



Different scales determine the occurrence of aquatic macrophyte species in a tropical stream

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ABSTRACT

Distributions of aquatic macrophyte species are commonly associated with water chemistry characteristics. However, other environmental factors that can lead to the occurrence of aquatic plants in lotic ecosystems, such as dynamic habitats linked to the surrounding landscape, have been underestimated. This study aims to evaluate landscape features that may influence the occurrence of species of euhydrophyte aquatic macrophytes in a tropical river basin. We assessed the occurrence of the following seven species: *Egeria densa*, *Cabomba furcata*, *Potamogeton pusillus*, *Potamogeton polygonus*, *Utricularia foliosa*, *Pistia stratiotes* and *Salvinia molesta*. We also measured environmental variables related to three spatial scales, local (limnological), channel and riparian landscape, along 25.5 Km of the Itanhaém River basin (São Paulo, Brazil). We found that local (limnological) and channel characteristics were important variables in determining the occurrence of aquatic macrophyte species while the landscape scale had little influence on species composition. Channel depth and margin slope were especially relevant abiotic variables in explaining the occurrence of four of the species but not *P. pusillus*, *P. polygonus* and *U. foliosa*. Our results highlight the importance of channel morphology for understanding aquatic plant occurrence and community composition in tropical rivers.

Keywords: aquatic plants, environmental gradients, landscape, lotic ecosystems, riparian vegetation

Introduction

Aquatic macrophytes occur in different types of aquatic ecosystem, but their distributions in lentic and lotic environments differ because of the distinct dynamics between these two habitats (Szoszkiewicz *et al.* 2014). They are usually more abundant in lakes when compared to rivers, because of their higher water light incidence and low water flow (Bornette & Puijalon 2011). Their occurrence and distribution are mainly related to water characteristics, for instance, water transparency,

temperature, pH values, electrical conductivity, and water and sediment nutrient concentrations (Alahuhta *et al.* 2012; Lopes *et al.* 2016; Moura-Júnior *et al.* 2019).

Lotic ecosystems are dynamic habitats because they are connected flowing water systems and are influenced by the upland areas (Vannote *et al.* 1980). Channel morphometry, for instance, channel width and depth, and hydrological characteristics, like water current velocity, are important environmental factors in rivers that differentiate them from lakes (Janauer *et al.* 2010; Gurnell *et al.* 2012; Steffen *et al.* 2014; Schneider *et al.*

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2015). In large floodplain tropical rivers, besides nutrient concentrations, the water dynamics due to the flood pulse (Junk & Piedade 1993; Neiff *et al.* 2014), water connectivity (Thomaz *et al.* 2009; Sousa *et al.* 2011; Bleich *et al.* 2014) and climatic factors (Lopes *et al.* 2017; Nascimento *et al.* 2020) drive aquatic macrophytes' composition and distribution.

Streams run across different landscapes being influenced by the surrounding land cover. Riparian forests protect streams against eutrophication and sedimentation by keeping channel structure stability and reducing light incidence, nutrient and sediment input into the water (Niles *et al.* 1998; Dosskey *et al.* 2010). Different vegetation characteristics, such as size and canopy openness for instance, can influence aquatic plants' composition (Mackay *et al.* 2010; Kroflič *et al.* 2018). These forests are also an important allochthonous source of organic matter, especially in shaded areas, where autochthonous primary production can be limited due to light reduction (Fletcher *et al.* 2000). Land use changes caused by human activities, as in urban areas and farms, can act as sources of pollution to the streams and impact aquatic biodiversity (Tockner & Stanford 2002). Different types of vegetation and changes in land use can, therefore, directly affect the aquatic ecosystems by altering the amount of nutrients, sediments and light that reaches the water bodies. Even in natural areas, the surrounding landscape can change along the river course, resulting in different habitats for biological communities and influencing downstream areas (Vannote *et al.* 1980).

Aquatic macrophytes are key components of aquatic ecosystems and are used worldwide as biological indicators of water quality and ecosystem integrity (Mackay *et al.* 2010; Beck *et al.* 2010; Radomski & Perleberg 2012). Despite the importance of aquatic macrophytes, the mechanisms that control their occurrence and distribution in the tropics are poorly understood and little explored (Junk *et al.* 2014), and studies on this topic consider only limnological variables and were conducted mainly in lentic habitats. We investigated the influence of different scales of environmental variables on the occurrence of seven species of aquatic macrophytes in tropical streams that do not undergo regular flooding, by comparing the relative importance of each scale separately and their combined contribution. We hypothesized that, besides water characteristics, aquatic macrophytes are also controlled by channel and landscape variables, because channel morphology, riparian vegetation and current velocity influence the capacity of bank formation by plants, while landscape influences the amount of light, nutrients, organic matter and sediments in the water. Limnological, channel and landscape variables together explain the macrophyte distribution better than each of these scales individually.

Materials and methods

Study area

The Itanhaém River basin is located on the southern coast of São Paulo State, Brazil (between 23°50' and 24°15' S; 46°35' and 47°00' W; Fig. 1) and has an area of approximately 950 Km². The climate is tropical humid without dry season (Köppen). The mean temperature is 22.7 °C and average annual rainfall is 2175 mm (Camargo *et al.* 2000). The river basin has three well-defined relief strata (plateau, escarpment and coastal plain): the plateau, with 700 to 900 m height, occupies approximately 28 % of the total area; the escarpment, with 20-700 m height occupies 26 % and the coastal plain, with 0-20 m height, occupies 49 % of the area. The plateau and escarpment are covered by the Atlantic Forest and are inside the 'Serra do Mar State Park', the coastal plain is covered by Coastal Plain Forest (*restinga*), banana cultivation, small farms and mangroves, and the areas close to the river mouth are urban area of the Itanhaém city (Camargo & Cancian 2016)

Sampling design

Our research area is 25.5 Km long ranging from the headwaters to the river mouth, including the coastal plain and the beginning of the escarpment relief strata. We defined the location of the research area using a Landsat 5 TN image with 30 m resolution from 2011 (United States Geological Survey/USGS) with ArcGIS 9.3 (ESRI 2018) and established sampling points distant 500 m apart, totalizing 51 points. The first sampling point was near the river mouth and the last in the escarpment, defined by the end of aquatic plant species occurrence. Sampling was conducted in two weeks in July of 2012, during the period of lower rainfall and at low tide to facilitate the visualization of submerged species and to standardize the tide influence. We covered the area with a boat and used a GPS (Garmin Etrex) to reach the previously defined point.

Environmental variables

We measured the abiotic variables on three scales: (1) local scales, including water chemical and physical variables; (2) channel scales, including channel characteristics and sediment phosphorus and nitrogen contents; and (3) landscape scales, including terrain elevation and land use categories (Tab. 1). Water and sediment samples were collected and stored for determination of nutrients at the laboratory (Laboratório de Ecologia Aquática LEA – UNESP Rio Claro) following standardized protocols (Allen *et al.* 1974; Koroleff 1976; Golterman *et al.* 1978; Mackereth *et al.* 1978; Carmouze 1994). Conductivity, pH, turbidity, salinity, water temperature, channel depth and current velocity were measured in situ at the center of the channel. Underwater radiation was recorded at the center of the channel at 0



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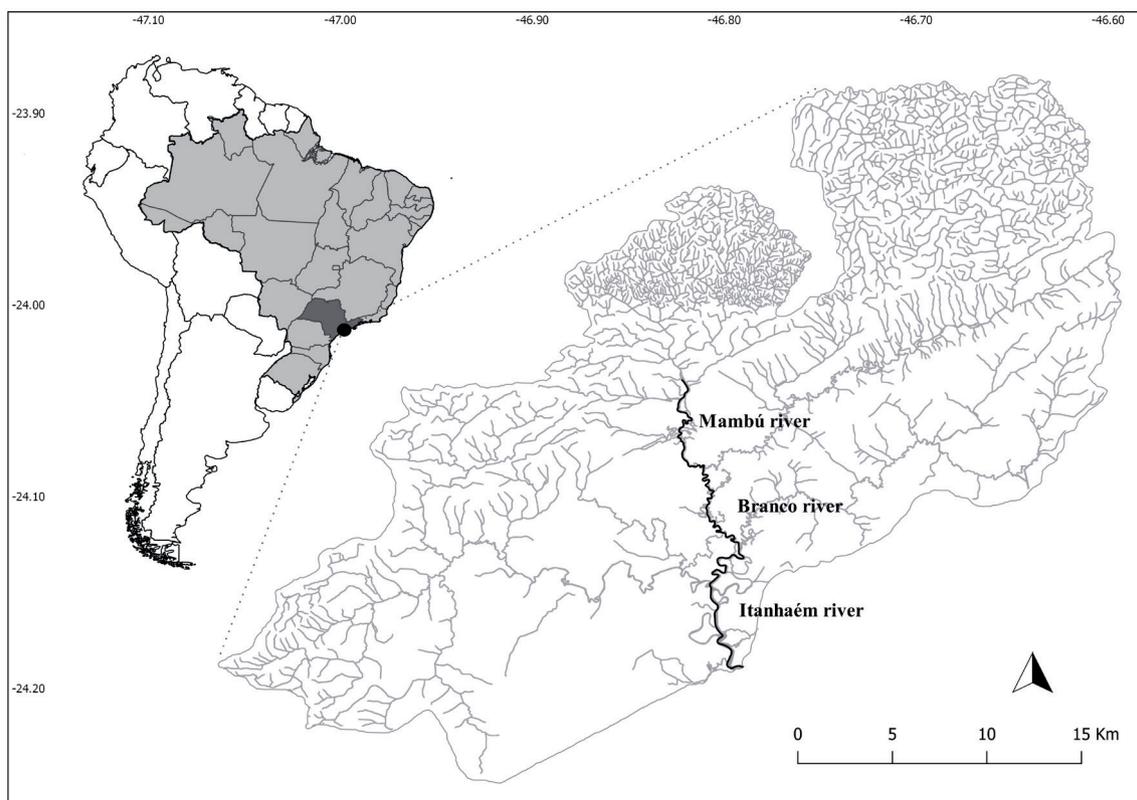


Figure 1. Location of the study area in the Itanhaém River basin, southern coast of São Paulo State (Brazil), highlighting the sampling area of 25.5 Km (bold): (1) Itanhaém River, (2) Branco River and (3) Mambú River.

Table 1. Overview of the abiotic variables measured in the study, with the scale considered, variable name, unit and method and/or equipment used.

	Variables	Method/Equipment
Local	Temperature (°C)	Horiba U10
	Hydrogenionic potential, pH	Horiba U10
	Salinity	Horiba U10
	Turbidity (NTU)	Horiba U10
	Electrical conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	Horiba U10
	Dissolved oxygen ($\text{mg}\cdot\text{L}^{-1}$)	Oximeter WTW Oxi 315i
	Underwater radiation	Underwater radiometer LI-COR LI-250
	Total Nitrogen ($\mu\text{g}\cdot\text{L}^{-1}$)	Mackereth <i>et al.</i> 1978
	N-nitrite ($\mu\text{g}\cdot\text{L}^{-1}$)	Mackereth <i>et al.</i> 1978
	N-nitrate ($\mu\text{g}\cdot\text{L}^{-1}$)	Mackereth <i>et al.</i> 1978
	N-amoniacal ($\mu\text{g}\cdot\text{L}^{-1}$)	Koroleff 1976
	Total phosphorus ($\mu\text{g}\cdot\text{L}^{-1}$)	Golterman <i>et al.</i> 1978
	Total alkalinity ($\text{mg}\cdot\text{L}^{-1}$)	Golterman <i>et al.</i> 1978
	Suspended sediment ($\text{mg}\cdot\text{L}^{-1}$)	Carmouze 1994
Channel	Channel width (m)	Measuring tape Western and Binocular distance measure Bushnell (>17 meters)
	Channel depth (m)	Metered rope
	Current velocity ($\text{m}\cdot\text{s}^{-1}$)	Global Water Flow Probe
	Sediment total Nitrogen (%)	Allen <i>et al.</i> 1974
	Sediment total phosphorus, SP (%)	Allen <i>et al.</i> 1974
	Canopy openness (%)	Clinometer Suunto Tandem
	Margin slope (°)	Clinometer Suunto Tandem
Vegetation cover (%)	Sferic densiometer Widco	
Landscape	Land use (%): farm, anthropic, early succession, mangrove, atlantic forest and coastal plain forest (<i>restinga</i>)..	ArcGis 9.3 (ESRI 2018)



and 0.2 m depths and subsequently the light attenuation coefficient (k) was calculated ($k = (\ln I_0 - \ln I) / z$, where I_0 corresponds to light at surface, I corresponds to light at 0.2 m depth, and z is the depth). Channel width was measured using a measuring tape and with a binocular when width was higher than 17 meters. Canopy opening, margin slope and vegetation cover were measured in both margins. All measurements were obtained as triplicates and subsequently we calculated the average values. Terrain elevation was obtained for each sample point and the percentage of land use categories was calculated for a 250 m buffer around each point.

Species occurrence

In order to verify the extent of the influence of riparian characteristics on the occurrence of aquatic plants, we chose seven euhydrophyte species that largely occur in the area (Nunes *et al.* 2019) and excluded the amphibian and emerging species because they also depend on soil nutrients (Murphy *et al.* 2003; Santos & Thomaz 2007; Meyer & Franceschinelli 2011; Demars *et al.* 2014; Kutschker *et al.* 2014). We selected species belonging to three different life forms (Schulthorpe 1967): (1) rooted-submerged: *Egeria densa* Planch. (Hydrocharitaceae), *Cabomba furcata* Schult & Schult. f. (Cabombaceae), *Potamogeton pusillus* L. subsp. *pusillus* and *Potamogeton polygonus* Cham. & Schltdl. (Potamogetonaceae); (2) free-submerged: *Utricularia foliosa* L. (Lentibulariaceae) and (3) free-floating: *Pistia stratiotes* L. (Araceae) and *Salvinia molesta* D. Mitch (Salviniaceae). We recorded species' presence (1) or absence (0) per point on both margins, covering a distance of 10 m from the margin. When it was not possible to see the channel bottom, we used a hook to verify the occurrence of submerged species.

Data analysis

To describe how abiotic characteristics and species occurrence vary along the sampling area we used graphs of species ordination in relation to environmental gradients. We tested correlation between environmental variables using Pearson's correlation analysis with a threshold of $r=0.7$. The variables included were temperature, turbidity, water total nitrogen and phosphorus, nitrate, channel width and depth, current velocity, sediment nitrogen and phosphorus, canopy openness, vegetation cover, margin slope, terrain elevation and land use categories. To evaluate how environmental variables affect species occurrence we used generalized linear models (GLM) because they produce predictive models and are appropriate for presence and absence data (Gotelli & McCabe 2002; Alahuhta *et al.* 2011), non-normal distribution assumption and different types of statistical errors (Gotelli & McCabe 2002; Alahuhta *et al.* 2011). We built a model for each species and a series of stepwise multiple regressions for each abiotic variable and included only the significant ones in the multiple models.

In addition, we corrected p-values for multiple comparisons using p adjustment of Holm (Holm 1979).

To evaluate the contribution of different scales of environmental variables (local, channel and landscape) on all species occurrence we used variation partitioning (Alahuhta *et al.* 2011; Borcard *et al.* 2011). We used variables' variance inflation factor (VIF) to test for collinearity. The data sets were divided into three environmental data matrices, where only variables with a VIF < 10 were included: local (temperature, turbidity, electrical conductivity, total nitrogen, nitrate and total phosphorus); channel (width, depth, margin slope, current velocity, sediment nitrogen and phosphorus, canopy openness and vegetation cover); and landscape (farm, anthropic activity and Atlantic forest) and a biological data matrix (species occurrence). All analyses were carried out using the R platform (R Development Core Team 2020) considering significance of 5 %.

Results

Macrophytes were more frequent at intermediate portions of the study area and absent in the areas close to the river mouth ([Fig. S1 in supplementary material](#)). The most frequent species were *E. densa* (33 points, 64.7 % of sampling areas) and *Cabomba furcata* (20 points, 39.2 %), followed by *S. molesta* (10 points, 19.6 %) and *P. stratiotes* (9 points, 17.6 %). The least frequent species were *Potamogeton pusillus* (5 points, 9.8 %), *P. polygonus* and *U. foliosa* (2 points, 3.9 %).

The water chemical and physical characteristics on a local scale influenced the occurrence of only two species, *C. furcata* and *P. pusillus* (Tab. 2). Higher water nitrate concentration was related to *C. furcata* (Fig. 2A) and low water alkalinity was related to *P. pusillus* (Fig. 2B).

Environmental variables of channel scale, especially channel depth and margin slope, influenced the occurrence of most species except *P. polygonus*, *P. pusillus* and *U. foliosa* (Tab. 2). Deeper portion of the channel (average of 6.9 m), steeper margins and lower sediment nitrogen concentration were related to *C. furcata* and deeper channel was related to *Egeria densa* (average of 6.4 m), *Pistia stratiotes* and *Salvinia molesta* (average of ~ 9.0 m; Tab. 2 and Fig. 3). When considering the adjusted p-value, channel depth was related to *C. furcata*, *E. densa* and *S. molesta* and margin slope was related to *E. densa*.

The land cover was predominantly of *restinga* vegetation, followed by early succession vegetation and mangrove, which are concentrated at the river mouth, the most anthropized portion of the basin. Atlantic forest covers only 3 % and farm covers 8 %, which are concentrated at the headwaters ([Tab. S3 and Fig. S4 in supplementary material](#)). This scale had less influence on species' occurrence compared to the previous ones, and only lower terrain elevation was related to *P. stratiotes* and *S. molesta* (Fig. 4), that is, flatter areas



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favor free-floating species. When considering the adjusted p-value, this scale had no influence on any species.

The combination of local and channel scales explained most of species' occurrence (15 %), followed by channel scale individually (11 %). Local scale individually explained 7 % and landscape scale individually explained 0.1 %. The combination of all environmental scales explained 3 % of species' occurrence.

Discussion

As we expected, besides water characteristics, the landscape and channel environmental variables were related to the occurrence of macrophyte species, mainly channel depth and margin slope. This is in line with the fact that landscape and channel characteristics are primary environmental factors influencing aquatic macrophyte species, due to the close relationship between streams, the

surrounding landscape, and upstream areas. In fact, the occurrence of most species was related to channel depth, margin slope and terrain elevation.

Deeper channels with steep margins were related to *E. densa* and *C. furcata*, probably because this life-form has higher capacity to colonize deeper areas compared to other life-forms (Gantes & Caro 2001; Bando *et al.* 2015). Lower sediment nitrogen concentration was related to *C. furcata*, a rooted-submerged species which is regulated by multiple factors but is usually linked to high water quality and preserved habitats (Søndergaard *et al.* 2010). These organisms can absorb nutrients via their leaves and roots but are more associated with nutrient availability in water (Lombardo & Dennis-Cooke 2003; Bornette & Puijalon 2011). Flatter areas were related to the free-floating species *P. stratiotes* and *S. molesta*, probably because the slow river flow favors non-rooted species. Interestingly, both species occurred in deeper parts of the channel. Depth is not a limiting factor linked to the free-floating life-form but seems

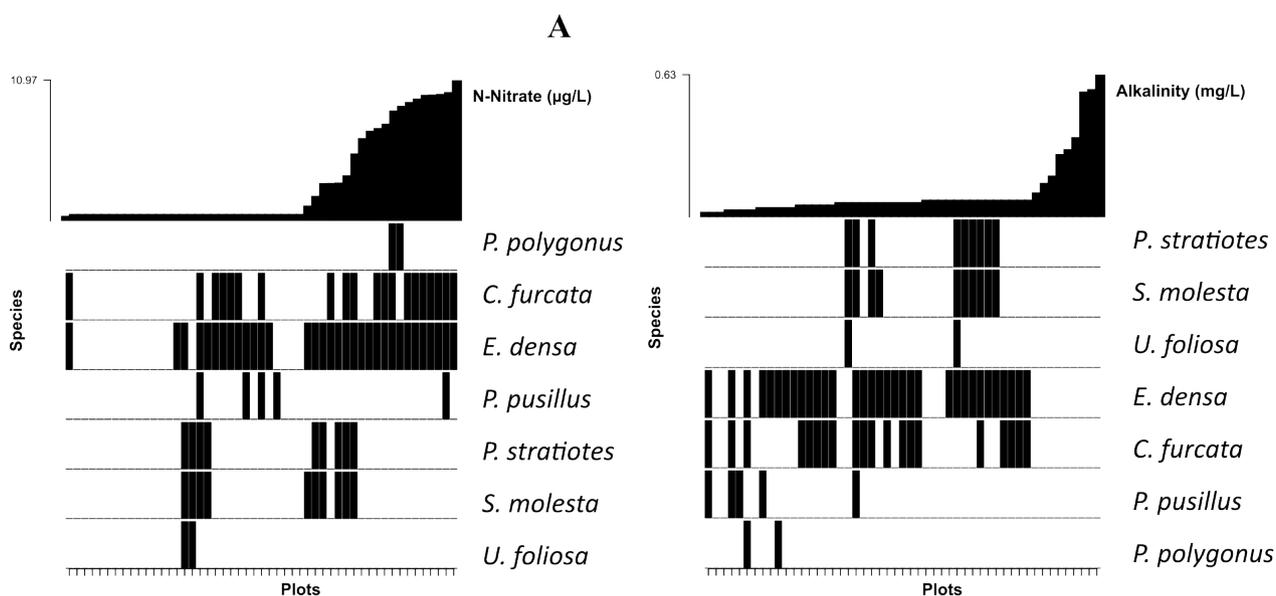


Figure 2. Correlation of aquatic macrophyte species (*P. stratiotes*, *S. molesta*, *E. densa*, *C. furcata*, *U. foliosa*, *P. pusillus*, *P. polygonus*) in relation to environmental variables of local scale: **A**) N-nitrate (µg/L) and **B**) total alkalinity (mg/L) at 51 points along the 25.5 Km. Black bars indicate plots with species presence.

Table 2. Generalized linear models (GLM) of aquatic macrophyte species in relation to environmental variables. The columns indicate species name, the regression beta coefficient, significance (p-value) and p-adjusted by Holms' correction.

Species	Variables	β-coefficient	p-value	Adjusted p-value
<i>Cabomba furcata</i>	Channel depth	1.19	0.007	0.049
	Margin slope	0.24	0.01	0.07
	Nitrate	0.92	0.01	0.07
	Substrate nitrogen	-73.5	0.01	0.07
<i>Egeria densa</i>	Channel depth	0.47	0.008	0.056
	Margin slope	0.19	0.007	0.049
<i>Potamogeton pusillus</i>	Total alkalinity	-77.41	0.02	0.14
<i>Salvinia molesta</i>	Channel depth	0.87	0.004	0.028
	Terrain elevation	-0.62	0.01	0.07
<i>Pistia stratiotes</i>	Channel depth	1.14	0.01	0.07
	Terrain elevation	-1.26	0.02	0.14



to be an important physical variable for aquatic plants, because it is related to other factors, such as turbidity and water transparency (Hrivnák *et al.* 2010).

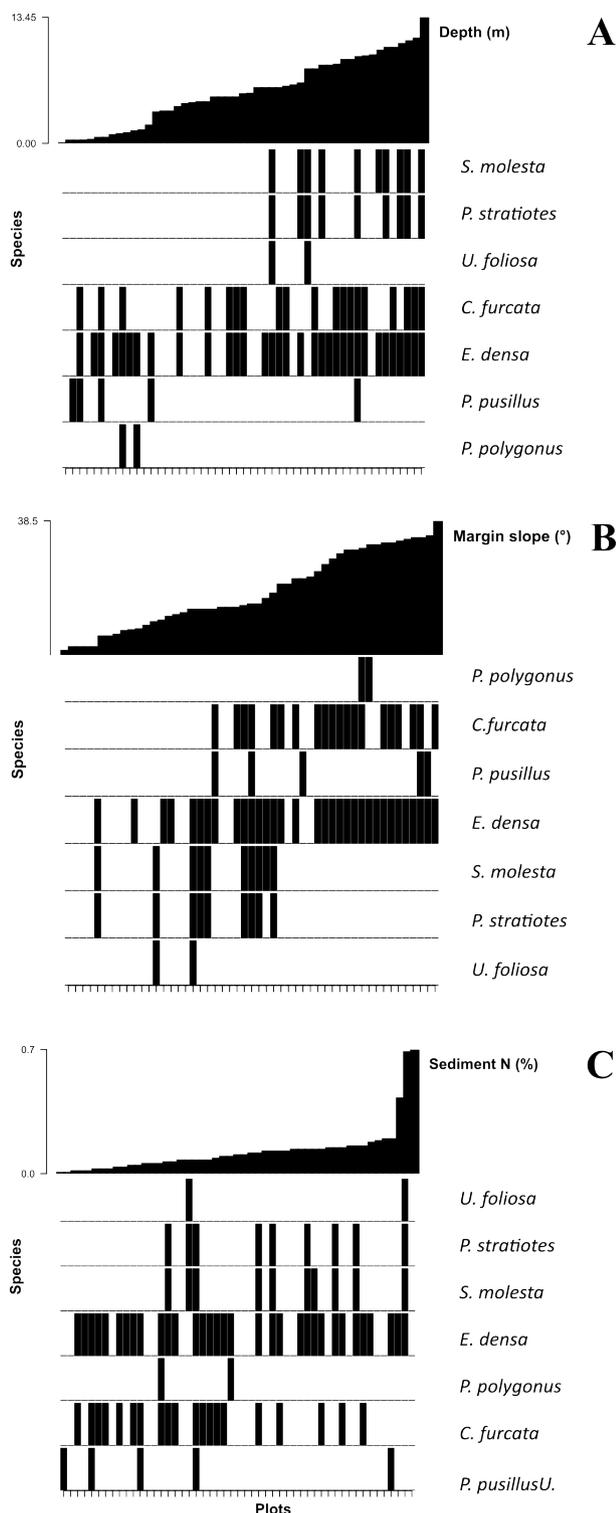


Figure 3. Correlation of aquatic macrophyte species (*P. stratiotes*, *S. molesta*, *E. densa*, *C. furcata*, *U. foliosa*, *P. pusillus*, *P. polygonus*) in relation to environmental variables of channel scale: **A)** channel depth (m), **B)** margin slope (°) and **C)** nitrogen of sediment (%) at 51 points along the 25.5 Km. Black bars indicate plots with species presence.

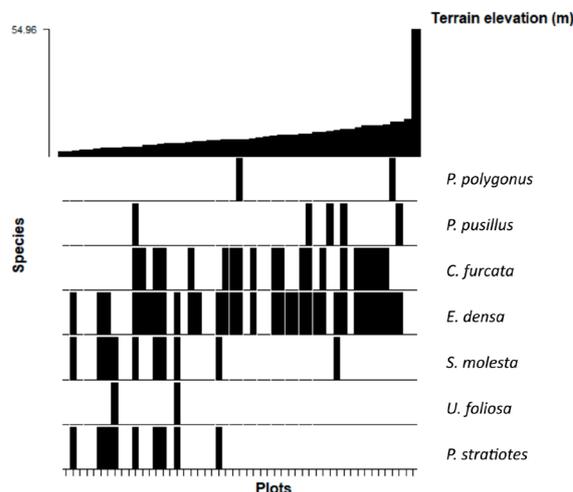


Figure 4. Correlation of aquatic macrophyte species (*P. stratiotes*, *S. molesta*, *E. densa*, *C. furcata*, *U. foliosa*, *P. pusillus*, *P. polygonus*) in relation to the environmental variable of landscape scale terrain elevation (m) at 51 points along 25.5 Km. Black bars indicate plots with species presence.

We expected that higher current velocity would favor *P. pusillus* and *P. polygonus* occurrence, since submerged species are assumed to be more resistant to physical damage caused by stronger water flows, and because higher flows may positively influence the gas exchange and sediment characteristics of this group of species (Chambers *et al.* 1991; Madsen *et al.* 2001); however, this was not verified. In fact, *Potamogeton pusillus* can thrive in lakes where there is no water flow (Lombardo *et al.* 2013), which can indicate that this species is not dependent on high current velocity and is not excluded in more lentic habitats. Besides that, we must consider that we sampled only during the low-rainfall season and we did not capture extreme rain events that certainly have occurred. Because these events can particularly affect current velocity and influence macrophyte distribution, further information about water current velocity is necessary to better understand its influence on species' distribution.

Followed by channel characteristics, water chemistry influenced species occurrence. Higher water nitrate concentration was related to *C. furcata*, which is an environmental driver of macrophyte composition (Kennedy *et al.* 2015). Water is probably the main source of nitrogen to this species, which explains the association with low nitrogen in the sediment we found. Lower alkalinity was related to the occurrence of *P. pusillus*, which is an important variable related to the genus *Potamogeton* (Hellquist 1980), but our results differed from those reported by (Riis *et al.* 2000), who found higher alkalinity associated with this genus, and can be a result of adaption of different species belonging to this genus to other environments. We expected that higher water nutrient availability would be especially related to free-floating species (Henry-Silva *et al.* 2008), but we did not find this relationship. In fact, higher growth

rates of *S. molesta* at reduced water nutrient concentration was described for this river basin (Rubim & Camargo 2001), and this result can indicate that channel variables have higher importance in lotic ecosystems rather than water variables (Schneider *et al.* 2018).

Surprisingly, land use categories were not related to species' occurrence. Some macrophytes are influenced by the increase of light, water nutrients and pollution caused by land cover change, like agriculture and urban areas (Alahuhta *et al.* 2011; Alahuhta *et al.* 2012). Our sampling area is mainly covered by Coastal Plain Forest, early succession vegetation and mangroves, with a small percentage of farm and anthropogenic uses. Probably, different types of natural vegetation do not restrict species' occurrence because they do not act as a source of pollution, increasing the amount of sediments and nutrients in the water bodies, and channel characteristics, for instance channel depth, influence more the underwater radiation, being more relevant for plant distribution along the river.

Local and channel variables combined were the environmental characteristics most related to macrophyte occurrence. Water chemical and physical characteristics are particularly important to vegetation establishment and growth because they are sources of nutrient supply and can be very limiting to species (Barendregt & Bio 2003; Bornette & Puijalón 2011). The free-floating species, for instance, usually grow under high water nutrient concentrations and can be related to disturbed areas, while submerged species can grow under a wide of water nutrient concentrations (Mjelde & Faafeng 1997; Lombardo 2005). Channel variables individually were also very important for species' occurrence, which highlights the importance of channel morphology for macrophyte establishment and growth. Channel morphology is related to changes in light incidence in the water column and influences water current velocity; a higher water flow increases nutrient processing and oxygen concentration in rivers, favoring plant growth (Bleich *et al.* 2014; Bleich *et al.* 2015). Channel morphology, therefore, seems to be important for the occurrence of five of these species. The variance of species' occurrence that was not explained by environmental categories can be related to biotic interactions, but further studies are necessary to investigate these relationships. We found a substitution of species along the gradient with some overlap of *E. densa* and *C. furcata* with the free-floating species (Fig. 2), probably because these species are related to multiple factors, such as streamflow, nutrient availability, and substratum. The differences in river channel combined with biotic interactions can lead to a substitution of aquatic plant species and/or patches of species distributions along the river course (Khedr & El-Demerdash 1997; Naiman & Decamps 1997; Neiff *et al.* 2014).

To our knowledge this study is the first comparing the contribution of different scales of environmental variables, highlighting the importance of considering

fine and landscape scales to better understand aquatic plant occurrence in tropical streams, which has been demonstrated only for lakes so far (Duarte & Kalff 1990; June-Wells & 2016). Our results show that water chemistry and channel characteristics are important factors shaping macrophyte species occurrence in tropical lowland streams, but landscape has no influence on species composition. Channel depth and margin slope were especially important, highlighting the influence of channel characteristics to better understand and predict aquatic plant occurrence and distribution in lotic ecosystems.

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