence of *H. verticillata* increases as the tested variable increases, while the opposite would indicate a negative effect of the variable.

To assess the effect of the distance between shores and depth on sediment organic matter values, a simple linear regression was applied. Finally, to determine the type of sediment the *H. verticillata* colonizes, a principal component analysis (PCA) was conducted using the grain sizes found at each sampling point. A factorial ANOVA was performed with the PCA axes to verify if there was a significant

difference between the sediment types of locations colonized and not colonized by *H. verticillata*. All tests and figures were conducted using StatisticaTM 7.0 software.

# Results

A total of 13 species of submerged macrophytes were recorded for the entire Rosana Reservoir, with an average of (2.8 ± 1.46) for large scale, (2.05 ± 1.19) for medium scale, and (1.18 ± 0.94) for small scale. In all scales, the probability of occurrence of *H. verticillata* was significantly positive related to the increase in richness of native species (Table 1: Fig. 2a,b and c). The occurrence of *H. verticillata* at each sampling point and across the three scales varied between 1 and 4 species.

Table 1
Results of logistic regression using the presence of *H. verticillata* as the dependent variable, and as continuous variables, the native species richness at three scales (small, medium, and large), and the abiotic variables, electrical conductivity, pH, Secchi disk transparency, fetch, distance between shores, % OMsed g DW, and reservoir depth.

| Parameters | Estimates | $\chi^2$ | McFadden's $rho^2$ | Odds ratio | *p* |
|---|---|---|---|---|---|
| Small scale | 1.982 | 310.618 | 0.269 | 7.258 | < 0.001 |
| Medium scale | 1.822 | 47.814 | 0.394 | 6.185 | < 0.001 |
| Large scale | 1.219 | 24.958 | 0.207 | 3.382 | < 0.001 |
| Electrical conductivity | 0.052 | 0.846 | 0.007 | 1.053 | 0.357 |
| pH | 0.339 | 0.860 | 0.007 | 1.404 | 0.353 |
| Secchi disk transparency | -0.303 | 0.174 | 0.001 | 0.738 | 0.676 |
| Fetch | 1.064 | 15.150 | 0.126 | 2.900 | < 0.001 |
| Distance between shores | 1.608 | 29.409 | 0.244 | 4.994 | < 0.001 |
| % OMsed g DW | -3.049 | 81.129 | 0.675 | 0.047 | < 0.001 |
| Reservoir depth | -10.655 | 89.216 | 0.742 | 0.000 | < 0.001 |
| McFadden's estimates the proportion of variation explained by the logistic model; | | | | | |
| The odds ratio tests the relative risk according to the richness of ENs at three scales: small, medium, and large, and the abiotic variables: electrical conductivity, pH, Secchi disk, fetch, distance between shores, % OMsed g DW, and reservoir depth. | | | | | |

# >>> Fig. 2

Considering the abiotic variables, the probability of occurrence of *Hydrilla verticillata* was not significantly affected by electrical conductivity, pH, and Secchi disk depth (Table 1). However, logistic regression showed that the probability of occurrence of *H. verticillata* significantly increases with the increase in abiotic variables of *fetch* and distance between shores (Table 1; Figs. 3a-b). Nevertheless, the distance between shores exhibited the best model generated by the analysis (Table 1). As for the variables of sediment organic matter and reservoir depth, with the gradual increase in these variables, there was a significant decrease in the probability of occurrence *H. verticillata* (Table 1; Figs. 3c-d), with the analysis result showing a better logistic model for the depth variable (Table 1).

# >>> Fig. 3

# >>> Table 1

The results of the linear regression between sediment organic matter versus depth and distance between shores showed that with increasing depth, there was a significant increase in the percentage of organic matter ($\beta = 0.74$, $R^2 = 0.54$, $p < 0.001$; Fig. 4a). However, for the distance between shores, the relationship was inverse, with a significant reduction in sediment organic matter percentage with increasing distance between shores of the reservoir ($\beta = -0.49$, $R^2 = 0.26$, $p < 0.001$; Fig. 4b).

# >>> Fig. 4

The results of the principal component analysis (PCA) using the grain size data demonstrated that the sediment of the Rosana Reservoir is composed of different types of granules (Fig. 5). However, the result of the ANOVA with the PCA axes showed that there was no significant difference in sediment type between locations where the *H. verticillata* was present and those where it was absent ($F = 1.02$; $p > 0.05$).

# >>> Fig. 5

## Discussion

The results of this study demonstrated that, contrary to what was expected by our hypothesis, the probability of occurence of *H. verticillata* was high with increases in species richness across all spatial scales. Moreover, the *fetch* and distance between the shores also significantly increased the probability of occurrence of *H. verticillata*, but its occurrence was negatively impacted by increases in organic matter sediment and reservoir depth.

Recent studies (e.g., Fridley et al. 2004; Herben et al. 2004; Grey 2009) have examined the role of spatial scales in explaining conflicting results between co-occurrence patterns of exotic and native species (Chen et al. 2010). However, it is common to find in the literature records of negative relationships between exotic and native species at small scales (e.g., Naeem et al. 2000; Brown and Peet 2003), and positive relationships at large spatial scales (e.g., Davies et al. 2005; Capers et al. 2007). The reason for

opposite patterns occurring at different scales is the predominant type of interaction. At smaller scales, competition determines community patterns, thus making the relationship between exotic and native species negative (Levine and D'Antonio 1999; Hector et al. 2001; Levine et al. 2004; Capers et al. 2007; Fridley et al. 2007). On the other hand, at larger scales, increased environmental heterogeneity and resource availability may elevate the co-occurrence between exotic and native species (Davis et al. 2000; Dunstan and Johnson 2004). In our results, the regression analysis showed that the probability of occurrence of *H. verticillata* was positively related to the increase in native species richness at the three spatial scales analyzed. Several studies have demonstrated that the presence of an exotic species can impact the development of other native species (Michelan et al. 2010; Silveira et al. 2018; Louback-Franco et al. 2019). However, other studies have demonstrated that the presence of an exotic species can facilitate the presence of other native species (Thomaz et al. 2012; Silveira and Thomaz 2019). Thus, possibly the competition between submerged macrophyte native species and *H. verticillata* may not have been important enough to affect the presence of *H. verticillata* at the small scales we addressed. At the same time, these findings allow us to reject the hypothesis that biological resistance to exotic species invasion, represented by species diversity, varies at different spatial scales. With these results, along with many other field studies in natural ecosystems, we can possibly demonstrate that the dominant general pattern in invasion ecology at multiple spatial scales is one of "biotic acceptance" in certain environments, where, natural ecosystems tend to accommodate the establishment and coexistence of introduced species despite the presence, abundance (Stohlgren et al. 2006), and/or native species richness.

Some authors have demonstrated using a competition-based model with negative relationships at small scales that these relationships can become positive when the number of resources available to the entire community is altered (Byers and Noonburg 2003). Despite the predominance of records of negative relationships at small spatial scales, a positive relationship has been reported between some communities containing exotic and native species at small scales in various systems such as California chaparral, savannas, and coniferous forests (Keeley et al. 2003). This suggests that the relationships between exotic and native species are not simply determined by competition but also by other factors such as increased resource availability for a wide range of species.

Fluctuation and resource availability have received considerable attention in ecological studies (Davis et al. 2000; Blumenthal 2005), as these mechanisms propose that invasion can be facilitated in locations with high resource availability (Funk and Vitousek 2007). Possibly, this resource fluctuation may occur at various spatial scales in natural or artificial ecosystems such as reservoirs, and consequently determine the locations to be invaded by new species. This would help explain why the hypothesis of biotic resistance is so often rejected under natural (non-experimental) conditions, as also suggested by our results (Sax 2001; Cleland et al. 2004; Dunstan and Johnson 2004; Stohlgren et al. 2008).

However, while native species richness in the reservoir did not influence the success of the exotic species here studied, it can be observed that the probability of occurrence of *H. verticillata* was determined by some abiotic factors. Firstly, dispersal can be an important factor in determining the

locations where the *H. verticillata* occurred. Thus, *fetch* (wave disturbance) played a significant role in the probability of occurrence of *H. verticillata* throughout the reservoir, especially in areas closer to the dam, where there is a wide distance between shores (see results), which possibly increases *fetch* values, and consequently dispersal. Therefore, even though our results have shown that native species richness did not influence the probability of occurrence of *H. verticillata*, we can predict that hydrilla could possibly colonize locations highly disturbed by waves in the reservoir.

Another important factor for the probability of occurrence of *H. verticillata* was the depth of the reservoir. Unlike what was found in the Itaipu reservoir, where the presence of hydrilla was recorded in deeper locations (Thomaz et al. 2009; Florêncio et al. 2021), it can be observed that the probability of occurrence *H. verticillata* occurred in shallower areas in the reservoir (see results), possibly because these areas have low concentrations of organic matter in the sediment and greater availability of sub-aquatic radiation. Consistently, the probability of occurrence of *H. verticillata* was negatively related to the increase in sediment organic matter concentrations, a fact also demonstrated by some authors in experimental studies (e.g., Barko and Smart 1986; Silveira and Thomaz 2015; Silveira and Thomaz 2022) and field observations (e.g., Sousa et al. 2009, 2010; Silveira 2015). In fact, this abiotic variable is directly related to the width of the reservoir and consequently to the probability of occurrence of *H. verticillata* (see Fig. 4b), as narrower locations possibly experience an increase in the amount of allochthonous material entering from the shores compared to wider locations. Thus, we found that there was an increase in sediment organic matter concentrations in narrower locations (see Fig. 5b). Some authors have evidenced the formation of toxic components generated by anaerobic decomposition in sediment (Barko and Smart 1983, 1986), which can cause anoxia and compromise the development of aquatic plants (e.g., Moore et al. 1992; Pezeshki 2001; Blokhina et al. 2003), a fact also demonstrated for *H. verticillata* (Spencer and Ksander 1995). Lastly, regarding the physical composition of the sediment, our results indicated that the reservoir has a heterogeneous sediment type, dominated by various types of granules, and the presence or absence of the *H. verticillata* was reported in all these different sediments. Thus, we predict that sediment grain size did not influence the colonization of *H. verticillata*, but rather the sediment quality concerning organic matter concentrations.

In summary, our results demonstrate that the probability of occurrence of *H. verticillata* in the Rosana reservoir was not influenced by native species richness at three spatial scales, and abiotic factors such as morphometry (*fetch*), distance of reservoir shores,sediment organic matter and depth of the reservoir where the plants were sampled, can determine the success or failure of the occurrence of this species. At the same time, the success of probability of occurrence of *H. verticillata* was positively related to the native species richness at three different spatial scales. These results suggest that biotic resistance is of little importance for *H. verticillata* success at the reservoir. But, at the moment, some abiotic factors are more important for inhibiting of probability of occurrence of *H. verticillata* in the reservoir than biotic resistance. Nevertheless, due to the various changes in environmental quality that these aquatic environments may undergo or even due to the presence of the exotic species being better established, this relationship may change in the future.

## Declarations

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# Figures

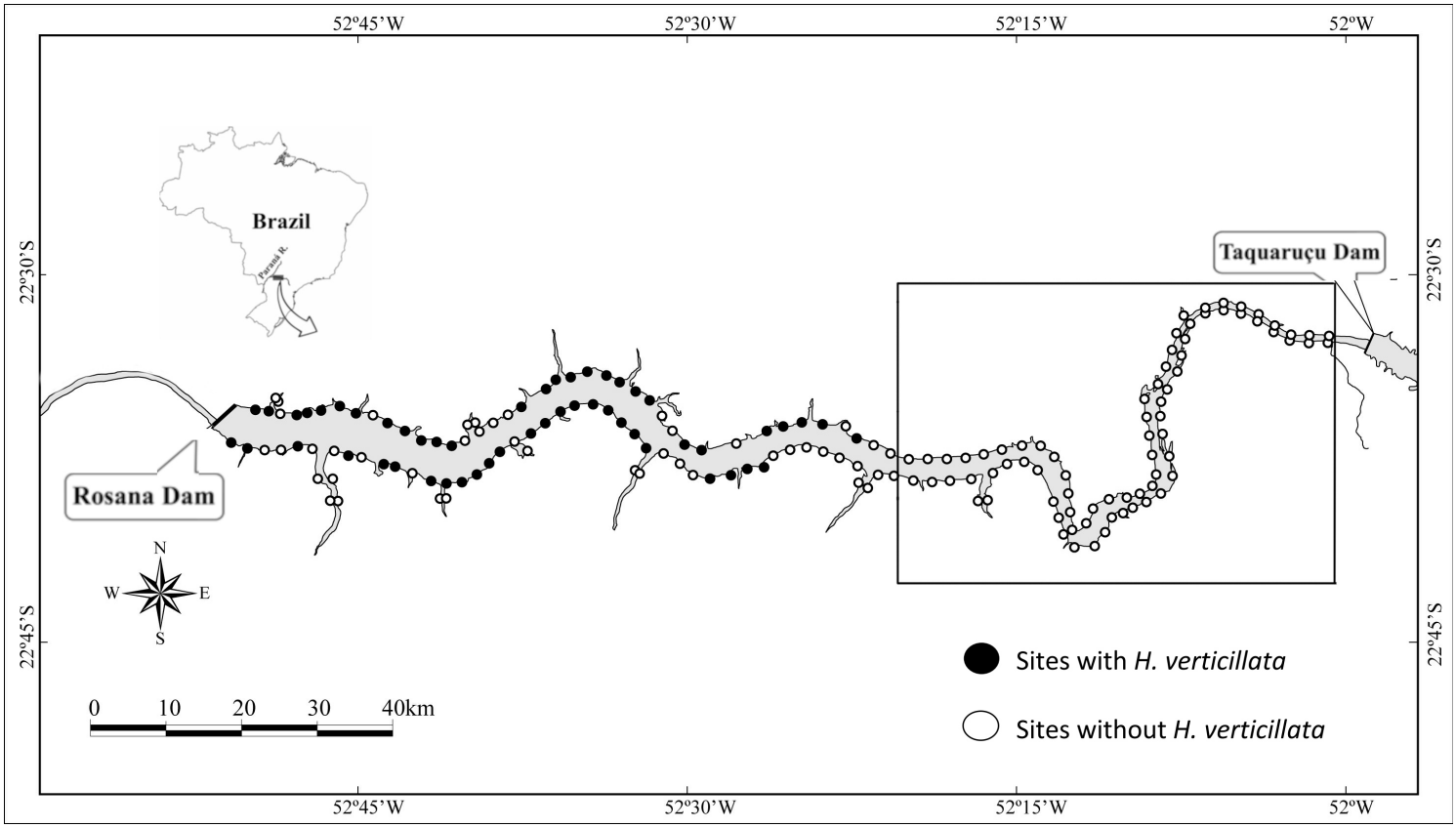
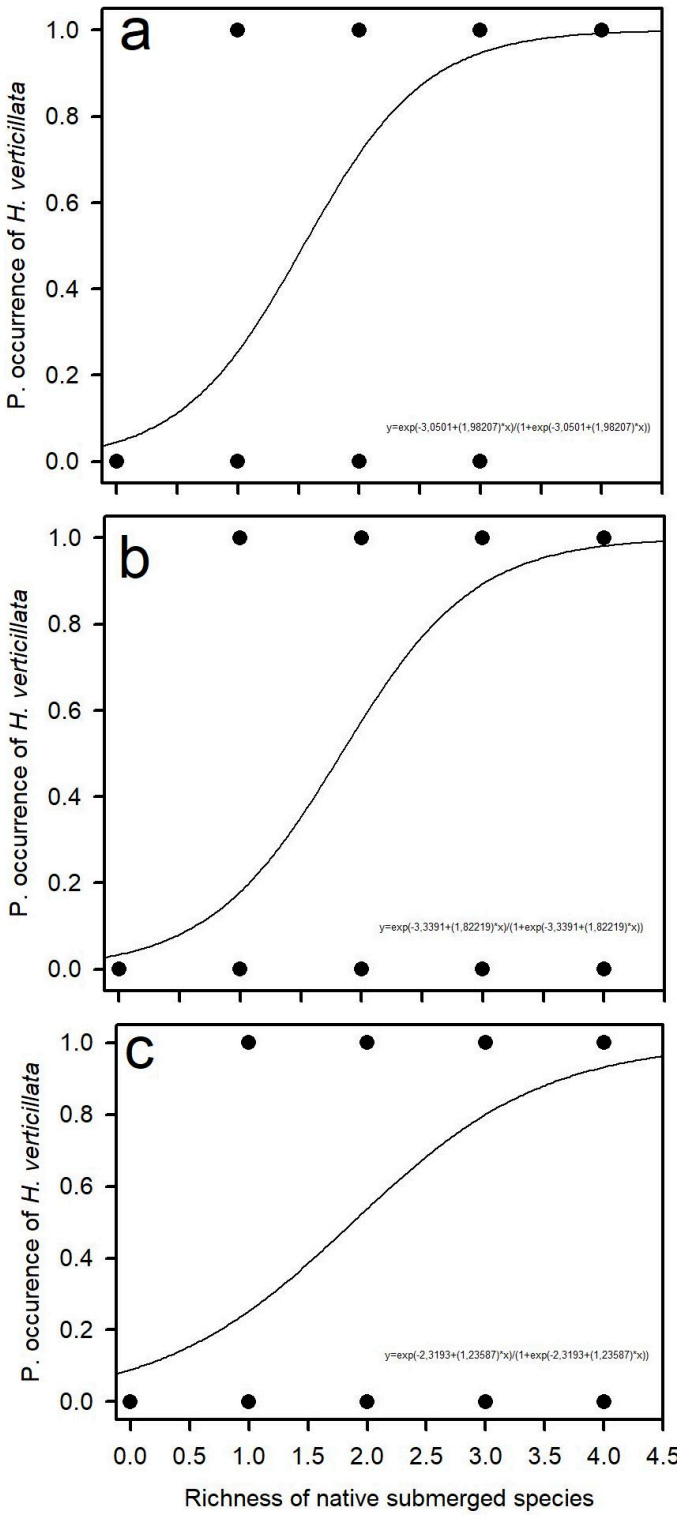


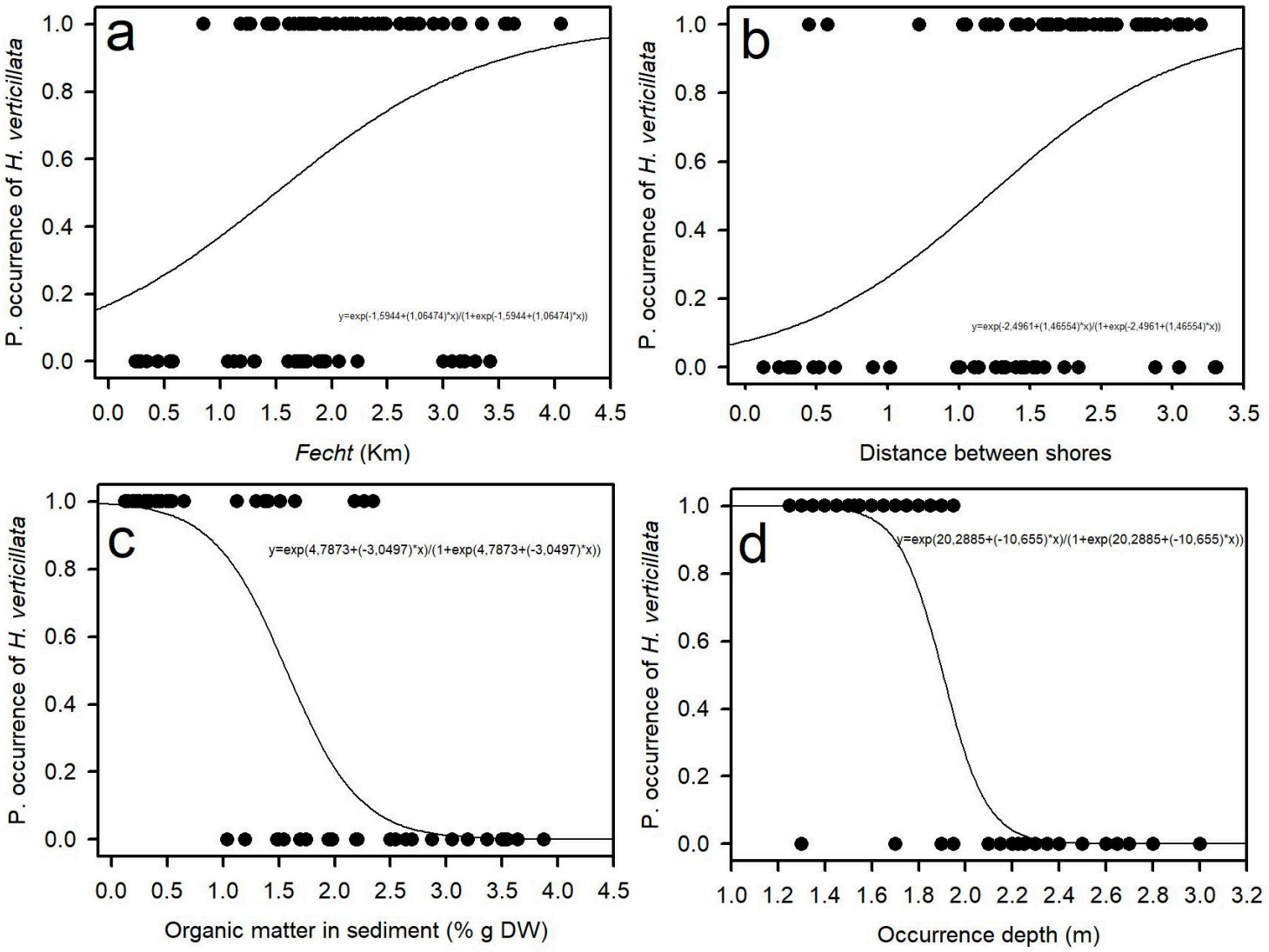

**Figure 1**

Rosana Reservoir demonstrating the sampled points colonized and not colonized by *Hydrilla verticillata*.



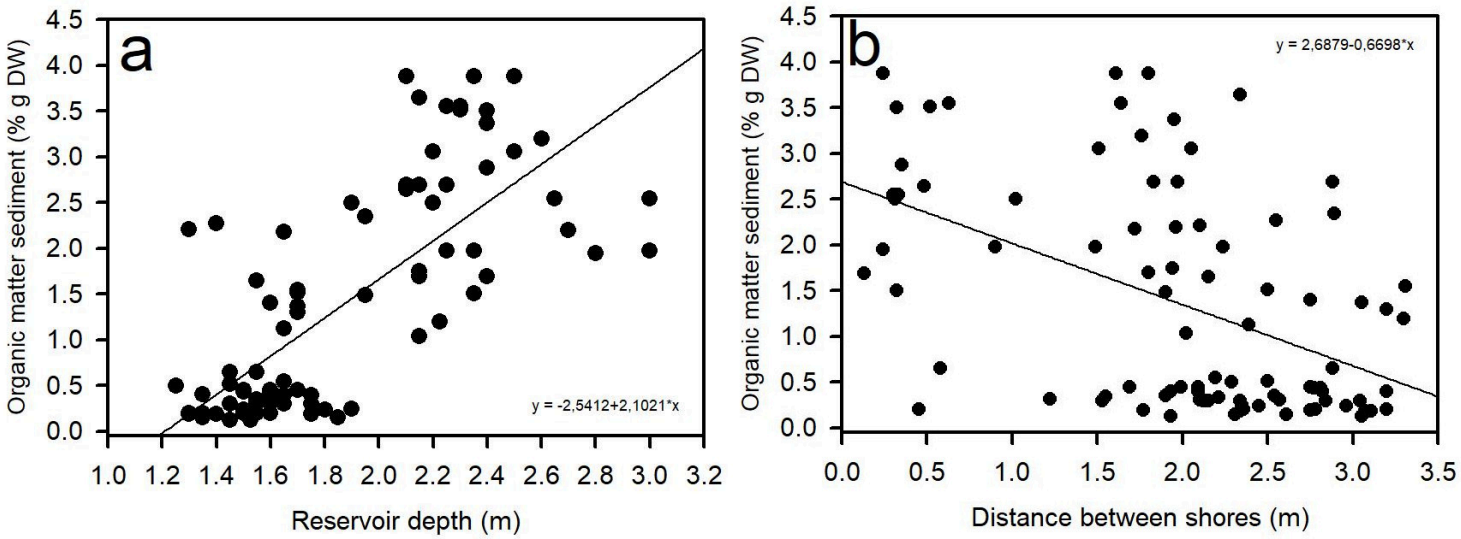

## Figure 2

Probability of occurrence of *H. verticillata* as a function of native speciesrichness at three different scales: small scale (a), medium scale (b), large scale (c).



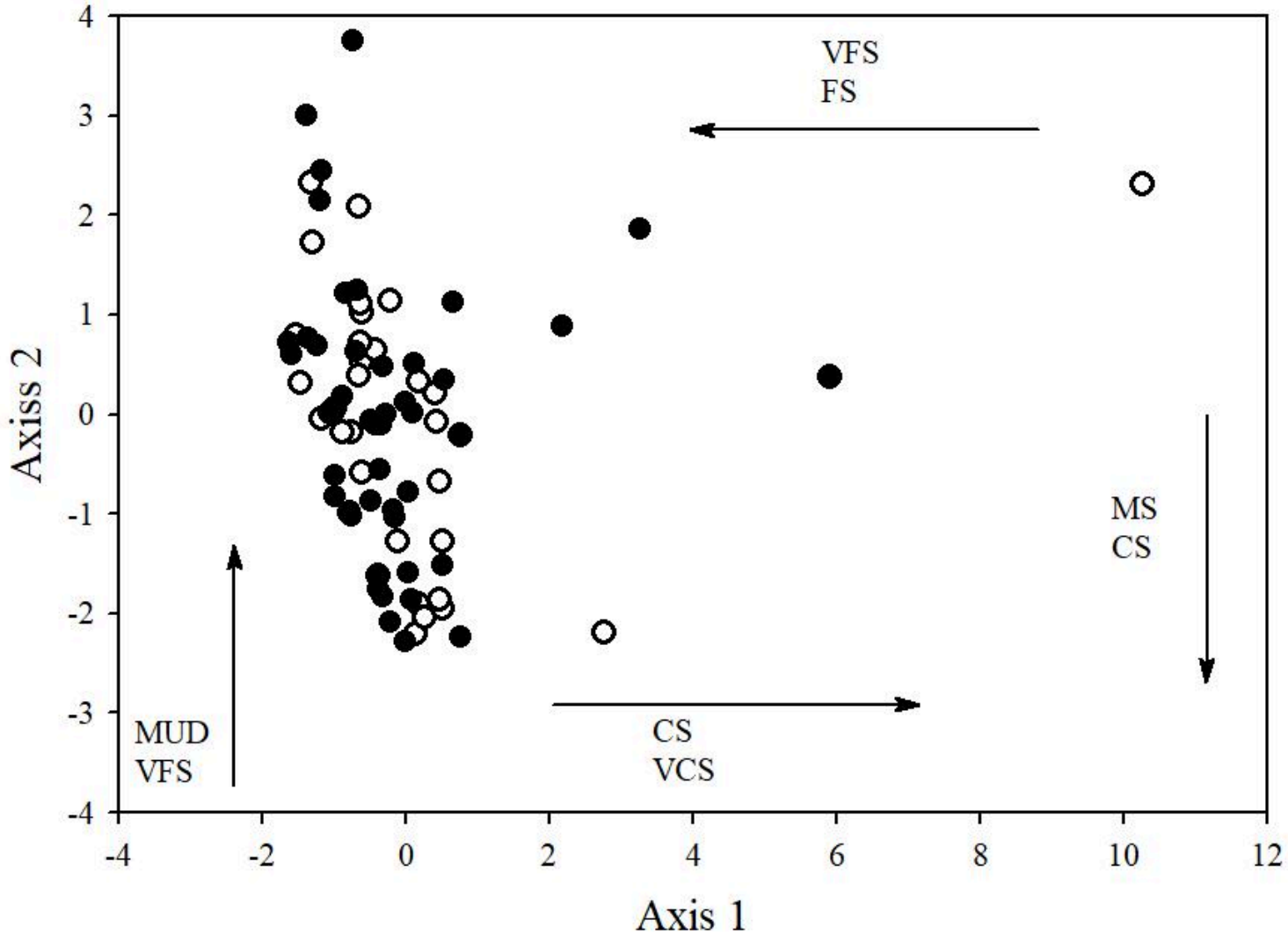

## Figure 3

Probability of occurrence of *H. verticillata* as a function of fetch (a), distance between shores (b), % OMsed g DW (c), and depth of the reservoir where the plants were sampled - "Reservoir depth (d).




## Figure 4

Linear relationship between sediment organic matter and Reservoir depth (a) and distance between reservoir shores (b).




## Figure 5

Scatter plot of sediment grain size analysis: Silt + Clay = Mud; Very Fine Sand = VFS; Fine Sand = FS; Medium Sand = MS; Coarse Sand = CS; Very Coarse Sand = VCS. Where *H. verticillata* was absent = hollow circles or present = black circles.