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Original Article

Facilitation in mangrove ecosystem: The role of herbaceous species in seedling recruitment and growth patterns of *Avicennia germinans* in a recovering mangrove in Northeastern Brazil

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ABSTRACT

The restoration of mangroves is crucial for preserving their vital role as ecosystems. Facilitation could assist in the restoration of degraded ecosystems, especially during the first life stages. This study investigated how herbaceous species can facilitate the recruitment and growth of *Avicennia germinans* in a degraded mangrove area undergoing restoration during extremely dry and rainy seasons typical of northeastern Brazil. The research assessed the densities and growth of *A. germinans* in the presence of *Batis maritima* and *Sesuvium portulacastrum*, and without any other plant species as control during the rainy and dry seasons from 2017 to 2019. The area had been previously disturbed by the salt pond industry abandoned since the late 1980s. The results revealed different facilitation mechanisms. *S. portulacastrum* and *B. maritima* promoted 2.6 and 1.7 times higher densities of *A. germinans* than control plots. While *B. maritima* had significantly faster growth of *A. germinans* than *S. portulacastrum* plots, associated with a capacity of decreasing salinity levels, facilitating mangrove seedlings during dry seasons, *S. portulacastrum* surpassed *B. maritima* and control plots in terms of density, which can be profitable for mangrove seedlings during extreme rainy seasons of floods.

Keywords: *Avicennia*; Facilitation; Herbaceous; Mangrove; Restoration.

Introduction

Modern ecological concepts and theories have only recently addressed the importance of a wide variety of facilitating interactions and their influence on the organization of terrestrial and aquatic communities, while advances in the past three decades have provided more accurate insight into natural communities (Bruno *et al.* 2003; Brooker *et al.* 2008; Huxham *et al.* 2019). Facilitation is a process where the presence of a species has a beneficial effect on other species (Levin *et al.* 2009). The facilitation theory can be applied in the restoration of ecosystems to

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benefit the community through pioneer species, a positive density dependence relationship, and facilitation cascades, all of which can influence individual physical conditions, population distribution, growth rates, species composition and diversity, and, at a landscape level, community dynamics (Bruno & Bertness 2001; Bruno *et al.* 2003; Halpern *et al.* 2007; Gedan & Silliman 2009).

However, these concepts have failed to influence the ecology of mangrove restoration and rehabilitation significantly (Huxham *et al.* 2019). Although little assessed, facilitation could be especially beneficial during the first life stages of mangroves, when recruiting and establishment are usually difficult due to harsh conditions of physical and biological stress, such as high temperatures and salinity, competition (Maestre *et al.* 2009), and propagule predation (Ferreira *et al.* 2013). Although propagules of several species of mangroves can adapt to extreme transitional environments, edaphic factors, such as low redox potential and high salinity of sediment, predominantly limit the establishment of propagules and the growth of mangrove seedlings, which are life stages that determine the success and survival of mangroves (Bruno *et al.* 2003; Gedan & Silliman 2009; Huxham *et al.* 2019).

The presence of pioneer herbaceous species is known to increase the deposition of fine sediments such as silts and influence the supply of nutrients and water, leading to changes in the composition of microflora and fauna and the creation of microclimates (Chapman 1974). Furthermore, patches of herbaceous plants can facilitate the retention, recruitment, and settlement of mangrove propagules via the physical complexity of their structures. These herbaceous plants can also modify the composition of the sediment through its physiology in a way that improves physical-chemical environmental conditions such as temperature, salinity, and moisture, which may increase the settlement, survival, and growth of mangrove seedlings (Bruno *et al.* 2003; Huxham *et al.* 2019).

In this regard, *Batis maritima* and *Sesuvium portulacastrum* are pioneer herbaceous halophyte plants cited as facilitators of the colonization of propagules and seedlings of *Avicennia germinans* (Milbrandt & Tinsley 2006; McKee *et al.* 2007; Peterson & Bell 2012; Teutli-Hernández *et al.* 2017; Pickens *et al.* 2019). However, the extent of this facilitation in the early life stages of mangrove trees is unclear since it is unknown whether facilitation extends beyond the establishment and growth of mangrove seedlings and the point at which herbaceous species operate as facilitators before becoming competitors. Moreover, the behavior of this facilitation during stressful environmental conditions, without regard to the condition of degradation/rehabilitation, must be evaluated since the stress level is known to model facilitation (Maestre *et al.* 2009).

It is important to understand how the facilitation process occurs in mangrove ecosystems and gain insight into the dynamics in these ecosystems, especially the varied interactions and complex processes that are still not fully known. Moreover, a better understanding of these processes could help establish high-priority environmental solutions both for the conservation of biodiversity and for the mitigation of the effects of climate change (Huxham *et al.* 2019). Also, further insight into the fundamental role of pioneer herbaceous species as facilitators in restoring degraded mangrove ecosystem functionality would help improve restoration projects in degraded areas such as abandoned saltworks (Bruno *et al.* 2003; Huxham *et al.* 2019; Renzi *et al.* 2019).

In Brazil, few studies have addressed co-specific facilitation in mangrove ecosystems (Vogt *et al.* 2014; Pranchai *et al.* 2018) and evaluated interspecific interactions throughout the mapping of *A. germinans* (Pranchai *et al.* 2021). Moreover, none have addressed interspecific facilitation during the early stages of mangrove seedling establishment and seedling growth monitoring at population and individual levels. This data can shed light on fine-scale processes to transfer, replicate, and make basic decisions in restoration projects in the region. Furthermore, no studies investigate the role of nurse plants in the semiarid mangroves of northeastern Brazil, the driest region of the Brazilian coast (Soares *et al.* 2021). The climate in the semiarid coast of Brazil alternates between extreme seasonal periods of dry climate and rains, known to model ecological aspects of marine communities of the region and transform into a laboratory in which biological interactions can be observed in different environmental stress conditions during the rainy and dry seasons (Soares *et al.* 2021).

To examine how facilitation by herbaceous vegetation might improve forest restoration after disturbance in northeastern Brazil, we tested the hypotheses that 1) changes in densities and growth of *A. germinans* are related to the presence of patches of herbaceous species in the mangrove ecosystem and 2) when variation is detected, these changes are related to environmental variation during the rainy and dry seasons in the region as environmental stressors. We expect the herbaceous species to act as a physical trap mechanism and as mitigators of extreme conditions (decrease in salinity and sediment temperatures) based on previous studies developed regarding these aspects (Milbrandt & Tinsley 2006; McKee *et al.* 2007; Peterson & Bell 2012; Teutli-Hernández *et al.* 2017; Pickens *et al.* 2019). These actions would promote higher densities at the population level and growth rates of *A. germinans* at the individual level in plots with *B. maritima* and *S. portulacastrum* compared to the control plots without the herbaceous plants in a mangrove area under recovery.

Material And Methods

Study site

The study site is in an Environmental Protected Area (Área *de Proteção Ambiental* or APA, in Portuguese) of the

Pacoti River in the municipality of Eusébio, state of Ceará, northeastern Brazil. The climate is tropical, with a maximum temperature of 34 °C and a minimum of 22 °C. The rainy season is concentrated in a few months (January to May), with an average annual rainfall of 1424.1 mm (IPECE 2020) (Figure S1). For the study analysis, we defined the months of the seasons from precipitation data from December 2017 to November 2019. Thus, the rainy season was defined as January to June with an average rainfall of 1289.9 mm, and the dry season as July to December with an average rainfall of 134.2 mm (FUNCEME 2020). Tides are semidiurnal, with a maximum tidal amplitude of around 3.1 m and a minimum of 0.9 m (Freire 1989). The mangrove vegetation of this area is predominantly composed of *Avicennia schaueriana* Stapf and Leechm., *Avicennia germinans* (L.) L., *Laguncularia racemosa* C.F.Gaerth, and *Rhizophora mangle* L., (Gorayeb *et al*. 2005; Ferreira *et al*. 2019).

The estuary harbored salt production ponds installed after clearing the original mangroves in the 1960s. However, most ponds were deactivated at the end of the 1980s (Fig. 1). The coastal basin, downstream from the last artificial reservoir, covers an area of approximately 132 km^2 (Ferreira *et al*. 2019).

From 2016 to 2018, a hydrological restoration project with a channel opening in the deactivated salt ponds was executed at the study site. During this period, the connection and water flow between the site and the adjacent estuary were re-established, thus helping to mitigate the hypersalinity caused by the historical impact of the salt ponds. After the channels were opened, the pioneer herbaceous species *Batis maritima* L., *Sesuvium portulacastrum* (L.) L., and *Sporobolus virginicus* (L.) Kunth colonized the area, leading to the settlement of *L. racemosa* and *A. germinans* propagules (the latter already established in the saltwork) and the development of planted *R. mangle* propagules (Ferreira *et al.* 2022). Real-time kinematic (RTK) topographical surveying was carried out in the study area to ensure the plots shared the same topographical characteristics (Figure S2). We verified that all observational plots were in a plane area with similar influence from the tides. During the study period, all plots of herbaceous species maintained full coverage, and species did not intermingle in the plots. Our study site covers approximately 1,900 m^2, in which rainfall drainage, radiation, wind, and other factors may similarly affect all observational plots of herbaceous species and mangroves, including the control plots.

Sampling strategy

In the area of approximately 1,600 m^2 (40 m x 40 m), two patches of pioneer herbaceous species, one with *S. portulacastrum* and another with *B. maritima*, were selected and monitored after the channel opening 3°49'S - 38°25'W,3°49'S – 38°25'W, 3°49'S – 38°25'W, 3°49'S – 38°25'W, Fig. 1A). Two patches of the pioneer herbaceous species *S. portulacastrum* and *B. maritima* of approximately 300 m2 (15 m x 20 m) were selected (Fig. 1B). All plots had seedlings of the mangrove tree *A. germinans*. We randomly allocated five plots of 4 m2 (2 m x 2 m) to each patch of herbaceous species (Fig. 1C-F). One area adjacent to the two patches and equivalent in size with the total absence of herbaceous species and with the presence of *A. germinans* seedlings was designated as a control area. No other mangrove or herbaceous species occurred in the plot areas other than those mentioned above throughout the study period.

Samplings were performed monthly from December 2017 to November 2019. Seedlings of *A. germinans* from 10 cm to 20 cm in size (Pickens *et al.* 2019) were counted and measured regarding height from the ground to the last apical bud. Plants in each plot were labeled with serially numbered plastic tags in each treatment and measured monthly from February 2018 onwards (Fig. 1G-I). The growth rate was calculated (Equation 1) by subtracting the final height (Hf) from the initial height (Hi) of each labeled individual. The height difference was divided by the number of days elapsed between one sampling and another (d) and multiplied by 30 to obtain a growth value in centimeters per month (Teutli-Hernández *et al.* 2017).

$$\text{Growth rate (cm/month)} = \text{Hf - Hi/d x 30} \qquad (1)$$

For logistic reasons, we had to adjust a possible overestimation in the sampling effort to monitor the individual growth rate of *A. germinans* and adjust the number of samples based on the Central Limit Theorem (Martínez-Abraín 2014). Standard deviations were represented graphically using randomly obtained growth rates versus the number of samples (x = number of values considered for each standard deviation). Moreover, the extent to which the standard deviation of growth rates became less variable and more stable as the sample size of the measured individuals increased was evaluated, and the point at which this occurred showed the value X (number of samples) for the collection of growth rates. For our study, the standard deviations of growth rates using data from the first months of sampling (February to April) stabilized at 18 individuals for long-term growth rates. Thus, 18 labels of *A. germinans* individuals were randomly selected for each plot, and the plastic tags were removed for the rest of the seedlings. The sampling frequency was adjusted and standardized by collecting density data every two months since the densities did not vary monthly but seasonally. Due to missing tags, mortality, or growth loss, some individuals were censored for the data analysis and were not replaced.

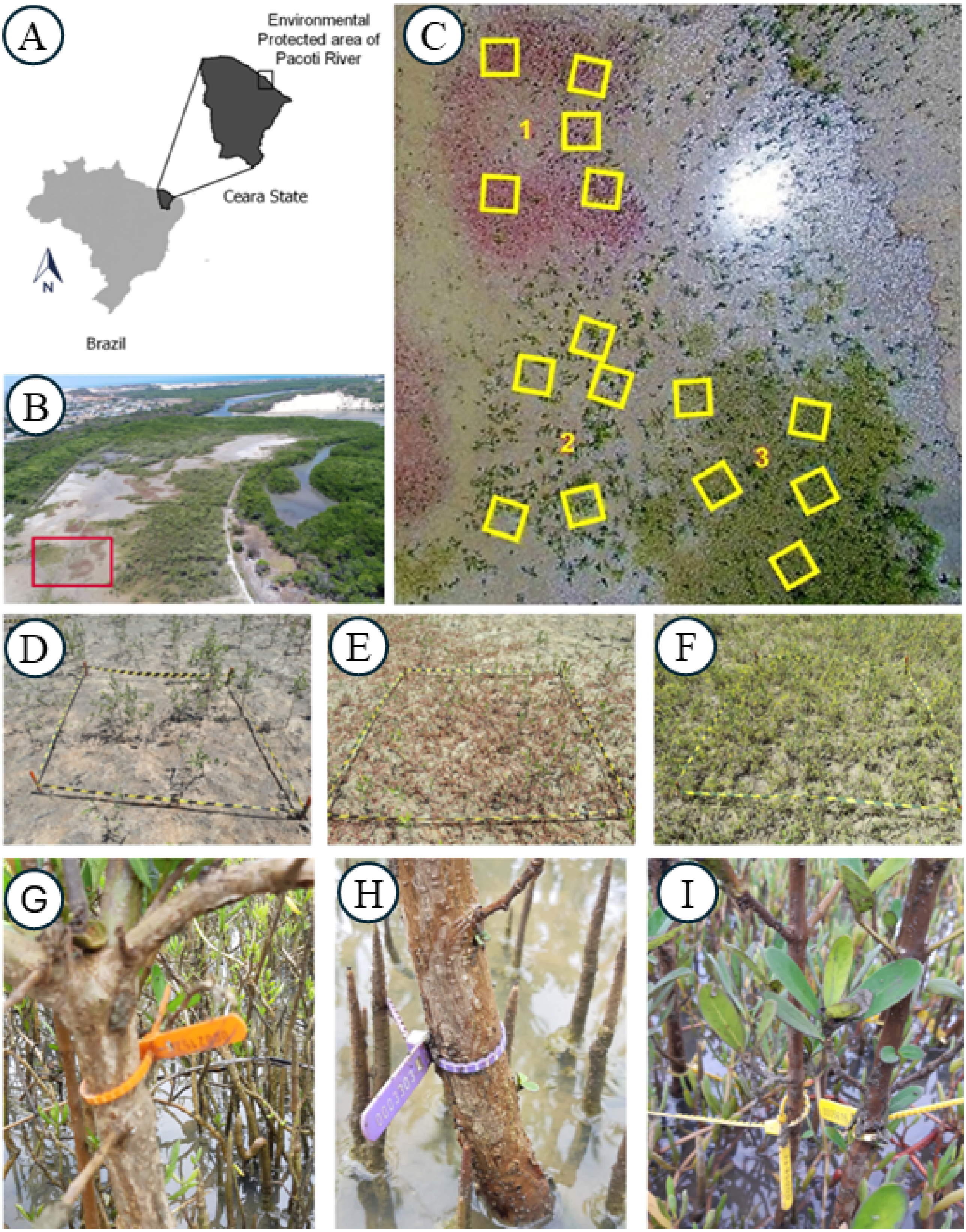

Figure 1. Location of the study site in the state of Ceara, Northeast Brazil. A. Study site in Ceará state. B Aerial view of deactivated salt production ponds. C. Plots were randomly allocated in patches of *S. portulacastrum* (1), control (2), and *B. maritima* (3). D. Detail of 4 m^2 plots in Control. E. Detail of 4 m^2 plots in *S. portulacastrum*. F. Detail of 4 m^2 plots in *Batis maritima*. Plants labeled with serial plastic tags in: G. *Batis maritima* patch. H. Control patch and I. *S. portulacastrum* patch.

Abiotic data collection

Salinity and Temperature. Environmental variables such as the surface temperature of the substrate were measured using a digital thermometer, and the salinity of the percolated water of the sediment was measured using a refractometer. These variables were measured in each plot for each monthly sampling between 11:00 am and 12:00 pm at 20-minute intervals.

Sediment. A surface sediment sample was collected using a core of 15 cm in diameter to 25 cm in depth. One sample was taken in each herbaceous patch and control area for each season in each year. Several subsamples of each core sample were collected as replicates for content analysis. Each sample was collected in a central area of each herbaceous patch outside the demarked plots and a central area of the control plots.

Humidity. The sediment was collected using the mentioned core, stored in plastic bags, labeled, sealed, and transferred in a thermal box to the laboratory. Wet samples were weighed and dried in the stove at 45-50 °C for approximately 48 hours. The humidity content of each homogenized sample was determined as follows (Suguio 1973) (Equation 2):

$$h = (WW - DW) / DW \qquad (2)$$

where WW = wet soil weight in grams and DW = dry soil weight in grams.

Organic matter. The organic matter content was determined using an adaptation of the method of Dean (1974) (Equation 3), where fractions of 2 g of each sample were burned in a muffle furnace at 450 °C. After two hours, the samples were placed in a desiccator for complete cooling free of moisture and weighed again. Organic matter content was calculated using the formula:

$$MO = Pi - Pf \qquad (3)$$

where MO is the organic matter, Pi is the initial weight (before burning), and Pf is the final weight (after burning).

For granulometric analysis, sediment samples were dehydrated in an oven at 60 °C for 72 hours, then quartered and weighed in an analytical balance to obtain six subsamples of 100 g of sediment. The muddy fraction was separated by wet screening on a mesh of 0.062 mm (phi 4), and the largest particles were subjected to dry sieving on 13 sieve drums for 15 minutes (Wentworth 1922). All fractions obtained were weighed and analyzed using ANASED 5.0 software following the particle size classification of Folk and Ward (1957).

Experimental design

To assess the growth of *A. germinans* and density variation associated with facilitation, we used a factor treatment that included three levels of variation corresponding to the substrate with the presence of *S. portulacastrum,* the substrate with the presence of *B. maritima*, and the substrate without the presence of any pioneer herbaceous species but with *A. germinans* as a control. Each level of the treatment factor had five replicates (plots of 4 m^2). To explain the temporal differences in the density patterns and growth rates of *A. germinans*, the factor year was considered as the temporal variation, with two levels of variation corresponding to the years 2018 and 2019; the factor period with two levels of variation corresponding to dry and rainy seasons in each year, defined according to rainfall data for the municipality of Eusébio (FUNCEME 2020); and the factor month, including levels of variation of calendar time corresponding to the months that constitute each period (from January to June for the rainy period and from July to December for the dry period). The response variables to test these hypotheses were the density and growth rates of *A. germinans*.

For analysis, we considered the dry period as a factor that could operate as an environmental stressor. The dry season accentuates the hyper-salinity of the sediment, which is already saline due to past impacts on the site. High salinity would affect the individual condition of the mangrove in the short term, as it has to spend more energy in the secretion of salt during this season than during the rainy season. Moreover, it would affect the condition of the *A. germinans* population in the medium or long term, thus providing opportunities for competition. In contrast, heavy rains in the rainy season can decrease the recruitment of *A. germinans* by dispersing the propagules from the estuary, thus hampering rooting and settlement and affecting the population densities in the short term.

Statistical analysis

Facilitation effect on A. germinans

Densities and growth were independently evaluated using uni-variate PERMANOVA run on a Euclidean distance similarity matrix and 999 permutations with the PRIMER-E & PERMANOVA v6 package, based on the factors described in the previous section (Anderson *et al.* 2008).

A significance level of 0.05 was established for decision-making on the hypothesis of a no-difference test. In the case of growth rate analysis, salinity and temperature were included as covariates due to the data available for analysis. Subsequently, as part of the PERMANOVA analysis, multiple comparison tests were run to detect differences between levels of factors or interactions that were statistically different.

Facilitation effect on physical sediment conditions

Temperature and salinity data were analyzed using multifactor ANOVA considering the treatment factor (Tr), period (Se), and month (Mo). The sedimentological variables moisture and organic matter were compared to detect significant differences between treatments using the Student t-test of a sample assuming equal variances (Zar 2010).

Results

The densities of *A. germinans* differed between the treatments and the control plots (Table 1). Plots with *Sesuvium portulacastrum* had greater density (12.5 ± 0.76 ind./m^2, median ± SE) than those reported with *B. maritima* (8 ± 0.64 ind./m^2) and the control plots (4.75 ± 0.32 ind./m^2).

The densities of *A. germinans* between treatments were the same in the sampled years. However, the densities were higher during the dry season than the rainy season for all. It should be noted that although all treatments differed from one another, the seasonality of *A. germinans* densities in plots with *B. maritima* and *S. portulacastrum* were more marked than the density trends observed in the control area (Fig. 2).

Comparisons of densities between treatments differed in each season, except at the start of the study period (December 2017), when densities were the same in all three treatments (control, *B. maritima*, and *S. portulacastrum)*, reflected in the significant interaction Se (Year) × Tr (Fig. 2, Table 1).

Facilitation influencing the growth of *A. germinans*

The growth rates of seedlings of *A. germinans* were generally higher with the presence of *B. maritima* (4.80±0.37 cm/month, median ± se) and did not differ from those in the control area 3.41±0.51 cm/month), while patches of *S. portulacastrum* had the lowest growth rates of *A. germinans* (2.88±0.26 cm/month) (Fig. 3, Table 2).

The growth rates of *A. germinans* did show a seasonality pattern (Se; p<0.05, Table 2), which was unrelated to the herbaceous species (Se × Tr; p=0.797, Table 2). More

Table 1. PERMANOVA analysis for densities of *A. germinans*.

Source of variation	df	SS	MS	Pseudo-F	P(perm)
Year –Year	2	4374.1	2187.1	2.6	0.149
Treatment -Tr	**2**	**1745.5**	**872.7**	**18.3**	**0.005**
Season (Year) –Se	**2**	**2774.3**	**1387.2**	**50.4**	**0.001**
Year x Tr	4	610.5	152.6	2.2	0.128
Month (Se (Year)) –Mo	**15**	**408.7**	**27.2**	**2.2**	**0.008**
Se (Year) × Tr	**4**	**439.6**	**109.9**	**10.4**	**0.001**
Mo (Se (Year)) × Tr	29	303.6	10.4	0.8	0.665
Residual	234	2855.0	12.2		
Total	292	14389.0			

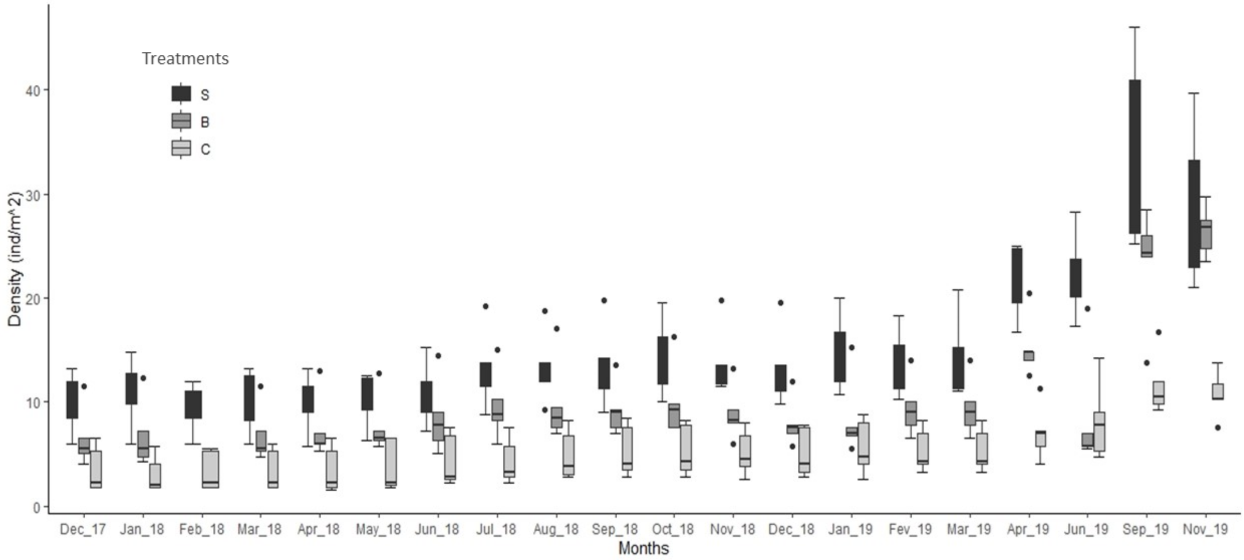

Figure 2. Densities of *A. germinans* associated with facilitation treatments *S. portulacastrum* (S), *B. maritima* (B), and Control (C) in the Pacoti River mangrove from December 2017 to November 2019.

specifically, *A. germinans* growth rates varied among the herbaceous species during the study months (Mo (Se) × Ef; p<0.05; Table 2). Growth rates of *A. germinans* in *B. maritima* and the control plots were higher during the first months of the rainy season (March and April). Subsequently, these rates changed at the end of the rainy season and during the dry season (June, September, and November), when *B. maritima* maintained high and different growth rates from the control and *S. portulacastrum*. This result indicates the potential of *B. maritima* to counterpose the harsh conditions of the dry season for the growth of *A. germinans* during the early stage of life.

Facilitation effect on the physical sediment condition

Temperature values only showed monthly variation but did not differ between the treatments and control patches. Herbaceous patches did not influence soil temperatures. However, there were significant differences related to seasonality in temperatures from 28 °C in the rainy season to 37 °C in the dry season (Fig. 4A). In contrast, salinity values differed among the months, treatments, and the interaction between these factors, ranging from 0 to 88 ppt (Fig. 4B). *B. maritima* differed from other plots, with significantly lower salinity in January, February, March, and June, (result from a posteriori analysis of the treatment vs month interaction), which are months of moderate rainfall. No significant differences were associated with facilitation during the month of heavy rains (April) and the dry period (September and November).

Grain-size analyses classified the sediment type as "very fine" in all treatments sampled throughout the study period, and very poorly selected, with a positive asymmetry in the distribution curve, tending to finer grains. The organic matter content showed significant differences between treatments and marked seasonality in plots of *S. portulacastrum*, with the highest levels during the dry season (Fig. 4C). This seasonality was less marked in the control plots, while no differences were observed between seasons in the presence of *B. maritima*.

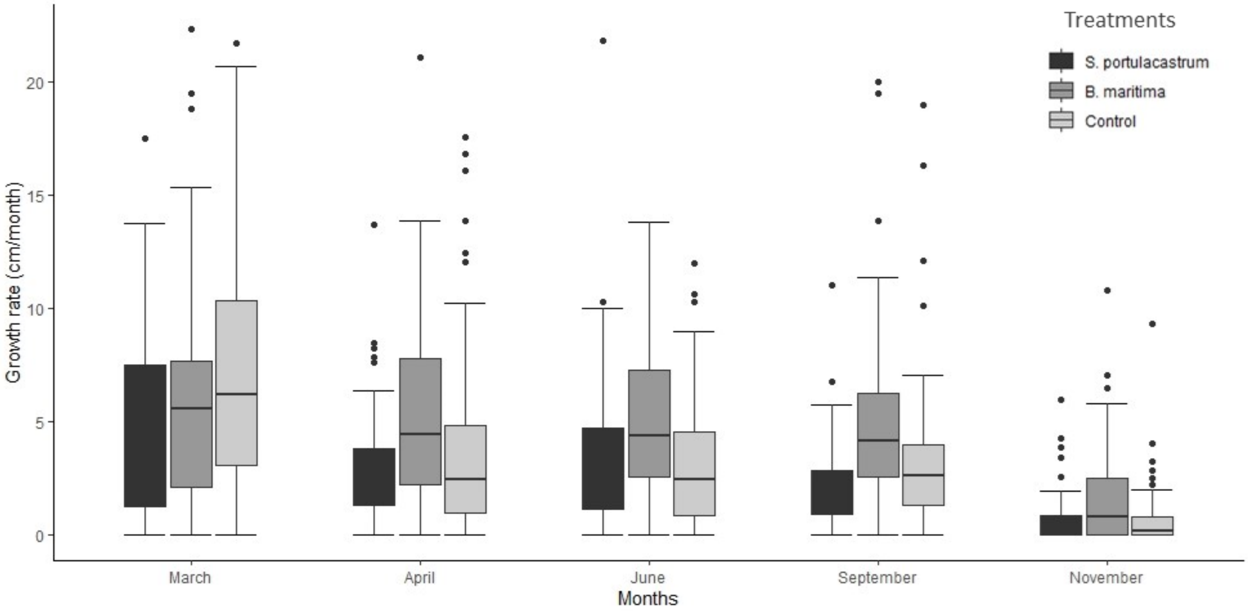

Figure 3. Growth rates of *A. germinans* during the study months by treatment.

Table 2. PERMANOVA analysis for growth rates of *A. germinans*

Source of variation	df	SS	MS	Pseudo-F	P(perm)
Season-Se.	**1**	**1469.4**	**1469.4**	**3.5**	**0.001**
Treatment - Tr	**2**	**710.6**	**355.2**	**32.3**	**0.052**
Month – Mo (Se)	**3**	**1275.9**	**425.3**	**37.2**	**0.001**
Se x Tr	2	21.9	10.9	0.2	0.797
Mo (Se) × Tr	**6**	**274.21**	**45.7**	**3.9**	**0.002**
Residual	1135	12984	11.4		
Total	1149	16682			

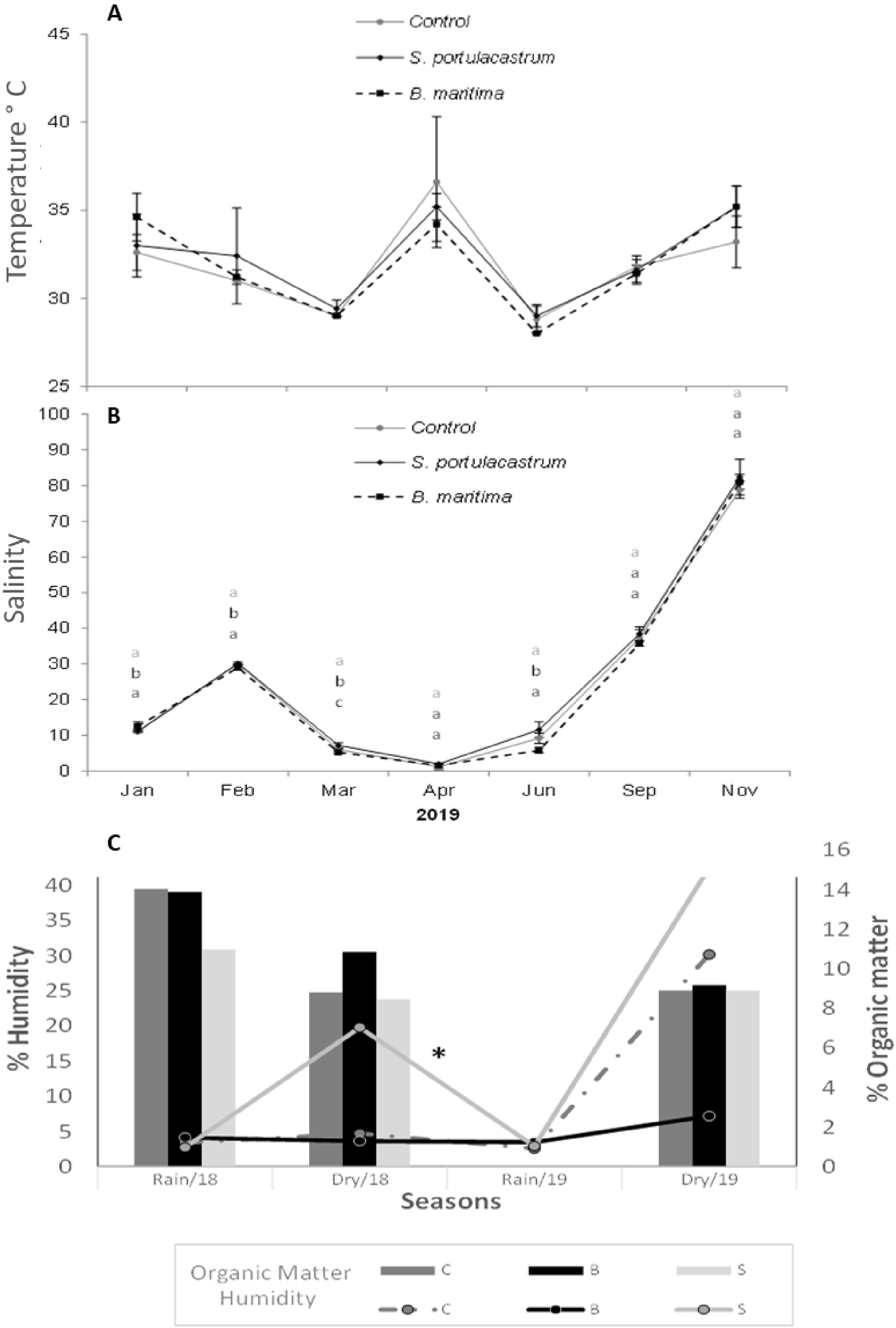

Figure 4. Trends in salinity, temperature, humidity, and organic matter (mean ± standard deviation) during 2019 in the treatments associated with facilitation. Letters indicate groups of salinity data following the order of treatments in the legend.

In summary, patches of *S. portulacastrum* present more individuals of *A. germinans* than those of *B. maritima*, which are more numerous in terms of individuals of *A. germinans* than the control plots. In contrast, the growth rates of seedlings were greater in patches of *B. maritima*. The patches of herbaceous plants did not significantly affect temperature but did significantly affect salinity, humidity, and organic matter (Fig. 4).

Discussion

Our results suggest that the species *B. maritima* and *S. portulacastrum* naturally facilitate the density of the first life stages of *A. germinans* during the recovery of an impacted mangrove ecosystem. These results agree with other studies where herbaceous species facilitate the recruitment and survival of propagules and seedlings of *A. germinans* under experimental conditions (Milbrandt & Tinsley 2006; Peterson & Bell 2012). However, under natural conditions, mangrove seedlings have established without clear patterns between herbaceous species patches and areas devoid of vegetation (McKee *et al.* 2007). In this sense, we observed natural responses associated with each herbaceous species' influence as facilitators on a very fine scale. These herbaceous species facilitate the establishment and growth of seedlings of *A. germinans* differently in the study area, with differing seasonal trends caused by climate stressors such as the extremely dry and rainy seasons of the northeastern region of Brazil and by previous impacts due to an abandoned salt pond in the study area.

S. portulacastrum stood out between the two herbaceous species in terms of trapping *A. germinans* seedlings, with higher black mangrove densities than *B. maritima* and more than two times greater densities than the control area. These findings confirm those of McKee *et al.* (2007), who reported that this species successfully traps dispersed propagules and positively influences a reduction in mortality. Both *S. portulacastrum* and *B. maritima* showed a distinct seasonality of *A. germinans* densities, which were higher during the dry season and lower during the rainy season. We argue that high densities of *A. germinans* during the dry season could be a delayed effect of the trapping mechanism by the physical structure of both herbaceous species, particularly due to our criteria of the minimum size of 15 cm required to count black mangrove individuals. In contrast, densities of black mangrove seedlings in the control area were always the lowest during the study period and did not show any seasonality (Fig. 2), probably because of the lack of the trapping mechanism given by herbaceous species. However, densities were generally higher in the presence of herbaceous species than in the control area. During the rainy season, densities of *A. germinans* in herbaceous species would be lower due to the effect of rainfall drainage stress, which is not present in the dry season, leading to reduced recruits and lower densities.

In contrast, growth rates tended to decrease in all the plots over the study period, which is expected as the dry season increases the already hypersalinity of soil and is expected with seedling size increase. Furthermore, we observed lower growth rates when densities were higher, as observed in plots with *S. portulacastrum*. In this regard, when comparing densities for *B. maritima* and the control area, higher black mangrove growth rates are expected in the control area than in the *B. maritima* plots because there is less probability of competition when there are fewer individuals in a determined area. We also assume facilitation does not influence control plots since they only have *A. germinans*, and competition has no influence due to the low black mangrove densities in these plots. In this regard, higher growth rates during harsh conditions combined with lower salinities, as well as bigger individuals of *A. germinans* (68.4 ± 39.4 cm), with significantly higher black mangrove densities than in the control plots and greater opportunities for competition, support the hypothesis that *B. maritima* facilitates the growth of black mangrove during stress conditions. This facilitation also could be due to its known high tolerance to hyper-salinity already present in the study area after the deactivation of an abandoned salt pond and even during the dry season when higher salinities are expected (Lacerda 2002; Debez *et al.* 2010; Donnelly & Walters 2014). In addition, *B. maritima* has been cited as responsible for increasing seedlings' survival after an environmental stress event such as a hurricane (Milbrandt & Tinsley 2006).

Pranchai *et al.* (2021) found that herbaceous species facilitated recolonizing and promoted the growth of black mangroves. However, in our study, high densities of *A. germinans,* associated with lower growth rates in black mangroves in plots of *S. portulacastrum,* leads us to speculate that competition occurred in this treatment. Sinsin *et al.* (2021) found a negative correlation between salinity and the growth of *A. germinans*. Furthermore, as it becomes more structurally complex, the higher densities of *A. germinans* added to the presence of herbaceous species could increase the trap of suspended particles (Chapman 1974), which explains the high salinity values in plots of *S. portulacastrum*. Therefore, the trap mechanism and the dry season could be contributing to higher salinities, which influence the growth rates of the black mangrove, exceeding the small-scale facilitation influence of herbaceous species, thus showing interactions of facilitation and competition shifts.

Further studies are needed to evaluate the mechanisms acting behind the establishment and growth variation during the first life stage of mangroves in recovery at small spatial and temporal scales in variable stress conditions and, thus, identify changes in biological interactions. Our study observed that high densities and hypersalinity could affect the growth rates of mangrove seedlings in all plots. Moreover, *B. maritima* mitigates hypersalinity and exhibits higher growth rates for *A. germinans* than *S. portulacastrum*.

However, higher densities and hypersalinity were observed in *S. portulacastrum*, leading to low growth rates for *A. germinans*. Lastly, this "effect" does not occur in the control plots, with low densities and high salinities, which do not seem to affect the growth rates of *A. germinans*.

In contrast, none of the herbaceous plants significantly influenced sediment temperature, probably because the temperature values of the region are relatively stable, thus contrasting with the description of *B. maritima* as a facilitator for sediment temperature conditions (Milbrandt & Tinsley 2006; Guo *et al.* 2013).

The low content of organic matter during the rainy season in all plots indicates an influence of rainfall on sediment, which leads to a greater transport of particulate matter. Otherwise, during the dry period, the absence of rain could promote the retention of particulate matter, especially with a trapping effect of herbaceous species, which could explain the high levels of organic matter during the dry period compared with the control, when the density of *A. germinans* is higher. In this regard, *Spartina alterniflora* has proven to influence sediment fixation and the trapping of chemical elements (Lacerda 2002). We speculate that this herbaceous species could bring organic matter to the system, particularly during the dry period (autochthonous organic matter), due to the high densities of *A. germinans* in these plots or organic matter from the herbaceous species. We also deduce that low levels of organic matter found in the plots of *B. maritima,* compared to the control, indicate that *B. maritima* could be taking advantage of the organic matter that is naturally retained during the dry season. This organic matter can be used (i.e., nutrient reabsorption) to minimize hyper-salinity stress through its growth process and may be used for the growth of *A. germinans*.

Although the origin of the organic matter is unknown, the marked differences between treatments in such a reduced area and the seasonal variation along with humidity and salinity between the herbaceous species suggest that these environmental variables are mediated by a unique influence for each herbaceous species. The variability of the abiotic factors in mangrove ecosystems emphasizes the importance of studying facilitation pathways with site-specific factors (i.e., identity, abundance, and architecture of mangrove associates) in future investigations of the facilitation features of 'nurse' plants in harsh environmental conditions (Padilla & Pugnaire 2006; Guo *et al.* 2013; Coldren & Proffitt 2017). The result also highlights the importance of studying the early stage of this process in impacted mangrove ecosystems that are the main target of mangrove restoration projects in arid environments (McKee *et al.* 2007; Teutli-Hernández *et al.* 2017).

Vogt *et al.* (2014) and, more recently, Pranchai *et al.* (2018) evaluated an intraspecific interaction in a mangrove degraded forest in natural recovery in northern Brazilian and found positive interactions between dwarf *A. germinans* in a low-density forest. Although their study area was in an impacted mangrove forest beside a road construction, mangrove trees were available to evaluate how intraspecific interactions may drive natural recovery. Nevertheless, impacted mangrove ecosystems in northeastern Brazil are characterized mainly by abandoned salt ponds and shrimp culture infrastructures (Ferreira & Lacerda 2016), constructed after the deforestation of littoral areas that are cleared areas that only depend on pioneer species. Furthermore, the climate in northeastern Brazil causes drastic environmental changes in a semi-arid ecosystem, in which we found salinities from 0 ppt in the rainy season to almost 90 ppt during the dry season and temperatures from 28 °C to more than 40 °C. It has been shown in other ecosystems that environmental stress, such as extended rainy seasons or very long dry periods, can change positive (facilitation) and negative (competition) interactions depending on species tolerance (Maestre *et al.* 2009; Guo *et al.* 2013; Coldren & Proffitt 2017). We infer that herbaceous species positively interacted with *A. germinans* during the study period at a population level of the seedlings, revealed by the density trends compared with the densities found in the control area. Nevertheless, we infer that only *B. maritima* could exert a positive interaction with *A. germinans* at an individual level, revealed through higher growth rates during almost the entire study period until November 2019. In this period, the dry season and high densities of *A. germinans* caused the environmental stress to exceed the facilitation effect on growth rates in this herbaceous species. Hence, since the impacted mangrove ecosystem in the region shares certain characteristics, such as hydrobiological interruption through dams and hyper-salinity due to the lack of water flow, we suggest the combination of hydrological restoration and pioneer herbaceous species for mangrove restoration in areas with these characteristics.

Our study has some important limitations. First, the shortage of areas with similar features (extension, distance to the estuary mouth, colonizing herbaceous, and human impact) prevented replication, which is a common problem when working in dynamic areas such as estuaries subjected to human impacts (Ferreira *et al.* 2015). Another limitation may be the lack of monitoring herbaceous species and control for potential confounders (e.g., potential differences in soil nutrients between plots and herbaceous shade levels). To mitigate this limitation, we ensured that all plots shared the same tidal inundation, elevation, and proximity to mangrove trees, and we observed that patches of herbaceous species did not change significantly in cover and did not overlap each other throughout the study period. These limitations did not allow us to make a cause-effect relationship between the herbaceous species and the mangrove variables, although we can associate them based on the trends observed in the obtained results. These factors, added with the clear patterns in each herbaceous species that always differed from the results obtained in the control area, allowed us to confidently attribute to facilitation the higher densities found in *S. portulacastrum* and the higher growth rates in high-density plots of *B. maritima,* compared to the control plots.

Our results show the dynamic and complex nature of the mangrove ecosystems, particularly in northeastern Brazil. These ecosystems are characterized by climatic variations well-defined by dry and rainy seasons, well-maintained temperatures, and salinity variations influenced by seasons, which can compromise the recovery capacity of these ecosystems. These findings are critical when including facilitating species in projects to restore mangrove ecosystems in the region. Moreover, the information presented here provides valuable insight into the response of species to other environmental stressors on a global scale, as in the case of climate change and sea-level rise.

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Data availability

The spreadsheets with the data obtained in the field are available in the supplementary data of this study at the link: https://doi.org/10.6084/m9.figshare.12982421.v3 DOI:10.6084/m9.figshare.12982421.v3

Author's Contrbutions

CBV developed the theoretical formalism, performed the experiment, laboratory procedures, analytic calculations and wrote the manuscript; ACF developed the theoretical formalism, verified the analytical methods, encouraged to investigate, supervised the findings of this work, and wrote the manuscript; RCC verified the analytical methods, and revised the manuscript; JVM developed the theoretical formalism, performed the experiment, laboratory procedures, analytic calculations and wrote the manuscript; CVC developed the theoretical formalism, performed the experiment, laboratory procedures, analytic calculations and wrote the manuscript; MFM verified the analytical methods, and revised the manuscript; LEAB verified the analytical methods, encouraged to investigate, coordinate the project and supervised the findings of this work. All authors discussed the results and contributed to the final manuscript.

Conflicts of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary Material

The following online material is available for this article:

Figure S1 – Pluviometry of Eusebio Municipality during the study period.

Figure S2 – Study area in the Pacoti River mangrove.

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