



Changes in Abiotic Factors Drive Non-native Plants Colonization in Subtropical Mangroves

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Abstract

The colonization and spread of non-native species are recognized as a critical driver of environmental change in mangrove ecosystems. However, environmental factors that favor non-native plant colonization in mangroves are still poorly understood. To fill this gap, we investigated the effect of selected abiotic factors controlling non-native plant species colonization in mangroves in Southeastern Brazil. We selected 18 plots in mangrove forests under different levels of anthropogenic N inputs, both colonized and non-colonized by non-native plants in the Estuarine-Lagoon Complex of Cananeia-Iguape, southeastern Brazil. We measured interstitial salinity, sediment nitrate and ammonium concentrations, and sediment physicochemical properties. We found that interstitial salinity at 10 cm depth followed by nitrate concentrations in sediment were the main factors associated with the occurrence of non-native species in the studied mangroves. Low salinity and increased N availability in sediment allowed for the success of non-native plants into mangrove forests, also resulting in high amount of dead mangrove trunks. Aiming to conserve and restore such areas, the restoration of abiotic conditions is the first step in the management of non-native species in this region.

Keywords Exotic species · Biological invasion · Tropical forests · Nitrogen pollution · Salinity · Anthropogenic alterations

Introduction

Mangroves are the only forest formations that occur at the interface of terrestrial, freshwater, and marine ecosystems (Alongi 2002). Because of their key location, mangrove forests have important biogeochemical roles that translate into the provisioning of critical ecosystem services (Van Lavieren et al. 2012; Lee et al. 2014). For instance, mangroves usually

store large quantities of carbon (C) per unit of area in both above and below ground biomass as well as in soil compared to upland tropical forests and marine ecosystems (Donato et al. 2011; Alongi 2014).

Although there is wide recognition of the social, economic and ecological relevance of mangroves, these ecosystems are still under strong human pressure (Valiela et al. 2001). One of the main drivers of ecosystem degradation is biological invasion. Despite the fact biological invasion is worldwide well recognized as one of the main vectors of global change promoting modification in the structure and functioning of ecosystems (Vitousek et al. 1996; Dukes and Mooney 1999; Mack et al. 2000; Liao et al. 2008; Vila et al. 2011; Lu et al. 2014), such driver has not received enough attention in mangrove ecosystems (Biswas et al. 2018). This is especially true considering the lack of investigations of environmental factors that favor the colonization of non-native species (Ren et al. 2014) and the functional attributes of non-native species that thrive in mangroves (Biswas et al. 2018).

Environmental factors that make an ecological system more susceptible to the colonization of non-native species

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are widely discussed, though there is a consensus that disturbance plays a key role in this process (Dukes and Mooney 1999; Mack et al. 2000; Biswas et al. 2012; Zhang et al. 2012). At the regional scale, human interventions such as building canals, roads, and dams promote deep alterations of river flows in the upstream watershed which, in turn, modify the freshwater input (and associated nutrient loads) to downstream estuarine ecosystems (Gopal and Chauhan 2006; Röderstein et al. 2013; Sathyanathan et al. 2014; Reis et al. 2019). These disturbances change environmental conditions and, as a consequence, may facilitate the colonization of non-native species into mangroves (Lugo 1998; Dahdouh-Guebas et al. 2005; Biswas et al. 2018). For example, measures to recover streamflow to mangroves have been taken in Colombia. Moreover, rivers were dredged to restore the river flow that had been altered for the construction of highways. Nonetheless, the combination of large rain events at the same time of these interventions caused a salinity reduction which, in turn, led to the colonization of aquatic macrophytes (*Typha domingensis* Pers) in these mangroves (Röderstein et al. 2013).

Under non-disturbed conditions, abiotic factors such as (i) low oxygen levels in sediment, (ii) periodic floods, and (iii) large variations in salinity act as barriers to the colonization of non-native species in mangroves (Schaeffer-Novelli et al., 2000; Spalding, Kainuma & Collins, 2010). That works for both terrestrial and freshwater plant species that hardly survive when competing with mangroves (Lugo 1998). Therefore, the success and significance of the effects of the colonization and spread of non-native species will depend not only on the abiotic factors of the ecosystem under disturbance but also on the functional attributes of non-native species relative to native vegetation (Van Kleunen et al. 2010; Pyšek et al. 2012; Lee et al. 2017). In a context of disturbance, alterations in salinity and nutrient availability (especially nitrogen) may directly favor non-native species by promoting rapid growth and reproduction. This, in turn, leads to changes at the community level through, for example, the increase in mortality rates of native species (Dukes and Mooney 1999; Bradley et al. 2010; Vila et al. 2011; Gufu et al. 2018). Thus, it is important to understand both the abiotic and biotic factors controlling the colonization of non-native species as well as the effects at the native community level to prevent, minimize, and manage its changes (Pyšek et al. 2012; Ren et al. 2014).

The Estuarine-Lagoon Complex (ELC) of Cananeia-Iguape, São Paulo State, Brazil is a Ramsar site (Ramsar 2017). Mangroves at the southern region of the complex are the widest and best conserved in São Paulo State (Cunha-Lignon et al. 2011). On the other hand, in the northern part of the complex, there was a significant increase in freshwater input due to the building of a canal in 1852 (locally known as “Valo Grande”) to deviate flow from Ribeira de Iguape

river (Mahiques et al. 2009, 2013). This deviation, as well as the input of sewage and excess nutrients from agricultural activities in the Ribera de Iguape river basin resulted in important changes in the estuary (locally known as “Mar Pequeno”) and associated mangroves. This possibly favored the colonization non-native species in the adjacent mangrove (Cunha-Lignon et al. 2011; Cunha-Lignon and Menghini 2016; Reis et al. 2019).

To shed more light on the controls of the colonization of mangrove ecosystems by non-native species, here we investigated the effect of selected abiotic factors affecting the colonization of aquatic species in the subtropical mangrove occurring at the ELC of Cananeia-Iguape.

Materials and Methods

Study Area

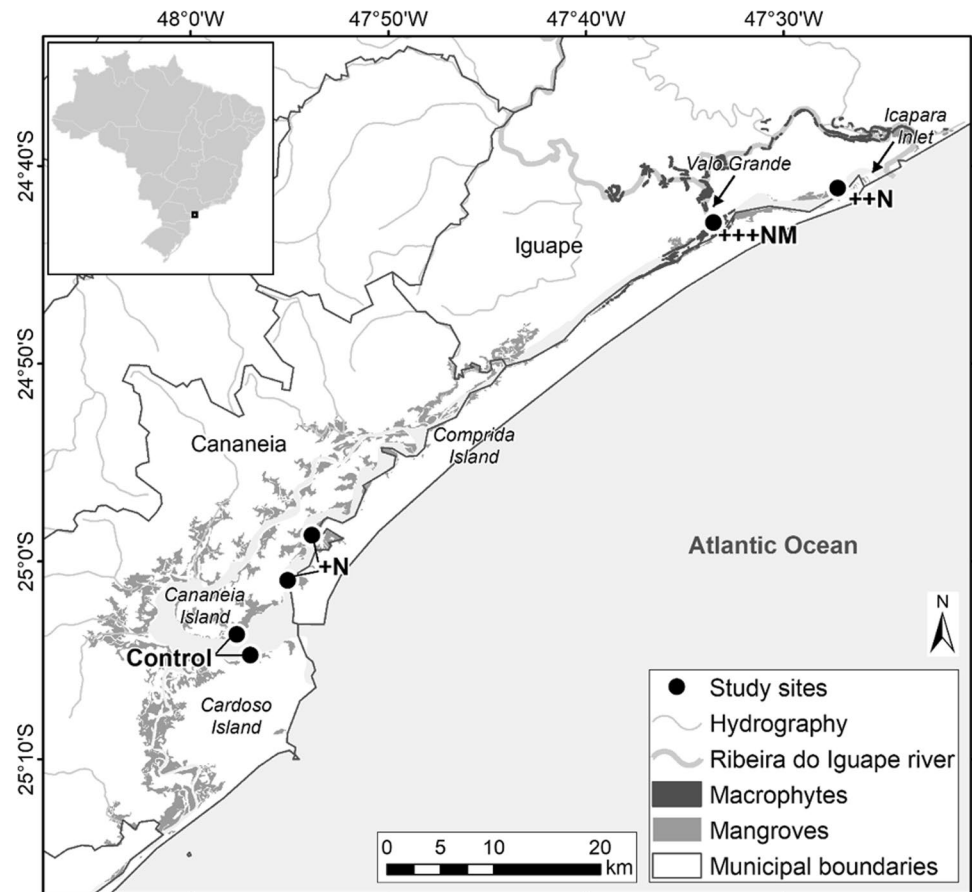
The study was conducted in the ELC of Cananeia-Iguape, southeastern Brazil in 2015 (Fig. 1). Mangrove vegetation in the ELC of Cananeia-Iguape is composed by the species *Rhizophora mangle* L. (Rhizophoraceae), *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae), and *Avicennia schaueriana* Stapf & Leechm. ex Moldenke (Acanthaceae) (families according to APG 2009) (Schaeffer-Novelli et al. 1990). Landsat time series indicated the absence of non-native plants in the mangrove areas adjacent to the Valo Grande canal in 1997. The occurrence of non-native plants was first recorded in 2010 (Cunha-Lignon et al. 2011), but the exact year of colonization is unknown. The forest structure of these mangroves has been recently clarified by Rovai et al. (2021). Based on this paper, mean values of basal area, diameter at breast height, height and stems per hectare are, respectively, 20 m² ha⁻¹, 5 cm; 6000 stems ha⁻¹.

The climate in the ELC of Cananeia-Iguape is classified as subtropical, “Cfa” according to the climatic classification of Köppen-Geiger (Alvares et al. 2014). Mean monthly temperature ranges from 24.5 °C in January to 7.8 °C in July. Mean annual precipitation is about 2,300 mm, without a marked dry season. Tides are semidiurnal with a mean amplitude of 0.82 to 1.25 m in spring tides (Schaeffer-Novelli et al. 1990). The ELC of Cananeia-Iguape was previously reported to experience sporadic frosts (Schaeffer-Novelli et al. 1990).

Sampling Design

The study was conducted in 18 plots inserted in 8 fringe mangrove sites in the ELC of Cananeia-Iguape, southeastern Brazil in 2015 (Fig. 1). The study plots integrate a

Fig. 1 Location of mangrove study sites in the Estuarine Lagoon-Complex of Cananeia-Iguape, southeastern Brazil. Study sites included two non-N-enriched and free of non-native species reference sites (Control); two sites free of non-native species and subjected to medium N inputs (+N); two sites without the presence of non-native species and subjected to medium to high N inputs (++N), and two sites colonized by non-native species and subjected to high N inputs (+++NM). Because of the map scale, the two study sites at +++NM and at ++N were overlaid. Source of the shapefiles of mangrove forests and aquatic macrophytes areas: Cunha-Lignon et al. (2011)



permanent plot network where mangrove vegetation structure has been monitored since 2001.

The study sites differ mainly in two aspects: (i) levels of anthropogenic N inputs (Reis et al. 2019) and (ii) occurrence of non-native plants. We selected two conserved mangrove areas under high marine influence, free of any non-native plants and anthropogenic N as control plots. We also selected two mangrove sites free of non-native plants but subject to medium N inputs from sewage discharge of a small urban area in the Cananeia Island (hereafter

+N). Lastly, we selected four mangrove sites close to the Valo Grande canal that were strongly affected by excess N inputs from the Ribeira de Iguape river basin. Two of these sites comprised mangroves without the occurrence of non-native plants and subjected to excess N inputs ranging from medium to high (hereafter ++N). The other two sites included mangrove areas colonized by non-native and subjected to high N inputs (hereafter +++NM) (Reis et al. 2019) (Tables 1 and 1 Supplementary). All sites with the presence of non-native plant species had similar species to

Table 1 Mean and maximum concentrations of ammonium nitrogen ($\text{NH}_4^+\text{-N}$), nitrate nitrogen ($\text{NO}_3^-\text{-N}$), and Chlorophyll, and the trophic state of estuarine water in the Estuarine-Lagoon Complex of Cananeia-Iguape from 2010 to 2015

Treatments	$\text{NH}_4^+\text{-N}$ (mg/l)		$\text{NO}_3^-\text{-N}$ (mg/l)		Chlorophyll a ($\mu\text{g/l}$)		Trophic State
	mean	maximum	mean	maximum	mean	maximum	
Control	0.10	0.13	NA	NA	4.6	8.5	mesotrophic
+N	0.12	0.35	NA	NA	7.9	29.4	mesotrophic to eutrophic
++N	0.14	0.80	NA	NA	15.8	62.6	eutrophic to hypereutrophic
+++NM	0.35	1.43	0.47	3.55	10.4	47.6	eutrophic to hypereutrophic

Data from the monitoring the quality of coastal waters by Companhia de Saneamento Ambiental do Estado de São Paulo (CETESB); data is available at <https://servicos.cetesb.sp.gov.br/infoaguas/>. NA = Not applicable: all values were below detection limit <0.20

control sites prior to non-native plant species colonization (see Cunha-Lignon et al. 2015).

In summary, our treatments can be described as follows:

- (i) control plots dominated by native mangroves such as *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana* (n = 4; control);
- (ii) native mangroves subjected to a moderate amount of N (n = 6; +N);
- (iii) native mangroves subjected to a high amount of N (n = 4; ++N) and.
- (iv) mangroves with the occurrence of non-native species and subjected to a high amount of N (n = 4; +++NM).

The dominant non-native species at the +++NM plots were *Hymenachne amplexicaulis* (Rudge) Nees (Poaceae), *Bacopa monnieri* (L.) Wettst. (Plantagenaceae), *Crinum salsum* Ravenna (Amaryllidaceae), and other unidentified species of the families Poaceae and Cyperaceae.

In July 2015, vegetation structure was measured and sediment and foliar samples were obtained in each plot. To avoid trampling and possible interferences in the vegetation structure inside the plots, all foliar and sediment samples were obtained immediately outside each plot. The interstitial salinity was also obtained *in situ* next to each plot.

The plots have varying sizes, according to the stem density (Schaeffer-Novelli and Cintrón 1986; Schaeffer-Novelli et al. 2015). In each plot, all trees taller than 1 m were identified and had their diameter at breast height (DBH) recorded with a metric diameter tape, and their height measured using a telemeter or a telescopic pole. The condition of the trunks (alive or dead) was also registered (Schaeffer-Novelli and Cintrón 1986; Schaeffer-Novelli et al. 2015).

A sediment sample (0–10 cm depth) was collected per plot to quantify the concentrations of NH_4^+ -N and NO_3^- -N. Extra sediment samples at 0–10 and 10–20 cm depths were also collected next to each plot to characterize sediment physicochemical properties. The sediment samples for physicochemical analyses from plots in the same site were pooled together, totaling two composite samples by treatment (i.e., Control, + N, ++ N, and +++NM). All sediment samples were kept refrigerated until analysis.

Next to each plot, mature foliar samples (i.e., green and fully expanded) from three mangrove trees with DBH \geq 4 cm were obtained, as well as foliar samples of the non-native plants, one sample per species. Foliar samples were analyzed for the $\delta^{13}\text{C}$, and concentrations of C and N. The foliar samples were washed with tap water and then oven dried at 40 °C for 48 h immediately after fieldwork.

Abiotic Factors

Physical and Chemical Properties of Sediment

The sediment samples at 0–20 cm depth were analyzed for concentrations of organic matter, Na^+ , K^+ , Ca^{2+} , Mg^{2+} , and available P, sum of exchangeable bases, and cation exchange capacity according to Embrapa (1997, 2009). Sediment texture was analyzed using the hydrometer method (Bouyoucos 1932) and classified using the U.S. Department of Agriculture textural triangle. Organic matter (OM) was extracted with potassium dichromate in sulfuric medium and quantified by titration using ammonium ferrous sulfate. Available exchangeable bases were extracted with ammonium acetate 1 M. Concentrations of Na^+ were analyzed by flame photometry, K^+ by atomic emission, and Ca^{2+} and Mg^{2+} by atomic absorption spectrophotometry. Available P was extracted with Mehlich 1 solution and quantified with ammonium molybdate using a spectrophotometer. These analyses were carried out in the Department of Soil Science of the Luiz de Queiroz School of Agriculture, University of São Paulo.

Also, in each plot, we used an optical refractometer to measure *in situ* the interstitial sediment salinity at 10 cm (Sal10) and 50 cm (Sal50) depth.

Concentrations of Available N in Sediment

Concentrations of NH_4^+ -N and NO_3^- -N in sediment were quantified according to the extraction procedures described by Reis et al. (2017a). Extracts were analyzed for concentrations of NH_4^+ -N with a Nessler reagent (Greweling and Peech 1960) and NO_3^- -N (Meier 1991, cited in Sutton et al. 2014) using a UV spectrophotometer in the Laboratório de Ecossistemas of the Universidade de Brasília. Concentrations of mineral N (Nmin) were calculated by summing the concentrations of NH_4^+ -N and NO_3^- -N in sediment.

Biotic Factors

Vegetation Structure

From the data obtained in the field, we calculated the mean values of height (H) (m), DBH (cm), and basal area of live trunks (BALT) and dead trunks (BADT) (%) for each plot.

Foliar Attributes

Foliar samples were ground with a knife grinder and powdered with liquid nitrogen in a mortar. The carbon isotope ratio was determined by combustion using an elemental analyzer (Carlo Erba, CHN-1100) coupled to a Thermo Finnigan Delta Plus mass spectrometer at the Laboratory of Isotope Ecology of the Centro de Energia Nuclear na

Agricultura (CENA/Universidade de São Paulo), Piracicaba, SP, Brazil. The results were expressed in delta notation (δ), in parts per thousand (‰), based on internationally recognized standard. We used the following equation: $\delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1.000$, where R_{sample} and R_{standard} represent the heavy/light isotope molar ratio of the sample and standard, respectively. The standard used for carbon analysis was Pee Dee Belemnite (Vienna Pee Dee Belemnite - Vienna PDB; $^{13}\text{C}:^{12}\text{C}$ ratio = 0.01118). Internal standards (tropical soil and sugarcane leaves) are routinely interspersed with target samples during analysis runs. Long-term analytical error for the internal standards are of 0.2 ‰ for $\delta^{13}\text{C}$, 1 % for organic C, and 0.02 % for total N.

Statistical Analyses

The normality of raw data and residues was tested using the Shapiro-Wilk W-test. The homoscedasticity of the variances was verified by the Barlett test.

Multiple comparisons between the treatments (i.e., Control, +N, ++N, and +++NM), regarding the sediment physicochemical properties and biotic and abiotic data, were evaluated using the Permutational Multivariate Analysis of Variance (PERMANOVA), using Euclidean distance matrix with 999 permutations after standardization of the data with the function “scale” (Anderson 2001). A Pearson correlation matrix was used to evaluate the correlation between abiotic and biotic variables in order to eliminate highly correlated variables from the analyses ($r > 0.9$) (Supplementary Fig. 1). Given that BADT and BALT were highly correlated, only BADT was used for PCA and further analyses (Supplementary Fig. 1).

The study plots and the abiotic and biotic variables were ordered through Principal Component Analysis (PCA) to verify the environmental distance between treatments (Legendre and Legendre 2012).

Univariate comparisons of abiotic and biotic variables between treatments were performed using the one-way ANOVA F-test followed by *pos-hoc* Tukey HSD test.

The variance inflation factor (VIF) values of the predictor variables were evaluated. Variables with VIF > 20 were excluded because they presented high collinearity. We conducted a redundancy analysis (RDA) to evaluate the effect of the selected abiotic factors ($\text{Sal10} + \text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) on the biotic variables that presented significant differences between treatments on univariate comparisons (BADT, foliar C:N and foliar $\delta^{13}\text{C}$) and also foliar N, which is an important foliar attribute. The statistical significance of the RDA axes and groupings were tested by the analysis of similarities (ANOSIM). A partial RDA (pRDA) was performed to evaluate the individual effect of each predictive abiotic

variable on the set of response biotic variables (Legendre and Legendre 2012). The significance of the effect of each predictor variable on the response variables was tested by an analysis of variance (ANOVA).

All analysis was performed using the software R (R Core Team 2017) at $p < 0.05$.

Results

Physical and Chemical Properties and Available N in Sediment

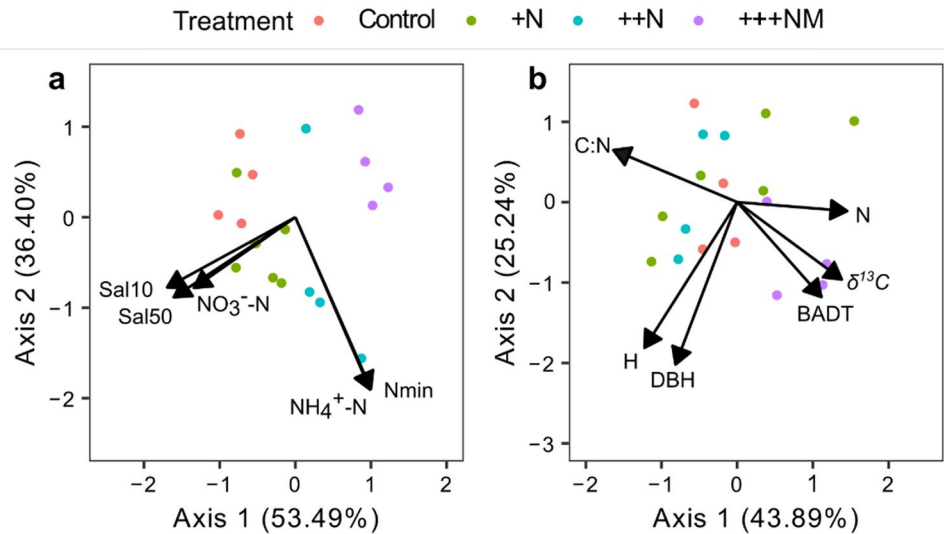
Sediment texture and the active, potential, and exchangeable pH values were similar among treatments. That was also the case for concentrations of organic matter (OM), available P, Na^+ , K^+ , Ca^{2+} , and Mg^{2+} , as well as SEB and CEC in sediment at 0–20 cm depth (PERMANOVA, $F_{(3,4)}=1.6919$, $p=0.385$) (Supplementary Table 2). There were drastic variations in salinity in our sites. In those close to the Valo Grande channel (i.e. +++NM and ++N), the salinity was extremely low compared to the other plots (Supplementary Table 3). In general, the abiotic variables (i.e. Sal10, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and Nmin) were significantly different between treatments (PERMANOVA, $F_{(3,14)}=10.088$, $p=0.001$).

Biotic Factors: Vegetation Structure and Foliar Attributes

Biotic variables including foliar attributes (i.e., N concentrations, C:N ratios, and $\delta^{13}\text{C}$) and vegetation structure data (i.e., DBH, H, BALT, and BADT) also differed among treatments (PERMANOVA, $F_{(3,14)}=5.5376$, $p=0.012$). These abiotic and biotic variables were also consistently different among treatments on univariate comparisons, except for DBH, H and foliar N concentrations, which were similar among study plots (Supplementary Table 3). A high basal area of dead trunks (BADT) and a lower C:N ratio of the plants were recorded in sites subjected to high N inputs and colonized by non-native plant species (+++NM) (Supplementary Table 3).

Foliar C:N ratios of the native and non-native species were, respectively 15.4 ± 3.9 and 22.5 ± 4.4 . There was a significant difference between these two groups ($t_{(19)}=3.8489$, $p=0.001$). Foliar N concentration of non-native species was significantly higher ($26 \pm 5.3 \text{ g kg}^{-1}$) compared to mangrove species ($15 \pm 3.9 \text{ g kg}^{-1}$) ($t_{(19)}=3.8489$, $p<0.001$).

Fig. 2 Principal component analysis (PCA) of mangroves according to abiotic (A) and biotic variables (B). Dots of different colors identify the treatments: non-N-enriched and free of non-native species plots (Control), plots free of non-native species and subjected to medium (+N) and medium to high (++) N inputs, and plots colonized by non-native species and subjected to high N inputs (+++NM)

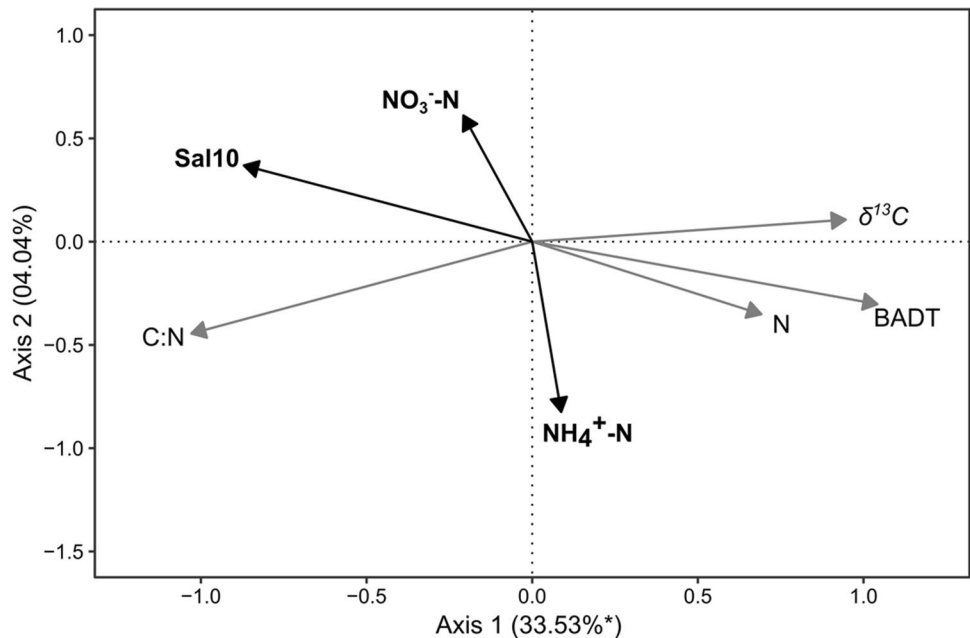


Abiotic and Biotic Factors Related to the Colonization of Non-native Species

The PCA axes of abiotic variables explained 89.9 % of the total variance in the data set (Fig. 2A). Ordination axis 1 was negatively correlated to NO₃⁻-N concentrations and interstitial salinity at 10 and 50 cm, which grouped Control and +N. The ordinations of +++NM plots was negatively correlated with the variables Sal10, Sal50, and NO₃⁻-N. Ordination axis 2 was negatively correlated with the Nmin and NH₄⁺-N that grouped the ++N 2-4 plots, which presented the highest concentrations of these

variables (Fig. 2A). The PCA axes of biotic variables accounted for 69.1 % of the variance (Fig. 2B). Ordination axis 1 indicated that the invaded areas subjected to high N inputs (+++NM plots) were positively correlated with the foliar δ¹³C and N concentrations and with BADT, while were negatively correlated with foliar C:N ratios. The ordination of plots of Control, +N, and ++N was positively correlated with C:N and by the variables DAP and H (Fig. 2B).

Fig. 3 Redundancy analysis (RDA) of the influence of abiotic on biotic factors associated with the colonization of non-native species in mangroves. Black arrows indicate predictor variables and gray arrows indicate response variables



Influence of Abiotic Factors on the Colonization of Non-native Species

Axes 1 and 2 of the RDA, accounting for the influence of abiotic on biotic variables, explained 37.57% of the total variance ($F_{(3,14)}=4.6744$, $p=0.001$) (Fig. 3). Axis 1 of the RDA explained 33.53% of the variance and the clusters were statistically significant ($F_{(1,14)}=11.9557$, $p=0.002$). RDA axis 1 was negatively correlated with interstitial Sal10 and foliar C:N ratios and positively correlated with BADT and foliar $\delta^{13}\text{C}$ and N concentrations. However, interstitial Sal10 was the only predictor variable that had significant influence on axis 1. RDA axis 2, on the other hand, was not significant ($F_{(1,14)}=1.4414$, $p=0.481$), explaining only 4.04% of the variance.

Considering the individual influence of each predictor abiotic variable on the biotic variables related to the colonization of non-native plants (pRDA), Sal10 and NO_3^- -N exhibited the highest coefficients of determination (adjusted R^2) and significant p-values (Sal10: $R^2_{(\text{adj})}=0.422$, $F=11.443$, $p=0.001$; NO_3^- -N: $R^2_{(\text{adj})}=0.101$, $F=6.3702$, $p=0.002$). The influence of NH_4^+ -N was not significant ($R^2_{(\text{adj})}=0.010$, $F=1.2704$, $p=0.306$).

Discussion

Many studies have addressed how human alterations in the upstream of hydrological fluxes can modify environmental conditions in downstream mangrove forests (Dahdouh-Guebas et al. 2005; Röderstein et al. 2013). However, most of these studies reported alterations following the reduction of freshwater input into mangrove ecosystems leading to increased salinity, degradation of the mangroves and dominance by tolerant mangrove species (Gopal and Chauhan 2006; Sathyanathan et al. 2014). Here, we showed the opposite situation, that is, we evaluated the effects of increasing freshwater inputs into mangrove forests. We found large alterations on the structure of native vegetation in the presence of non-native species, in agreement with previous studies showing the marked sensibility of mangrove ecosystems to changes in the hydric regime (Lugo 1998; Zhang et al. 2012; Röderstein et al. 2013; Biswas et al. 2018).

The PCA analysis indicated the association between the mangrove areas subjected to high N inputs and colonized by non-native plant species (+++NM plots) with the concentrations of NO_3^- -N in the sediment, interstitial Sal10 and Sal50 and by the biotic variables BADT, foliar $\delta^{13}\text{C}$, N foliar and foliar C:N. The RDA and pRDA analysis indicated that the biotic variables BADT, foliar N concentrations, C:N ratios and foliar $\delta^{13}\text{C}$ were significantly influenced by interstitial salinity at 10 cm depth followed by NO_3^- -N concentrations in mangrove sediment. This suggests that colonization such

plants is mainly controlled by these variables at our study sites. The Valo Grande canal opening has facilitated the entrance of propagules and banks of non-native plant species into the estuary and mangrove areas in the Iguape region. Our results suggest that a salinity reduction to 1.7 g kg^{-1} following excess freshwater inputs was the main factor contributing to the colonization and subsequent establishment of non-native plant species in these mangrove forests. These results add to previous studies that indicated high salinity as the main environmental filter preventing non-native plant colonization into mangroves (Lugo 1998). The plants that invade mangrove forests are usually able to tolerate high salinity to some extent (Biswas et al. 2018). For this reason, species like aquatic macrophytes and grasses would not be able to colonize mangroves unless salinity was significantly reduced in these systems (Lugo 1998; Dahdouh-Guebas et al. 2005; Biswas et al. 2012; Ren et al. 2014). Accordingly, Röderstein et al. (2013) reported that a salinity reduction to $1.0\text{--}2.0 \text{ g kg}^{-1}$ was the main factor leading to the establishment of the aquatic macrophyte *Typha domingensis* Pers in mangroves on the Caribbean coast of Colombia.

Concentrations of NO_3^- -N in sediment were the second factor that mostly affected the colonization by aquatic macrophytes at our study sites. It can be explained by the fact that nutrient concentrations in sediment affect the growth of non-native species (Ren et al. 2014). For instance, while the occurrence of non-native species in mangroves and other coastal areas in south China was negatively correlated with sediment salinity, their biomass was positively correlated with total N content in sediments (Ren et al. 2014) underscoring the importance of N availability for the growth of non-native species. The Valo Grande canal also carries excess N inputs from human activities resulting in high N availability in mangrove sediment at the +++NM and ++N plots. Despite the ++N plots exhibited higher NO_3^- -N and mineral N concentrations in sediment relative to the +++NM plots, non-native plants were not recorded inside the mangrove stands where the ++N plots were located. Because these stands were located closer to an open ocean inlet, salinity ranged from 13 to 20 g kg^{-1} at the ++N plots. Thus, the high salinity likely prevented the establishment of non-native plant species at these sites, despite propagules and floating banks of aquatic macrophytes being found in the surrounding estuarine waters. This highlights that salinity is the main factor controlling the establishment of non-native species at our study sites.

The co-occurrence of non-native plant species and mangroves has been found in ecotonal zones and bordering mangrove forests (Tomlinson 1986; Lugo 1998). The establishment and dominance of aquatic plants inside mangrove stands, however, is a consequence of disturbance and can result in negative effects on the native vegetation (Biswas et al. 2007, 2018). We observed large alterations on mangrove vegetation structure at the plots colonized by

non-native plant species (+++NM) (Cunha-Lignon et al. 2011; Cunha-Lignon and Menghini 2016). The BADT data indicated the higher amount of dead mangrove trunks at the +++NM plots (53% of basal area) compared to the other plots (up to 20%). In fact, the gradual and progressive increase in dead mangrove trees in areas close to the Valo Grande channel has been reported by long-term monitoring (e.g., Cunha-Lignon et al. 2015). This can be related to a higher competitive advantage of non-native plant species versus mangroves under low salinity and high N availability allowing the fast growth of non-native species (Dukes and Mooney 1999; Vilà and Weiner 2004; Bradley et al. 2010; Biswas et al. 2012, 2018; González-Muñoz et al. 2013; Gufu et al. 2018). Further studies using an ecophysiological approach per species are needed to understand the mechanisms underlying the displacement of native mangroves by the non-native plant species in these areas.

The lower NO_3^- -N concentrations in mangrove sediment at the +++NM compared to the others likely reflected a higher absorption of N by the non-native plant species along with higher N losses to the atmosphere via denitrification as a consequence of excess inorganic N inputs and intensified N cycling (Reis et al. 2017b, 2019).

In summary, the abiotic factors interstitial Sal_{10} and NO_3^- -N concentrations in sediment facilitated the colonization by aquatic macrophytes in the studied mangrove areas. We also verified the higher foliar N concentrations and lower foliar C:N ratios of non-native relative to native plants, possibly reflecting a greater N demand and assimilation of N by non-native plants. The combination of these abiotic and biotic factors and the competitive interactions of the native and non-native communities have resulted in the dominance of aquatic macrophytes in the mangrove understory and the high amount of mangrove dead trunks (BADT) in the plots colonized by non-native plant species (+++NM). Additionally, we did not observe the occurrence of young mangrove individuals at +++NM likely as a consequence of the high biomass of non-native plants that forms a physical barrier to the dispersion of mangrove propagules, thus affecting the recruitment and succession of mangroves (Cunha-Lignon et al. 2011; Biswas et al. 2012, 2018).

Considering that most non-native plant colonization and establishment in mangroves result from changes in abiotic conditions as a result of disturbances (Biswas et al. 2018) and that these changes may be difficult to reverse (Bradley et al. 2010), management efforts should be focused on the major disturbance factors that control the colonization of non-native plants by promoting restoration of abiotic conditions and recolonization of native species (Röderstein et al. 2013). In the case of this study, the rehabilitation of regional hydrological conditions coupled with the reduction of excess

nutrient inputs, especially of N, should be the first step in the management of non-native species in this region.

Conclusions

The increased freshwater flow and associated abiotic changes verified in the north sector of the ELC of Cananeia-Iguape were determinant for the non-native species overcoming the geographic and environmental barriers, allowing their expansion and dominance in mangrove ecosystems. The reduction of salinity and increased N availability in the sediment allowed the occurrence and success of the colonization non-native species in the studied mangroves.

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Author contributions JAGS – Sampling, writing the manuscript, statistical analyses.

CRGR - Writing the manuscript, sampling design.

MCL – Sampling design, sampling, writing the manuscript.

GBN - Sampling design, writing the manuscript, funding.

LFS - Writing the manuscript, funding.

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Data Availability The authors may provide the data used in the manuscript upon request.

Declarations

Animal Research There were no clinical trials. We did not work with people. We worked with soils and plants. Thanks

Consent to Participate There were no humans used in the present research.

Consent to Publish The authors allow the data be published in case the manuscript is accepted.

Plant Reproducibility The present research did not use of plant reproducibility techniques.

Clinical Trials Registration The present research did not make use of clinical trials.

Gels and Blots/ Image Manipulation The present research did not make use of gels and blots and image manipulation.

Competing Interests

The authors declare that there are no competing interests.

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