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Spatial and Seasonal Variation of Species Richness and Biomass of Macroalgae (Rhodophyta) on Mangrove Roots on the Brazilian Amazon Coast

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ABSTRACT

Mangrove forests are a relevant coastal ecosystem, and Brazil holds the second-largest mangrove area worldwide, with over two-thirds of it located in the Amazon region. However, despite their singular environmental characteristics and ecological importance, macroalgal communities in Amazonian mangroves remain poorly understood. Therefore, this study investigates the composition and biomass of macroalgae from two mangrove forests on the Brazilian Amazon coast and their temporal variation. Overall, higher precipitation was observed in May and lower in September, while air temperatures were higher in November and lower in January. Estiva tidal creek exhibited higher salinity and conductivity, while Taici had higher turbidity, NO_2^-, and PO_4^{-3} levels. Seven Rhodophyta species were identified, with *Bostrychia calliptera, B. moritziana*, and *Catenella caespitosa* being the most frequent and dominant in terms of biomass across all months and substrates at both sites. Richness and biomass varied significantly across months, with the highest values observed in the dry season (September) and at the innermost site (Taici). Among the substrates, rhizophores had significantly higher biomass in Taici, whereas pneumatophores showed similar biomass across both sites. DistLM analysis indicated that salinity, precipitation, NO_2^- concentrations, and substrate type were the main drivers of macroalgal biomass. These findings highlight the significant spatial and temporal variations in environmental conditions and macroalgal biomass in mangrove ecosystems, emphasizing the need for site-specific management and conservation strategies.

1 | Introduction

Mangrove ecosystems are complex and dynamic environments situated at the interface between land and sea in tropical and subtropical regions (Alongi 2014, 2020). Although they occupy less than 1% (18.1 million hectares) of the world's coastal zones (Bunting et al. 2022), mangroves rank among the most productive ecosystems globally (Bouillon et al. 2008) and offer critical ecological services, such as shoreline protection, nutrient cycling, and carbon sequestration (Tasneem and Ahsan 2024).

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These services are especially relevant for several traditional coastal communities, which rely on mangrove systems for food, livelihood, and shelter (Carney et al. 2014).

This ecosystem is subjected to broad variations in environmental parameters, mainly due to tidal influences, river inputs, and local rainfall (Pinto et al. 2013). Therefore, the plant species are adapted to extreme salinity conditions and low soil oxygen content (Alongi 2020). Mangrove macroalgae are essential components of mangrove ecosystems, contributing to nutrient retention, primary productivity, and habitat provision for a range of organisms, including larvae, invertebrates, and fish of commercial interest (Yokoya, Pellizzari, Felício, et al. 2023). They also serve as an important carbon source due to their high primary productivity and decomposition rates (Cunha et al. 1999; Peña et al. 1999), and some species can be used as bioindicators of environmental disturbance (Miranda and Pereira 1989; Fortes 1992; Melville and Pulkownik 2006).

In mangrove ecosystems, macroalgal communities typically have low species diversity and are dominated by a few genera, mainly *Bostrychia* Mont., *Caloglossa* (Harv.) G. Martens, and *Catenella* Grev (Oliveira 1984). Several studies have already demonstrated the predominance of the Rhodophyta division in mangroves, considering their biomass and diversity; the most diverse genus (*Bostrychia* Mont.) is widely distributed (Menezes et al. 2015). These algae colonize a variety of substrates, including pneumatophores, rhizophores, seedlings, and lower trunks (Cordeiro-Marino et al. 1992). Their occurrence is influenced by environmental parameters such as salinity, light, turbidity, and nutrient availability (Eston et al. 1992; Kinne 1971). In Brazil, the current estimate of the most common macroalgae in mangroves identifies 22 species, comprising 15 Rhodophyta and 7 Chlorophyta (Yokoya, Pellizzari, Felício, et al. 2023). While some species show substrate preferences, these relationships remain poorly explored (Freire et al. 2020).

Brazilian mangroves are among the largest and best-preserved in the world (Lara 2003; Silva et al. 2011), with more than half (56.6%) located along the northern Amazon coast (Souza-Filho et al. 2009). The Amazonian mangroves are characterized by irregular geomorphology, with 23 estuaries and 30 catchment areas that drain 330,000 km^2 (Souza-Filho 2005). In this setting, mangroves thrive in ideal conditions for colonization and persistence, including a tropical, humid climate, ample freshwater, a sediment supply, and tidal mixing driven by a macrotidal regime. This combination of factors contributes to their lush development, with trees reaching heights of 30–45 m (Vale et al. 2023). These conditions create unique ecological gradients that shape the structure and distribution of associated communities, including macroalgae.

Despite its unique environmental characteristics and high economic and ecological importance, studies on Brazilian mangroves have primarily focused on evaluating distribution, seasonality, biomass variation, zonation, colonization, and succession, with limited attention given to ecological dynamics, especially in the Amazon region (Yokoya, Pellizzari, Felício, et al. 2023). Consequently, significant knowledge gaps remain regarding how environmental and spatial–temporal variability affects the structure and biomass of macroalgal assemblages in this region.

Therefore, this study aims to describe the composition, species richness, and biomass of Rhodophyta macroalgae associated with *Rhizophora mangle* (rhizophores) and *Avicennia germinans* (pneumatophores) in two Amazonian mangrove forests located in different parts of the continent (internal and external) and their temporal variation. Three hypotheses were tested: the composition and biomass of macroalgae are different between (i) mangroves (internal and external position within the estuary), (ii) substrates (rhizophores and pneumatophores roots), and (iii) different months. Thus, our results aim to contribute ecological insights into the functioning of Amazonian mangrove systems, advance the understanding of macroalgal assemblages in tropical estuaries, and support informed conservation strategies for mangroves.

2 | Materials and Methods

2.1 | Study Area

The Brazilian Amazon coast represents 35% of the country's 8500 km-long coastline (Isaac and Barthem 1995), and the Bragança coastal plain is situated in northeastern Pará State, Brazilian Amazon coast (Figure 1). The regional climate is equatorial, humid with a mean annual temperature of 25.5°C and annual rainfall of 2500 mm (Lara 2003), with a dry season from September to November when mean precipitation is near to zero, and a rainy season from January to April, when 73% of the annual rainfall occurs (Martorano et al. 1993). The main hydrodynamic features are mean tidal height variations of 4 m in a semi-diurnal cycle; although this range can reach 6 m during equinoctial spring tides (Souza-Filho et al. 2003). The Caeté and Taperaçu estuaries border the region, characterized by approximately 25 km of mangrove forests, saltmarshes, and other coastal environments (Souza-Filho and Paradella 2002; Souza-Filho et al. 2003; Santos et al. 2020, Santos et al. 2024).

The present study was conducted at two mangrove areas located on Ajuruteua Peninsula (Figure 1): (i) Taici channel (0°58′05,27″S-46°44′14,98″W)—in the innermost portion of the peninsula, with more significant freshwater influence, and (ii) Estiva channel (0°50′37″ S-46°36′36,89″W)—in the outermost portion of the peninsula, with more significant marine influence. The two work sites are formed by mixed mangrove forests, dominated mainly by *R. mangle* and *A. germinans* trees, and are approximately 20 km apart (Figure 1).

2.2 | Sampling Procedures

Bimonthly samples occurred from January to November 2010 during spring low tides along a 30 m transect perpendicular to the waterline at each site. Five sampling points (P1–P5) equidistant (5 m) from the edge of the mangrove forest towards the interior were established. Five pneumatophores and five rhizophores (cut to where macroalgae are present) were randomly

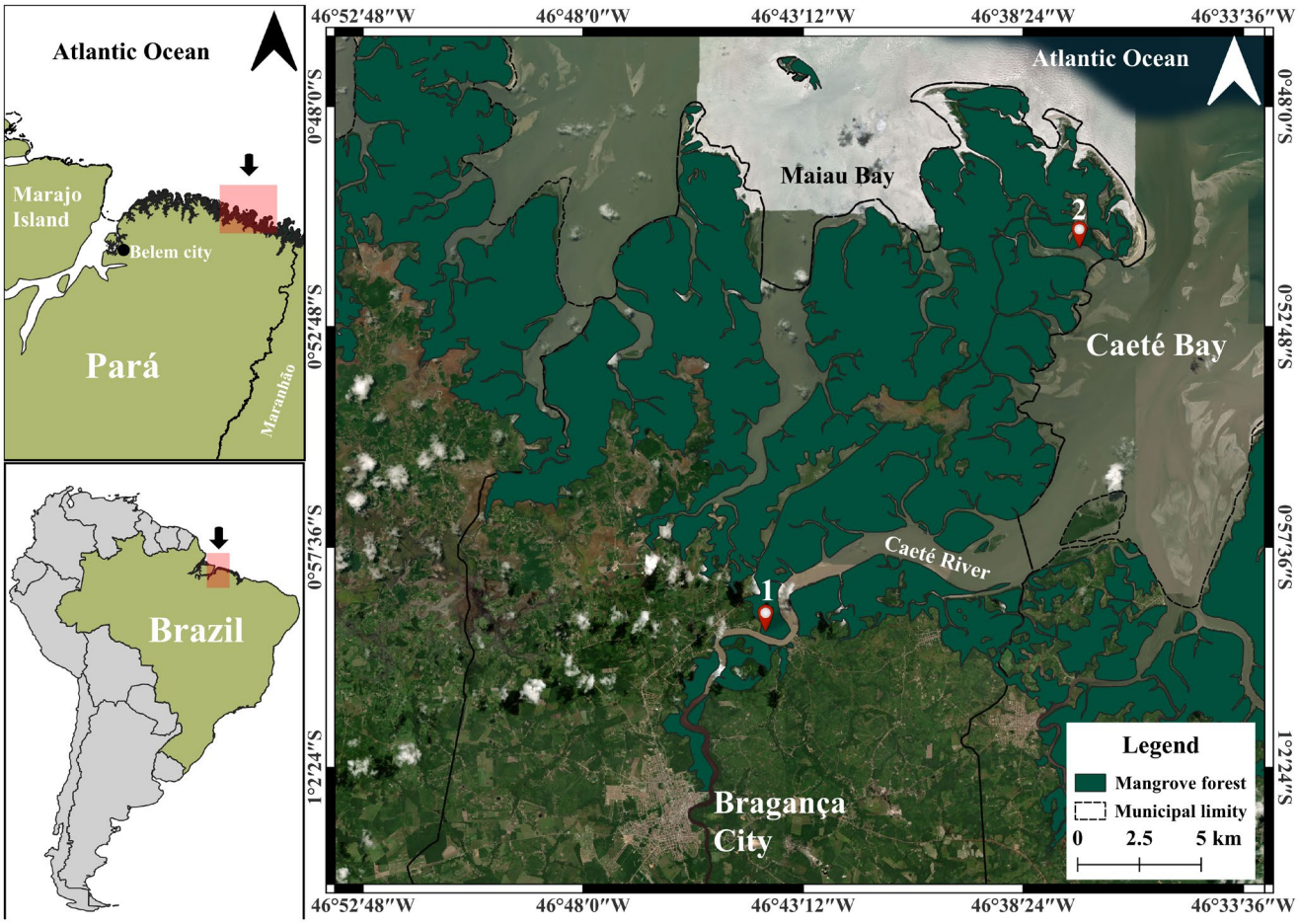


FIGURE 1 | Map of the study area locating the studied locations (1: Taici tidal channel and 2: Estiva tidal channel).

collected at each sampling point. After collection, the samples were immediately frozen for later *laboratory* analysis.

For nutrient analysis, three water samples were collected from the main tidal channel of each site during both low and high tide using a Kemmerer bottle. Samples were stored in plastic bottles that had been pre-treated with 5% hydrochloric acid and then rinsed with distilled water before being frozen for later analysis. The concentrations of nitrite (NO_2^-; mg/L), nitrate (NO_3^-; mg/L), phosphate (PO_4^{3-}; mg/L), and ammonia (NH_3; μg/L) were measured. Water temperature (°C), salinity (‰), conductivity (mS/cm), pH, turbidity (NTU), and dissolved oxygen (O_2; mg/L) were measured in situ using a multi-parameter analyzer.

2.3 | Laboratory Procedures

The estimate of the area of attachment of macroalgae on the substrates was obtained by multiplying the total length measurement and the average circumference (measurements of the top, base, and median region) of the pneumatophores and rhizophores. Subsequently, the samples of rhizophores and pneumatophores were washed with water, and the macroalgae were removed with the aid of tweezers to be then separated and identified with the help of a stereoscopic microscope and dichotomous keys (Cordeiro-Marino 1978; Fortes 1992; Caridade and Ferreira-Correia 2007), following the review by Wynne (2005). After identification, each taxonomic group was dehydrated separately in an oven at 70°C until it reached a constant weight and was subsequently weighed on an analytical balance to estimate the biomass of each species ($g\,cm^{-2}$).

After the cooled water samples reached room temperature, they were filtered to carry out the following nutrient analyses: Nitrite (NO_2^-) was estimated by the Diazotization method, Nitrate (NO_3^-) by the Cadmium Reduction method, Phosphate (PO_4^{-3}) by PhosVer 3 (CETESB 1978), and Ammonia (NH_3) by Indophenol (Paranhos 1996).

2.4 | Statistical Analyses

For each species, the frequency of occurrence (F) was determined using the Beanland and Woelkerling (1982) classification, where Abundant [$F \geq 70\%$], Common [$F < 70\%$ and $\geq 40\%$], Occasional [$F < 40\%$ and $\geq 10\%$], and Rare [$F < 10$]. Species richness (total number of species) and biomass ($g\,cm^{-2}$) were calculated for each biological sample. The assumptions of normality and homogeneity of variances were tested using the Kolmogorov–Smirnov and Levene's tests, respectively. When necessary, data were ($\log_{x+1}$) transformed to meet parametric assumptions.

Differences in biological descriptors (richness and biomass) were tested using a three-way analysis of variance (ANOVA), with site (Taici and Estiva) and month (January to November) as fixed factors, and root type (pneumatophores and rhizophores) as a random factor. Environmental variables (water temperature, salinity, pH, conductivity, turbidity, dissolved O_2, NO_2^-, NO_3^-, PO_4^{-3}, and NH_3) and root height data were analyzed between sites (Taici and Estiva) and months (January–November) using a two-way ANOVA. When ANOVA detected a significant difference, Tukey's a posteriori test was applied to identify significant pairwise differences.

A Principal Coordinate Analysis (PCO) of "area × month" was run on a Bray–Curtis similarity matrix of the fourth-root transformed species abundance data to visualize differences in macroalgae biomass in each substrate (pneumatophores and rhizophores). Species that showed Spearman correlation coefficients > 0.60 with the first two PCO axes were plotted to aid interpretation. SIMPER (Similarity Percentages) analysis was used to identify the species that contributed most (> 50%) to the dissimilarities between groups. Permutational multivariate analysis of variance (PERMANOVA) was applied to the same Bray–Curtis matrix to assess differences in community structure, using the same three-way design as ANOVA. Due to the limited number of permutations, pseudo-*p* values were adjusted using Monte Carlo simulations (Anderson and Robinson 2003). When significant, pairwise comparisons were also conducted using Tukey's post hoc test.

To identify the environmental drivers of biomass variation, a distance-based linear model (DistLM; Anderson 2001) was applied. This method assesses relationships between multivariate response data (biomass) and a set of predictor environmental variables. Resemblance matrices were based on Euclidean distance using log $(x+1)$ transformed data. Model selection was performed using a forward stepwise procedure with 9999 permutations and the AIC Information as the selection criterion (Anderson et al. 2008). A 5% significance level was considered for all analyses.

3 | Results

3.1 | Environmental Characteristics

A list of all environmental parameters is shown in Table 1. Precipitation varied between months, with the highest values recorded in May and the lowest in September. Air temperature was higher in November and lower in January (Table 1). Salinity, conductivity, turbidity, NO_2^-, and PO_4^{-3} showed significant differences between sites and months (Table 2). Overall, higher salinity and conductivity values were found at Estiva and turbidity, NO_2^- and PO_4^{-3} at Taici throughout the sampling period (Table 1). Conversely, pH, dissolved O_2, and NO^{3-} did not vary significantly between sites and months (Table 2), although slightly higher values were found at Estiva. An exception was observed for dissolved O_2 at Taici, which showed elevated levels in May and September (Table 1). Water temperature and NH_3 varied significantly only among months (Table 2). Higher water temperature values were recorded in September and November at both sites, and NH_3 was detected in May at Taici (Table 1).

3.2 | Macroalgae Richness

Seven species of the Rhodophyta division were identified: five from the genus *Bostrychia*, one from the genus *Caloglossa*, and one from the genus *Catenella* (Table S1). In general, the species *Bostrychia calliptera* (Mont.) Mont. and *Catenella caespitosa* (Wither.) L. M. Irvine, in Parker & Dixon, were the most frequently recorded, present in all months at both sites and substrates. On the other hand, *Bostrychia montagnei* Harv. and *B. tenella* (J.V. Lamour) J. Agardh were only found in January at Taici (Table 3). Among sites, Taici presented all species, while Estiva presented five (Table 3). Among substrates, *B. montagnei* was only found in rhizophores and *B. tenella* in pneumatophores (Table 3).

In general, *B. calliptera* was classified as abundant (82.24%), while *Caloglossa leprieurii* (Mont.) G. Martens was considered occasional (32.71%) in both sites. *Bostrychia radicans* (Mont.) Mont. in Orbigny, in turn, had different classifications among sites; at Estiva, it was considered an occasional species (39.22%), while at Taici, it was considered rare (1.79%). The species *B. montagnei* and *B. tenella* were considered rare in both sites. Among substrates, *B. calliptera* was classified as abundant in rhizophores in both sites and all months. However, it was classified as common in pneumatophores at both sites, except in May at Taici and November at Estiva, where it was classified as abundant (Table 3). *Bostrychia moritziana* was classified as abundant at Taici and rare at Estiva on both rhizophores and pneumatophores in all months (Table 3). *C. caespitosa* was classified as abundant in most months in both sites and substrates (rhizophores and pneumatophores). The species *B. radicans* and *C. leprieurii* were classified as common in most months, with pneumatophores and rhizophores, respectively (Table 3).

Species richness varied significantly among months [$F(5, 23) = 7.33$, $p < 0.01$], with May and September showing a significant difference from the other months (Figure 2). However, no significant differences were observed between sites and substrates [$F_{(1,23)} = 3.0$, $p > 0.05$; $F_{(1,23)} = 0.04$, $p > 0.05$; respectively], although Taici presented more species richness (7 species) than Estiva (5 species). The richness varied among roots, with *Rhizophora* roots presenting more species than pneumatophores at both sites (Figure 2).

3.3 | Macroalgae Biomass

Macroalgal biomass varied significantly between sites, months, and substrates. Overall, biomass was markedly higher at Taici ($43.94\,g\,m^{-2}$) than at Estiva ($8.49\,g\,m^{-2}$), with the highest values recorded in March at Taici and the lowest in November at Estiva (Figure 3A). Among substrates, rhizophores supported significantly greater biomass than pneumatophores at Taici, while no significant differences between substrates were observed at Estiva (Figure 3B,C). Three species accounted for the majority of macroalgal biomass: *Bostrychia calliptera* ($3.38\,g\,m^{-2}$), *B. moritziana* ($2.76\,g\,m^{-2}$), and *C. caespitosa* ($1.71\,g\,m^{-2}$), collectively contributing to over 70% of the total biomass across sites and substrates (Table 4).

TABLE 1 | Characterization of the Taici and Estiva tidal channel study sites. Seasonal variation of the environmental data.

	Months[a]					
Meteorological variables	**Jan**	**Mar**	**May**	**Jul**	**Sep**	**Nov**
Precipitation (mm)	54.6	64.8	360.0	163.4	3.4	5.8
Air Temperature (°C)	25.7	26.5	26.7	26.9	27.6	28.0

		Months					
Water variables[b]	**Sites**	**Jan**	**Mar**	**May**	**Jul**	**Sep**	**Nov**
Temperature (°C)	Taici	28.8	27.4	27	27.9	29.05	29.2
	Estiva	28.7	27.4	28	28.7	29.5	30.2
Salinity (‰)	Taici	18.9	2.5	12.4	14.5	22.9	20.5
	Estiva	30.4	14.3	22.5	32.1	38.3	36.1
pH	Taici	7.09	6.95	6.7	6.79	7.06	7.07
	Estiva	7.6	7.43	7.35	6.3	7.45	7.36
Conductivity (mS/cm)	Taici	32.55	20.45	4.5	7.77	30.45	35.85
	Estiva	49.2	23.8	35	46.8	54.55	57.45
Turbidity (NTU)	Taici	114.5	95	584.5	1151.5	119	41
	Estiva	190.66	85	35.38	39	45.5	28.5
O_2 (mg/L)	Taici	3.12	4.335	4.65	4.19	5.635	4.54
	Estiva	5.7	4.92	4.15	5.445	5.09	4.135
NO_2^- (mg/L)	Taici	0.011	0.0153	0.0106	0.0038	0.0183	0.057
	Estiva	0.005	0.004	0.004	0.003	0.003	0.004
NO_3^- (mg/L)	Taici	0.016	0.183	1.4	0.1	0.26	0.316
	Estiva	0.171	0.066	0.216	0.2	0.66	0.316
PO_4^{-3} (mg/L)	Taici	0.201	0.083	0.163	1.353	0.03	0.1
	Estiva	0.198	0.135	0.19	0.363	0.06	0.175
NH_3 (μ/L)	Taici	642.85	481.65	918.25	428.925	3.75	48.75
	Estiva	451.65	281.65	214.35	274.125	2.70	103.75

[a]Jan = January; Mar = March; May = May; Jul = July; Sep = September; Nov = November.
[b]O_2 = Dissolved Oxygen, NO_2^- = Nitrite, NO_3^- = Nitrate, PO_4^{-3} = Phosphate, and NH_3 = Ammonia.

A significant site × substrate interaction showed that the effect of substrate type on biomass varied between sites, with rhizophores supporting higher biomass than pneumatophores at Taici, but not at Estiva. The month × substrate interaction demonstrated that biomass differences between substrates were not consistent across months, being more pronounced during the rainy season. The significant site × month × substrate interaction confirmed that the influence of substrate type on seasonal biomass patterns differed between sites, highlighting a complex spatiotemporal structure in macroalgal biomass distribution.

The PCO plot revealed clear segregation of macroalgae biomass samples between study sites and substrates (Figure 4A). Axis 1 explained 72% of the total variation and distinguished samples between sites, while Axis 2 (17.4%) separated substrates (Figure 4A). At Taici, axis 1 (57.7%) also discriminated between rhizophores and pneumatophores, with *B. radicans*, *B. moritziana*, and *B. calliptera* strongly associated with pneumatophores (Figure 4B). At Estiva, substrate separation was also evident (axis 1 = 45.3%), though less pronounced (Figure 4C). In both cases, axis 2 (30.5%) captured temporal variation, likely reflecting seasonal shifts in environmental conditions.

In general, the dissimilarity between the study sites (Average dissimilarity = 41.53%) and substrates (Average dissimilarity = 29.56%) and months was due to the contributions of one species, specifically the high biomass of *B. moritziana* (see Table S1). The DistLM model identified salinity, precipitation, nitrite (NO_2^-), and substrate type as the main predictors of biomass variation, accounting for 65% of the total variance (Table 5). At Taici, biomass was primarily influenced by precipitation, salinity, NO_2^-, and substrate, while at Estiva, salinity and precipitation were the most important drivers (Table 5).

TABLE 2 | Comparison between month and site.

	Temperature (C°)		Salinity (‰)		pH		Conductivity (mS/cm)		Turbidity (NTU)		O_2 [a] (mg/L)		NO_2^- (mg/L)		NO_3^- (mg/L)		PO_4^{-3} (mg/L)		NH_3 (μ/L)	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Month	4.49	0.02	25.45	0.00	1.39	0.29	27.77	0.00	4.84	0.01	0.21	0.95	34.45	0.00	1.44	0.28	27.00	0.00	3.94	0.02
Site	2.45	0.14	149.29	0.00	2.39	0.15	159.11	0.00	12.77	0.00	0.52	0.49	125.86	0.00	0.33	0.58	8.16	0.01	4.24	0.06
Month vs. Site	0.89	0.52	6.88	0.00	0.68	0.64	7.74	0.00	5.85	0.01	0.55	0.73	33.05	0.00	1.46	0.27	13.14	0.00	1.28	0.33

Note: ANOVA-one-way (*F*-Value, *p*-value <0.05) results based on water variables.
[a]O_2 = Dissolved Oxygen, NO_2^- = Nitrite, NO_3^- = Nitrate, PO_4^{-3} = Phosphate, and NH_3 = Ammonia.

4 | Discussion

4.1 | Environmental Parameters as a Structuring Force

In the present study, salinity levels varied between months and study sites, with higher values observed at Estiva (in the lower estuary zone) and during the dry seasons (September and November). Similar results were found in previous studies in the Caeté estuary and other Amazonian estuaries where salinity increases downstream and during drier months (Barletta et al. 2005; Mesquita et al. 2006; Rosa-Filho et al. 2006; Asp et al. 2013; Rosário et al. 2016; Santos et al. 2024). The Amazonian coast has several unique features, including high volumes of river discharge and intense dry and rainy seasons, which contribute to marked fluctuations in the water salinity and hydrodynamics in coastal environments throughout the year (Pereira et al. 2016; Souza-Filho et al. 2009). Thus, the input of freshwater by the rivers and rainfall is one of the significant factors that cause variations in the salinity along the region's estuary (Asp et al. 2013).

4.2 | Species Composition and Richness Patterns

In the present study, three genera and seven species of macroalgae from the Rhodophyta division were recorded in association with rhizophores and pneumatophores in the mangroves studied. The species composition is similar to the composition recorded for other mangroves along the Brazilian coast (Yokoya et al. 2023) and worldwide (Table 5). In addition, the richness was similar on both substrates (rhizophore and pneumatophore), indicating that macroalgae in this environment associate broadly with any available surfaces, regardless of substrate type (Oliveira 1984).

Richness varied significantly between months, with September being the richest month and March having lower richness in both sites and substrates. This seasonal fluctuation is primarily linked to rainfall-driven changes in the estuary's salinity. It is well known that variations in salinity influence the abundance, composition, and distribution of macroalgae in several environments (Eston et al. 1991) and in tropical estuaries (Kinne 1971). During the rainy season (March and May), in the Amazon region, the increased freshwater input lowers salinity and increases turbidity, conditions that can suppress the development of marine-adapted macroalgae and restrict or exclude species that are exclusively marine or poorly adapted to low salinity (Kinne 1971; Correia-Ferreira and Brandão 1974; Eston et al. 1991). In contrast, the dry season (September and November) provides more stable and saline conditions, favoring higher species richness. This pattern likely reflects both reduced environmental stress and the greater physiological tolerance of dominant macroalgal species to fluctuating salinity, particularly when compared to the more extreme low-salinity conditions of the rainy season (Day Jr. et al. 2013).

Although no significant difference was observed between sites, Taici presented higher richness than Estiva. This difference might be related to the location of each mangrove. Taici is a channel located more internally on the continent. This location

TABLE 3 | Frequency of occurrence (%) of macroalgae attached to rhizophore (R) and pneumatophore (P) in the mangroves at Taici and Estiva tidal channels.

		Months[a]											
		Jan		Mar		May		July		Sep		Nov	
Species sites		R	P	R	P	R	P	R	P	R	P	R	P
Bostrychia calliptera	Taici	100	60	100	47	100	85	100	56	100	64	100	48
	Estiva	100	60	100	70	100	70	100	35	100	67	100	80
Bostrychia montagne	Taici	5	0	0	0	0	0	0	0	0	0	0	0
	Estiva	0	0	0	0	0	0	0	0	0	0	0	0
Bostrychia moritiziana	Taici	95	100	100	100	100	70	100	92	100	100	100	64
	Estiva	4	0	5	10	0	0	4	0	0	0	0	0
Bostrychia radicans	Taici	0	0	0	0	0	0	0	0	0	25	0	0
	Estiva	56	30	40	20	40	55	8	45	72	27	12	73
Bostrychia tenella	Taici	0	4	0	0	0	0	0	0	0	0	0	0
	Estiva	0	0	0	0	0	0	0	0	0	0	0	0
Caloglossa leprieurii	Taici	50	24	4	7	0	0	52	48	68	44	8	4
	Estiva	52	30	50	40	48	50	40	30	48	7	36	27
Catenella caespitosa	Taici	95	76	92	80	46	40	84	88	100	96	72	64
	Estiva	68	75	75	80	72	80	48	50	68	47	60	87

[a]Jan = January; Mar = March; May = May; Jul = July; Sep = September; Nov = November.

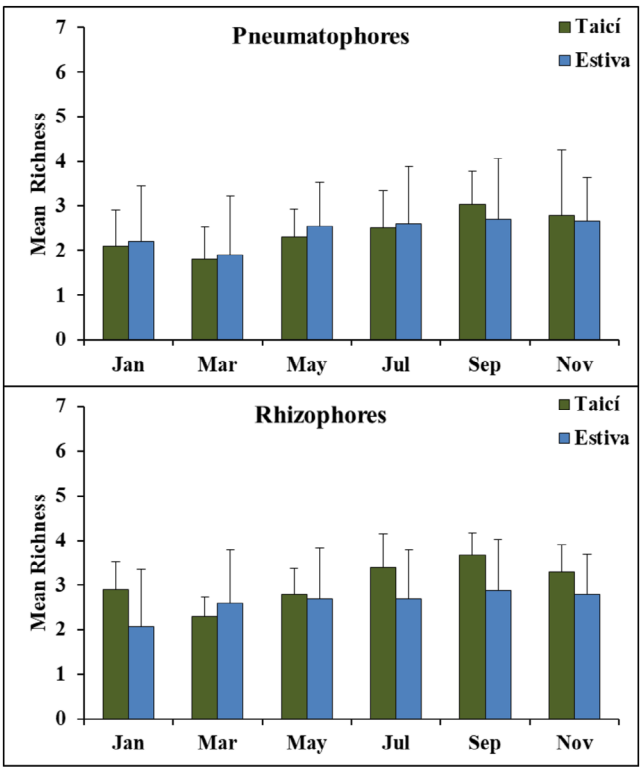


FIGURE 2 | Mean (±standard deviation) richness of macroalgae attached to rhizophores and pneumatophores in the mangroves at Taici and Estiva tidal channels.

may buffer it from wave action and marine salinity variation, promoting more stable and favorable conditions for macroalgal colonization compared to the Estiva channel, which is located in a region of the continent with more significant marine influence. A study on the occurrence of mangrove macroalgae in South Africa supports the hypothesis that the number of species is lower in waters with more significant salinity variations (Steinke et al. 2003), which was verified in the present study, where Estiva had significant differences in salinity over the months. Therefore, the reduced number of species in the sites studied is probably due to large fluctuations in local environmental forcing, such as (i) large fluctuations in salinity throughout the year, (ii) low level of water transparency, (iii) high tidal range (> 5 m), (iv) long period of flooding.

4.3 | Species-Specific Distribution and Environmental Tolerance

The most representative genera for the studied sites were *Bostrychia* and *Bostrychia*. *B. calliptera* was the most abundant species recorded in all months of the study and on all substrates. *Bostrychia* species are distributed worldwide in tropical and temperate regions, predominantly in mangroves (King and Puttock 1989). This genus is the most adapted to higher desiccation conditions (Wilcox et al. 1975), variations in emersion periods (Yokoya et al. 1999), and salinity (Borburema et al. 2020) experienced by macroalgae in mangrove areas. The species *B. calliptera* has been reported as one of the predominant species

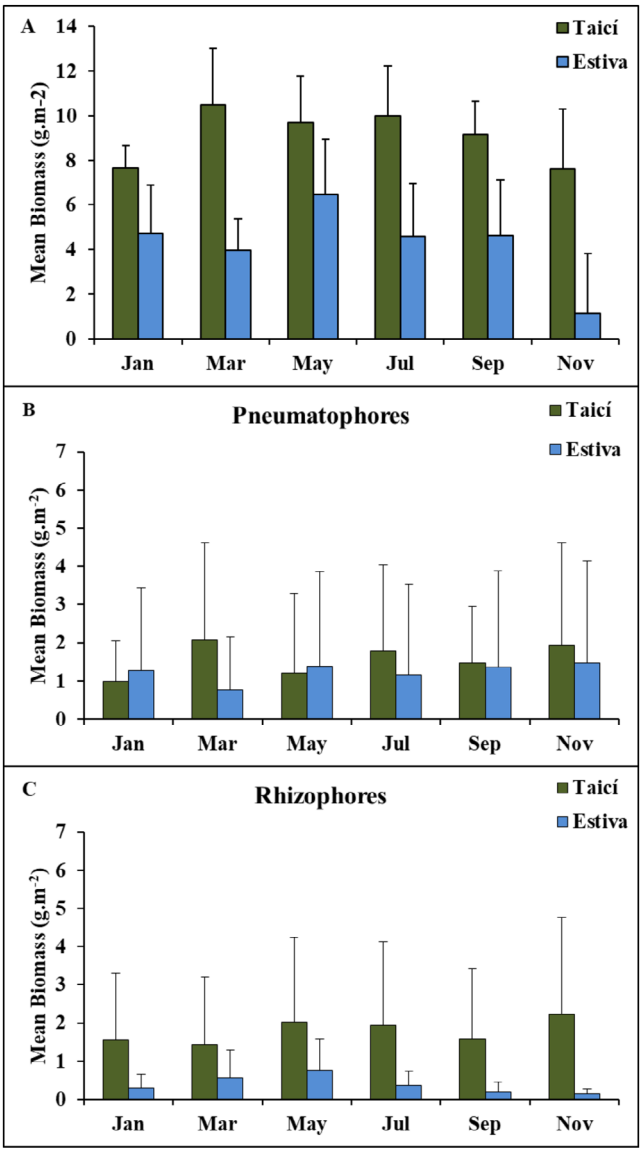


FIGURE 3 | Mean (±standard deviation) biomass (g m^{-2}) (A) of macroalgae attached to rhizophores (B) and pneumatophores (C) in the mangroves at Taici and Estiva channels.

considering the percentage cover in the majority of Brazilian mangrove macroalgal communities (Eston et al. 1991; Cunha et al. 1999; Cutrim et al. 2004; Machado and Nassar 2007; Fontes et al. 2016). Salinity tolerance in *Bostrychia* spp. occurs through the biosynthesis and storage of organic osmolytes (D-Sorbitol and D-Dulcitol) (Sanchez de Pedro et al. 2016). The ability of *Bostrychia* spp. to tolerate long continuous emersion periods (up to 6 days) (Yokoya et al. 1999) was also registered. Amazon mangroves are frequently flooded, and the Bragança mangrove peninsula is also commonly flooded, experiencing approximately 233 days of flooding per year (Souza-Filho et al. 2009). Therefore, the species that inhabit the mangroves might tolerate these variations in salinity and long periods of submersion.

Variations in the frequency of *Bostrychia* species were observed between sites. *B. moritziana* was abundant at Taici and rare at Estiva, likely due to differences in salinity, as this species prefers lower salinity and light conditions (Karsten et al. 1993), typical of the more inland Taici channel. Similar results were found in other mangroves on the Brazilian coast (Cunha and Costa 2002) and the Amazon region (Fernandes et al. 2005). Conversely, *B. radicans* was more frequent at Estiva, where intermediate salinity values prevail, and only appeared in Taici during the high-salinity month of September. This epiphytic species is widely distributed in environments with salinity levels ranging from 23 to 31 (Yarish et al. 1979), and its distribution is influenced by fluctuations in salinity (Bouzon and Ouriques 1999; Fernandes and Alves 2011). This condition was observed in most months at Estiva and in September at Taici. In turn, *B. tenella* and *B. montagnei* were considered rare both between sites and months and are also uncommon along other mangroves of the Brazilian Amazon coast, such as in Amapá (Paula et al. 1989), Maranhão (Cutrim et al. 2004; Cutrim and Azevedo 2005), and Pará (Fernandes and Alves 2011).

Regarding the genera *Caloglossa* and *Catenella*, *C. caespitosa* was abundant in Taici and common in Estiva during the rainy season, reflecting its affinity for lower salinity environments. This ecological preference is well documented across the Brazilian coast and in the Amazon mangroves (Cunha and Costa 2002; Fontes et al. 2007; Machado and Nassar 2007; Cutrim et al. 2004). In contrast, *C. leprieurii* was occasional across sites and months, consistent with its known sensitivity to desiccation and patchy distribution in mangrove environments (Oliveira 1984; Mann and Steinke 1988; Eston et al. 1992; Phillips et al. 1994, 1996; Peña et al. 1999).

4.4 | Biomass Variation and Substrate Influence

Total biomass was highest for *B. calliptera, B. moritziana*, and *C. caespitosa*, the most abundant species in the study area, which is consistent with the positive relationship between abundance and biomass (Melville and Pulkownik 2007). The results of the present study also showed that macroalgae biomass varied among the study sites, being higher in Taici than in Estiva. This difference is probably related to the structural development of mangrove forests. It is known that denser forests reduce light penetration and desiccation stress, creating conditions more favorable to macroalgal growth (Beanland and Woelkerling 1982; Almodóvar and Pagan 1971; Eston et al. 1992; Peña et al. 1999). Lower nutrient concentrations, particularly nitrite, at the Estiva channel may also explain the reduced biomass there. Nutrient availability, especially nitrogen and phosphorus, is a known limiting factor for macroalgal biomass in saline waters, particularly for Rhodophyta (Lapointe et al. 1987; Lapointe 1997, 1999; Lapointe et al. 2004; Fernandes et al. 2018).

Our results also showed that macroalgae had greater biomass in the rhizophore than in the pneumatophore substrate, with this difference being evident in Taici. This difference may be associated with the accumulation of excess sediment in the pneumatophores, as the density of pneumatophores on the forest floor promotes the retention and accumulation of sediment. Furthermore, large silt depositions in pneumatophores result in a reduction in biomass, as they reduce irradiance and gas exchange capabilities (Steinke and Naidoo 1990).

TABLE 4 | Average (±standard deviation) biomass ($g\,m^{-2}$) of macroalgae species attached to the two types of substrate *R* = rhizophore, *P* = pneumatophore) in the mangroves at Taici and Estiva tidal channels.

			Months[a]					
Species	**Sites**	**Substrate**	**Jan**	**Mar**	**May**	**July**	**Sep**	**Nov**
Bostrychia calliptera	Taici	R	2.75 ± 4.07	1.73 ± 2.75	1.46 ± 2.14	5.02 ± 3.12	3.42 ± 2.60	4.22 ± 2.15
		P	2.56 ± 5.32	1.24 ± 1.62	4.92 ± 7.55	2.34 ± 4.10	1.05 ± 1.37	1.80 ± 2.49
	Estiva	R	5.98 ± 4.84	4.79 ± 2.61	6.87 ± 4.94	6.43 ± 3.24	6.96 ± 2.60	7.39 ± 5.87
		P	0.81 ± 1.55	1.66 ± 2.20	1.86 ± 3.86	0.23 ± 0.32	0.95 ± 0.60	0.45 ± 1.09
Bostrychia montagne	Taici	R	0.15 ± 0.42	0	0	0	0	0
		P	0	0	0	0	0	0
	Estiva	R	0	0	0	0	0	0
		P	0	0	0	0	0	0
Bostrychia moritiziana	Taici	R	3.30 ± 5.00	9.86 ± 4.24	5.71 ± 4.12	4.89 ± 3.19	3.20 ± 1.30	6.90 ± 4.43
		P	4.77 ± 4.11	6.81 ± 5.29	7.37 ± 9.46	3.48 ± 3.65	3.87 ± 6.46	3.46 ± 5.18
	Estiva	R	0.08 ± 0.27	0	0	0	0	0
		P	0	0.30 ± 0.86	0	0	0	0
Bostrychia radicans	Taici	R	0	0	0	0	0	0
		P	0	0	2.32 ± 4.51	0	0	0
	Estiva	R	0.05 ± 0.08	00.01 ± 0.03	0.15 ± 0.24	0.05 ± 0.10	0.25 ± 0.29	0
		P	0.06 ± 0.16	0	0.20 ± 0.56	0.84 ± 0.94	0	0
Catenella caespitosa	Taici	R	0.89 ± 0.98	0.85 ± 1.00	0.03 ± 0.07	0.64 ± 0.95	2.05 ± 2.27	0.44 ± 0.74
		P	1.94 ± 2.01	6.18 ± 7.65	0.62 ± 1.75	5.80 ± 8.81	4.36 ± 5.39	3.43 ± 5.62
	Estiva	R	1.33 ± 1.92	2.25 ± 2.97	0.95 ± 1.4	0.40 ± 0.70	0.78 ± 1.42	1.23 ± 2.76
		P	1.10 ± 2.66	0.78 ± 0.95	1.41 ± 3.36	1.33 ± 1.88	0.90 ± 2.03	0.60 ± 0.74
Caloglossa leprieurii	Taici	R	0.34 ± 0.48	0.01 ± 0.02	0	0.09 ± 0.26	0.10 ± 0.11	0
		P	0.04 ± 0.13	0	0	0.03 ± 0.11	0.25 ± 0.54	0
	Estiva	R	0.25 ± 0.46	0.12 ± 0.24	0.33 ± 0.87	0.12 ± 0.18	0.10 ± 0.21	0.16 ± 0.27
		P	0.30 ± 0.58	0.06 ± 0.17	1.06 ± 2.71	0.34 ± 0.95	0	0.33 ± 0.80

[a]Jan = January; Mar = March; May = May; Jul = July; Sep = September; Nov = November.

Among sites at Taici, *B. moritziana* predominates on both substrates, which is certainly related to its high tolerance to the low salinity present in the waters of this channel (Karsten et al. 1993). At Estiva, *B. calliptera* predominates in the rhizophores, and *C. caespitosa* dominates pneumatophores. This difference appears to be because *Bostrychia* spp. are present even in the highest portions of the substrate, thanks to their exceptional tolerance to desiccation (Yarish and Edwards 1982; Mann and Steinke 1988). *Catenella caespitosa*, in turn, is present in the most basal portion of pneumatophores, suggesting that the size of the substrate is a relevant factor for the predominance of this species in pneumatophores, given that they remain submerged for longer and are less exposed to desiccation (Davey and Woelkerling 1985; Tanaka and Chiahara 1988).

Macroalgae productivity varied between months in the areas studied, indicating that rainfall in the region is related to the increase in biomass in the region's mangroves. Higher biomass was found in rainy months (March and May). Precipitation increases freshwater and nutrient inputs, enhancing organic matter deposition and reducing salinity (Alongi 1989; Aller and Stupakoff 1996; Geyer et al. 1996; Dittmar and Lara 2001; Schwendenmann et al. 2006; Souza-Filho et al. 2009). Thus, the decrease in salinity and increase in turbidity and nutrients in the rainiest months might act as a natural barrier to establishing algal flora throughout the Ajuruteua peninsula (Fernandes et al. 2005).

Variations in salinity influence the biomass, composition, and distribution of macroalgae in mangroves (Oliveira 1984; Eston et al. 1991). Increased salinity is often associated with increases in macroalgal diversity and biomass (Cunha and Costa 2002). However, the tolerance of *Bostrychia* (*B. calliptera* and *B. moritziana*) and *Caloglossa* (*C. caespitosa*) species to salinity variation (Bouzon and Ouriques 1999) likely enabled them to benefit from the increased resource availability during the rainy season

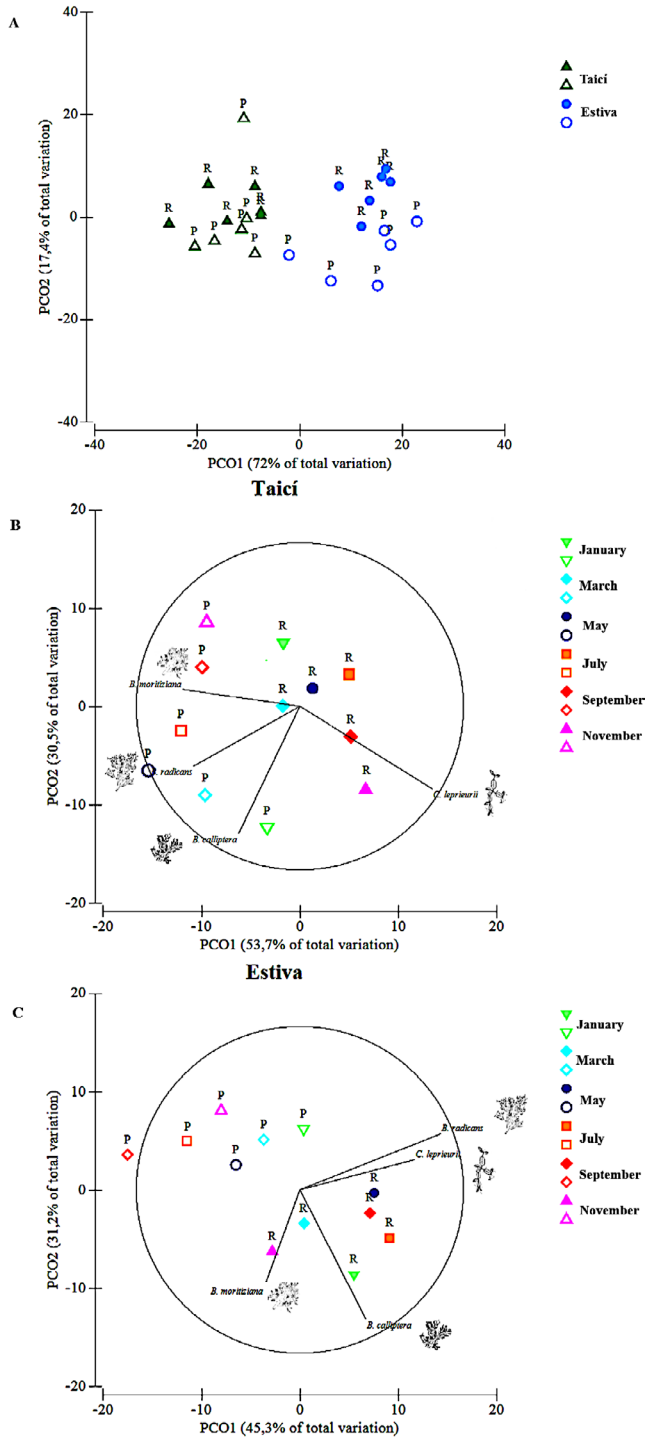


FIGURE 4 | Plots of the Principal Coordinates Analysis of the samples of the macroalgae biomass (A) collected from the two types of substrate (*R* = rhizophore, *P* = pneumatophore) in the mangroves at Taici (B) and Estiva (C) channels. The vectors represent species correlating more than 50% (based on Spearman correlation coefficients) with one of the first two PCO axes.

and reduced competition. Biomass was highest at Taici, particularly during the rainy season, attributed to increased nutrient input and reduced desiccation (Dittmar and Lara 2001; Schwendenmann et al. 2006). Species like *B. moritziana* and *C. leprieurii* also produce higher biomass at Taici during the rainy season, coinciding with peaks in nitrogen and phosphorus, which further supports the role of nutrients in driving biomass variation (Ryder et al. 1999). Rhizophores supported significantly more biomass than pneumatophores, likely due to more favorable microhabitats and reduced sediment accumulation (Steinke and Naidoo 1990). It is well known that competition for substrates available for fixation can influence the distribution and biomass of macroalgae (Melville and Pulkownik 2007). The abundance patterns of *B. calliptera, B. moritziana*, and *C. caespitosa* were similar, with their spatial and substrate-specific distributions reflecting their tolerance to emersion and light exposure (Tanaka and Chiahara 1988).

4.5 | Multivariate Patterns and Environmental Drivers

Macroalgal biomass showed significant spatial, temporal, and substrate-related variation, as evidenced by PCO and PERMANOVA analyses (Oliveira 1984; Eston et al. 1991). These results highlight the sensitivity of macroalgal communities to environmental gradients, with *B. moritziana* playing a key role in driving observed dissimilarities between sites and sampling periods (Bouzon and Ouriques 1999). The significant interaction between site, month, and substrate further highlights the complexity and interdependence of these factors in influencing biomass patterns (Cunha and Costa 2002).

Environmental variables played a key role in explaining biomass variability. DistLM analysis revealed that salinity, precipitation, nitrite, and substrate together accounted for 65% of the variation observed, indicating that a combination of physical and chemical factors regulates macroalgal growth (Dittmar and Lara 2001; Schwendenmann et al. 2006). Interestingly, while all these variables were significant at the Taici site, only salinity and precipitation were important at Estiva, suggesting site-specific differences in environmental controls (Ryder et al. 1999).

These findings reinforce previous research, which demonstrates that the interplay of multiple abiotic factors shapes the distribution and biomass of macroalgae in the mangrove ecosystem (Melville and Pulkownik 2007; Steinke and Naidoo 1990). The spatial and temporal variability in salinity and nutrient availability, especially during the rainy season, appears to create favorable conditions for species such as *B. moritziana* to increase biomass, reflecting their ecological tolerance and competitive advantage (Tanaka and Chiahara 1988).

5 | Conclusion

Our findings support the hypothesis that macroalgal biomass differs significantly between mangrove areas (Taici and Estiva), substrates (rhizophores and pneumatophores), and across months. Biomass was consistently higher at Taici, located further inland, particularly on rhizophores and during the rainy season (March and May). This pattern was associated with higher nutrient availability, reduced salinity, and forest structure favoring prolonged submersion. Furthermore, species dominance varied by site, with *B. moritziana* prevailing at Taici and *B. calliptera*

TABLE 5 | Best distance-based linear models (DistLM) fitted for macroalgae biomass against environmental variables attached to the two types of substrates (rhizophore and pneumatophore) in the mangroves at Taici and Estiva tidal channels.

Site biomass	Variables	R^2	AIC	Significance level
Taici	Precipitation (26%)[a], salinity (24%), NO_2^- (11%), substrate (5%)	0.79	31.37	$p < 0.01$—all
Estiva	Salinity (31%), pluviosity (22%)	0.75	25.34	$p < 0.01$—all
Both Sites	Salinity (21%), pluviosity (18%), NO_2^- (16%), substrate (10%)	0.83	28.80	$p < 0.01$—all

Abbreviations: AIC, Akaike information criterion; R^2, Coefficient of determination.
[a]Values in brackets mean the proportion of variability explained by each variable.

at Estiva, reflecting ecological responses to spatial and seasonal variability in environmental conditions. Additionally, the dominance of stress-tolerant species, such as *B. calliptera* and *C. caespitosa*, suggests a resilient macroalgal assemblage, while the restricted occurrence of others reflects environmental filtering. Seasonal and spatial variation in biomass underscores the role of hydrological cycles, nutrient availability, and substrate structure in shaping macroalgal communities. These results emphasize the importance of integrating local hydrological, chemical, and structural factors into conservation and monitoring strategies for Amazonian mangrove ecosystems.

Author Contributions

A.C.S.P. and M.E.B.F. conceived the ideas and designed the methodology; A.C.S.P. collected and curated the data, conducted the investigation, formal analysis, and led the original draft writing; T.M.T.S., C.F.B., and M.E.B.F. contributed to writing, review, and editing; M.E.B.F. supervised the work. All authors contributed critically to the manuscript and approved the final version for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available upon reasonable request to the corresponding authors.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** SIMPER analysis results reveal the dissimilarity of the macroalgae species that contributed most to the samples among the studied sites, substrates, and months.