From roots to burrows: how *Spartina alterniflora* (Poaceae) structure modulates brachyuran diversity in Amazonian saltmarshes

Das raízes às tocas: como a estrutura de *Spartina alterniflora* (Poaceae) modula a diversidade de Brachyura em marismas amazônicas

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Abstract: Saltmarshes dominated by *Spartina alterniflora* are highly productive coastal ecosystems that play key roles in sediment stabilization, organic matter accumulation, and the maintenance of benthic communities. While the ecological influence of *S. alterniflora* on macrofauna is well documented in temperate and subtropical regions, however, few studies about these interactions in the Amazon coast are reported. Based on that, this study evaluated the effects of *S. alterniflora* vegetation structure on the abundance, richness, and composition of Brachyuran crabs in saltmarshes at Maçarico Beach, Salinópolis, Pará, Northern Brazil. Fieldwork was conducted in June 2019 comparing two transects with contrasting vegetation zones. Vegetation attributes (above- and belowground biomass, height, organic matter content) and crab assemblage metrics (abundance, species richness, burrow density) were analyzed using ANOVA, PERMANOVA, and multivariate ordinations. Structurally complex areas with taller stems, higher root biomass, and greater organic matter content supported significantly higher crab abundance, richness, and burrow density. Community composition also varied between zones, with *Uca maracoani* and *Minuca* sp. dominating vegetated areas, while *Callinectes bocourti* was associated with less vegetated zones. These findings indicate that crab distribution in Amazonian saltmarshes is strongly associated with vegetation complexity, underscoring the ecological relevance of conserving *S. alterniflora* habitats under increasing coastal pressures.

Keywords: Wetlands. Decapoda. Macroinvertebrates. Amazon coast. Benthic ecology.

Resumo: Marismas dominadas por *Spartina alterniflora* são ecossistemas costeiros altamente produtivos que desempenham papéis fundamentais na estabilização de sedimentos, acúmulo de matéria orgânica e manutenção de comunidades bentônicas. Embora a influência ecológica de *S. alterniflora* sobre a macrofauna seja bem documentada em regiões temperadas e subtropicais, poucos estudos sobre essas interações são reportados na costa amazônica. Nesse contexto, este estudo avaliou os efeitos da estrutura da vegetação de *S. alterniflora* sobre a abundância, a riqueza e a composição de caranguejos braquiúros em marismas da praia do Maçarico, em Salinópolis, Pará, Norte do Brasil. O trabalho de campo foi realizado em junho de 2019, comparando dois transectos com zonas de vegetação contrastantes. Atributos da vegetação (biomassa aérea e subterrânea, altura e teor de matéria orgânica) e métricas da assembleia de caranguejos (abundância, riqueza de espécies e densidade de tocas) foram analisados por meio de ANOVA, PERMANOVA e ordenações multivariadas. Áreas estruturalmente mais complexas, com maior altura de caules, maior biomassa radicular e maior teor de matéria orgânica, apresentaram valores significativamente mais elevados de abundância, riqueza e densidade de tocas. A composição da comunidade também variou entre as zonas, com *Uca maracoani* e *Minuca* sp. dominando áreas vegetadas, enquanto *Callinectes bocourti* esteve associado a zonas menos vegetadas. Esses resultados indicam que a distribuição de caranguejos em marismas amazônicas está fortemente associada à complexidade da vegetação, destacando a relevância ecológica da conservação de *habitats* de *S. alterniflora* diante do aumento das pressões costeiras.

Palavras-chave: Planícies alagadas. Decapoda. Macroinvertebrados. Costa amazônica. Ecologia bentônica.

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INTRODUCTION

In tropical and subtropical estuaries, saltmarshes often occur in association with mangroves, typically occupying intertidal flats with low hydrodynamic energy (Braga et al., 2011). These environments form structurally complex habitats that sustain diverse faunal communities (Davy & Costa, 1992; Schaeffer-Novelli et al., 2023). The cordgrass *Spartina alterniflora* Loiseleur, 1807 is a pioneer species commonly established at the seaward edge of several Brazilian estuaries (Braga et al., 2009, 2011). Its extensive belowground root system enhances sediment retention and promotes organic matter accumulation, thereby modifying the physical and chemical properties of marsh substrates (Flynn et al., 1996; Netto & Lana, 1997). Such structural attributes are not only essential for the physical stability of the marsh but also exert profound ecological influences on associated macrofaunal assemblages (Lana & Guiss, 1992). Vegetation complexity shapes faunal spatial distribution by creating microhabitats, increasing habitat heterogeneity, and providing both food resources and refuge from predators (Whitcraft & Levin, 2007; Ferreira-Ramos et al., 2026).

Numerous studies have shown that vegetation characteristics (e.g. biomass, height, and root structure) are positively correlated with benthic macrofauna abundance and diversity (Rader, 1984; Lana & Guiss, 1992; Reis et al., 2019; Santos et al., 2025). In particular, the belowground biomass of *S. alterniflora* promotes the formation of burrows and shelters for crustaceans, while the accumulation of detritus from decomposing plant matter serves as a food source for deposit feeders and omnivores (Lillebø et al., 1999; Silliman & Bortholus, 2003). The result is a suite of direct and indirect interactions that link plant traits to faunal community composition and ecosystem functioning (Schaeffer-Novelli et al., 2023).

Crustaceans, particularly Brachyura, are key components of saltmarsh ecosystems (Bertness, 1985; Schaeffer-Novelli et al., 2023). Species from genera such as *Uca* Latreille, 1804, *Minuca* Bott, 1954, *Leptuca* Bott, 1973, and *Panopeus* H. Milne Edwards, 1834 are commonly associated with marsh environments worldwide (Bertness, 1985; Schaeffer-Novelli et al., 2023). These crabs are important bioturbators and often act as ecosystem engineers by modifying sediment properties, influencing vegetation growth, and contributing to nutrient cycling (Bortolus & Iribarne, 1999; Posey et al., 2003). In North America and Europe, the relationship between brachyuran crabs and *Spartina* vegetation is well established. Studies have shown that fiddler crabs (e.g. *Minuca pugnax* Smith, 1870 and *Minuca rapax* Smith, 1870) enhance plant productivity through their burrowing activity, which increases oxygenation and nitrogen availability in sediments (Szura et al., 2017).

Although saltmarsh fauna is well documented in the Northern Hemisphere (Santos et al., 2020) and along the southern and southeastern Brazilian coast (e.g. Lana & Guiss, 1991, 1992; Netto & Lana, 1996, 1997, 1999; Pagliosa & Lana, 2005), studies on Amazonian saltmarshes remain scarce. Research conducted in this region (Braga et al., 2009, 2011, 2013, 2024; Santos et al., 2020, 2025) has revealed important faunal differences across *Spartina alterniflora* vegetation gradients, but investigations specifically addressing brachyuran crabs and their functional roles are still limited. Consequently, the relationships between vegetation structure and crab assemblages in Amazonian saltmarshes remain poorly understood.

Therefore, this study evaluates how variation in the structural attributes of *S. alterniflora* (above- and belowground biomass, stem height, and organic matter content) shapes the abundance, richness, and composition of brachyuran crabs in Amazonian saltmarshes by comparing two intertidal zones with contrasting vegetation density and complexity. We hypothesize that areas with higher vegetation complexity (denser stands, taller stems, and greater root biomass) support greater crab abundance, species richness, and burrow density, and that community composition differs between areas according to vegetation structure.

MATERIALS AND METHODS

STUDY AREA

The study area is in the Atlantic Coastal Sector of North Brazil (Pará state), one of the most densely populated areas of this region (Sousa et al., 2011) with approximately 40,000 inhabitants, where the economy is based on tourism and fishing (IBGE, 2022). Furthermore, during the summer period (July) the municipality receives > 280,000 tourists (IBGE, 2022). The local climate is equatorial humid, classified as Af/Am according to the Köppen–Geiger system (Peel et al., 2007), with annual average temperature and rainfall of 26–27 °C and 2500–3000 mm, respectively, and with about 75–85% of the precipitation occurring during the rainy season (January–May) (Martorano et al., 1993). The main hydrodynamic features of the region are macrotides (4-6 m), strong coastal currents (up to 1.5 m/s) and wave energy modulated by wave attenuation on sandbanks at low tide (Monteiro et al., 2009; Pereira et al., 2009).

This study was conducted at Maçarico Beach, located in the western portion of Salinópolis city (0° 36' 49" S, 47° 21' 22" W). The beach is characterized by low exposure to oceanic energy due to its proximity to the Sampaio River (Figure 1). Its natural boundaries include the waterfront, cliffs of the Barreiras Formation, dunes, and areas of restinga vegetation (Ranieri & Robrini, 2015, 2016). Additionally, the presence of saltmarsh banks and muddy intertidal flats adjacent to mangrove forests contributes to the ecological and geomorphological complexity of the site (Ranieri & Robrini, 2015, 2016).

FIELD PROCEDURES

Samples were collected in June 2019 in the low intertidal zone of the Maçarico beach along two linear transects parallel to the waterline, 20 m apart from each other, covering two areas of differing *S. alterniflora* vegetation structure: (I) upper – located farther from the tidal edge, with denser and taller *S. alterniflora* vegetation; and (II) lower – closer to the waterline, where vegetation was sparser and shorter. For brachyuran crab sampling, in each transect, three equidistant (~10 m) sampling stations were established and all the crabs were collected manually from

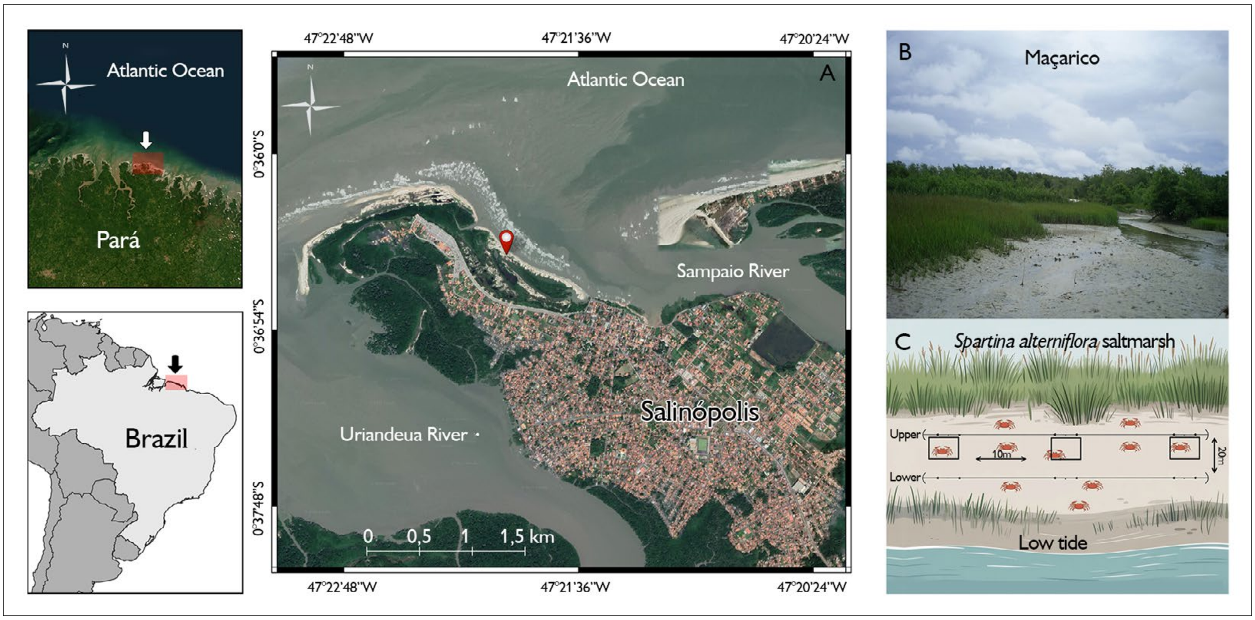

Figure 1. Map of the study area showing the location of the study areas in Salinópolis city, northern Brazil (A), the studied *Spartina* march (B) and schematic design of the sampling (C). Map: Thuareag Santos (2025).

within a 0.25 m^2 quadrat, stored in double plastic bags and fixed in 70% ethanol.

Additionally, Burrow counts were conducted within each 0.25 m^2 quadrat using a standardized search effort of five minutes per station. Counts were performed by two trained observers to minimize detection bias and ensure consistency across sampling points. All sampling occurred during spring low tide and under calm weather conditions, ensuring that burrows were fully exposed and detectability was maximized. Only burrows showing clear structural integrity (= recently maintained) were recorded to avoid including collapsed or inactive structures.

Because no direct capture–recapture validation or correlation between burrow counts and actual crab abundance was performed during fieldwork, burrow density is used here strictly as a proxy for crab activity and site occupancy, as commonly adopted in saltmarsh and mangrove studies.

Using a similar sampling design, a single plot (0.25 m^2) was randomly selected from each sampling station for the sampling of vegetation. Mean vegetation height (cm) was obtained by measuring all stems, and vegetation density was obtained by counting the number of saltmarsh stems inside each plot (Braga et al., 2011). The area in each plot was dug to a depth of 20 cm and all plant material, aboveground biomass (stems and leaves) and belowground biomass (roots and rhizomes), were removed to estimate vegetation H_2O content and organic matter (OM) (Santos et al., 2025). These samples were kept cool in the field and later frozen in the laboratory to prevent decomposition and loss of biomass until final processing in the laboratory (Santos et al., 2025).

Field activities were carried out under authorization from the Brazilian Ministry of the Environment through the Sistema de Autorização e Informação em Biodiversidade (SISBIO) (permit no. 58198-1). All sampling procedures complied with Brazilian environmental legislation and followed the guidelines established by Normative Instruction n°. 003/2014 (SEMAS-PA, 2014).

LABORATORY ANALYSIS

The biological samples were examined using a stereoscopic microscope, and the Brachyuran crabs were counted and identified to the lowest possible taxonomic level using the Identification Manual of the Brachyura (Crabs and Swimming Crabs) from the Brazilian Coast by Melo (1996) and literature review on the taxonomic classification of the group by Lima and Martinelli-Lemos (2019).

For vegetation, the aerial parts (stem, leaves, flowers, shoots) and underground parts (roots) were separated to determine the OM and H_2O contents. Saltmarsh H_2O content was estimated as water loss after drying the vegetation at 60 °C until constant weight. The saltmarsh OM content was estimated by burning 2 g of dry vegetation at 500 °C for 4 h (Braga et al., 2011).

DATA ANALYSIS

The Relative Abundance (RA) (the number of individuals of the species divided by the total number of individuals captured), density (ind/m^2), and the Frequency of Occurrence (FO) (the number of samples containing the species divided by the total number of samples) were calculated for each crab species. Crab species richness was expressed as the total number of species present in a given sample. In order to test the assumption of normality and the homoscedasticity of variance, the Shapiro–Wilk and Cochran's tests were applied, respectively. Whenever required, the values were fourth-root transformed. Differences in the crab richness and density and vegetation (area, H_2O content, OM, density, and height) were evaluated using a one-factor Analysis of Variance (ANOVA) where F represents the F-statistic and p the probability value. ANOVA was also applied to test for differences between the species densities and crab burrows between the intertidal areas.

To evaluate the effects of saltmarshes on Brachyuran crabs and validate our a priori clustering (upper and lower intertidal areas), a one-way Permutational ANOVA (PERMANOVA) based on Bray–Curtis dissimilarities of fourth root transformed abundance data, with 9,999 permutations designed with the same layout as the ANOVA. The P-values were adjusted using Monte Carlo random draws from the asymptotic permutation distribution, as the number of possible unique permutations was insufficient to generate a fully exhaustive permutation test (Anderson & Robinson, 2003). Ordination of community patterns was performed using Principal Coordinate Analysis (PCO). To identify the species that characterized each intertidal area, species that were correlated (Spearman's coefficient) with one of the first two axes by more than 60% were plotted in each PCO. This threshold follows standard practices in multivariate ecological analyses (Clarke & Gorley, 2015), as it highlights species with meaningful contributions to the ordination structure while avoiding excessive graphical clutter. The contribution of each taxon to the similarity and dissimilarity found among the groups was assessed using the similarity percentage (SIMPER) routine. The relationships between biological (crab species richness, density and burrow density) and vegetation parameters (biomass, height, OM) were evaluated using Spearman's rank correlation coefficient.

RESULTS

VEGETATION STRUCTURE

Marsh density showed no significant differences between areas (Table 1). In general, the vegetation structure varied significantly between the Upper and Lower transects (Table 1). Mean aboveground dry biomass was significantly higher (ANOVA: $F = 4.31$; $p = 0.02$) in the Upper transect (547.3 ± 62.1 g/m^2) than in the Lower (289.6 ± 41.5 g/m^2), and the same pattern was observed for belowground biomass (673.8 ± 78.4 g/m^2 *versus* 382.7 ± 56.2 g/m^2; ANOVA: $F = 11.27$; $p = 0.03$).

Stem height was significantly higher in the Upper area than in the Lower. Conversely, root length was greater in the Lower area compared to the Upper (Table 1). Overall, the H_2O content was consistently higher in the Lower area, both in stems and roots. In contrast, stem organic matter content was higher in the Upper area than in the Lower, while root organic matter did not differ significantly between areas (Table 1).

Table 1. Vegetation structural parameters (mean ± SD) of *Spartina alterniflora* in the saltmarsh intertidal areas (Upper and Lower) at Maçarico beach (Pará, northern Brazil). Results of one-way ANOVA are shown; significant differences ($p < 0.05$) are indicated with an asterisk.

Factors	Area	Mean (± SD)	Upper x Lower	
			F	p
Stem height (cm)	Upper	43.51 ± 1.09	14.85	0.00*
	Lower	35.55 ± 1.14		
Root size (cm)	Upper	21.91 ± 1.2	6.78	0.01*
	Lower	27.32 ± 1.17		
Marsh density (ind/m^2)	Upper	4.88 ± 1.38	0.38	0.55
	Lower	4.44 ± 1.36		
Steam H_2O content	Upper	22 ± 1.34	16.42	0.00*
	Lower	40.37 ± 1.31		
Root H_2O content	Upper	26.41 ± 1.68	4.85	0.04*
	Lower	39.2 ± 1.3		
Stem OM	Upper	0.47 ± 0.05	6.09	0.02*
	Lower	0.50 ± 0.13		
Root OM	Upper	0.83 ± 0.18	0.86	0.63
	Lower	0.8 ± 0.17		

CRAB ASSEMBLAGES: COMPOSITION AND SPATIAL DISTRIBUTION

In general, burrow density was significantly higher in the Upper area (mean 36.3 ± 5.1 burrows/m^2) than in the Lower area (22.1 ± 4.8 burrows/m^2). Similarly, higher crab density and richness were found in the Upper area (Figure 2).

A total 519 crab specimens were collected during this study (Table 2), corresponding to six species and distributed into three families: Ocypodidae (three species), Grapsidae (two species) and Panopeidae (one species). Among the species, *Uca maracoani* (Latreille, 1802) was the most abundant and frequent species overall (RA = 35.26%; FO = 100%), followed by *Minuca* sp. (RA = 29.47%; FO = 72%) and *Leptuca cumulanta* (Crane, 1943) (RA = 27.93%; FO = 65%). All the other species had low abundances and were infrequently recorded on the saltmarsh.

Overall, significant differences in the density were found between the areas for *U. maracoani* ($F_{(1,17)} = 129.73$; $p < 0.05$), *Minuca* sp. ($F_{(1,17)} = 71.32$; $p < 0.05$) and *Acantholobulus bermudensis* (Benedict & Rathbun, 1891) ($F_{(1,17)} = 4.00$, $p < 0.05$) with higher density was found in the Upper area, and for *Callinectes bocourtes* (A. Milne-Edwards, 1879) ($F_{(1,17)} = 12.46$, $P < 0.05$) with higher density was found in the Lower area (Figure 2). Although no significant differences in the density of *L. cumulanta* ($F_{(1,17)} = 1.60$; $P > 0.05$) and *Pachygrapsus gracilis* (Saussure, 1857) ($F_{(1,17)} = 2.43$; $P > 0.05$), higher values were found in the Upper area for *L. cumulanta* and for *P. gracilis* in the Lower area (Figure 3).

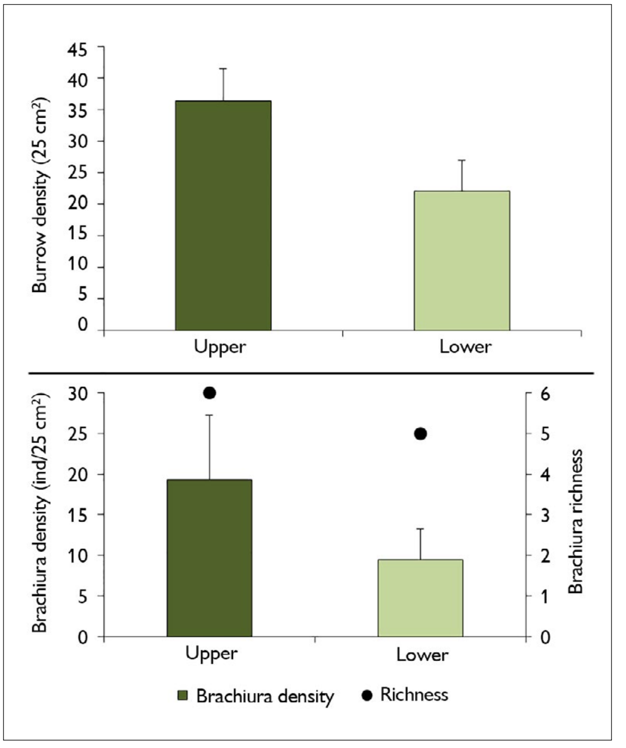

Figure 2. Burrow density (A), mean (± SD) density and richness (B) of brachyuran crab across the upper and lower intertidal areas in the Amazonian saltmarshes.

The PCO plot clearly distinguished the Brachyura samples between the study areas (Figure 4). Axis 1 explained 68.3% of the variation in the data and was responsible for separating the areas. On the positive side of this axis, crab species such as *U. maracoani*, *Minuca* sp., *P. gracilis*, and *A. bermudensis* were best correlated with the Upper area, while *L. cumulanta* and *C. bocourti* were associated with the Lower transect (Figure 4).

Table 2. Mean abundance (± SD) of crab species in the upper and lower intertidal zones of the Amazonian salt marshes.

Species	Upper	Lower
Uca maracoani	16.11 ± 1.17	7.33 ± 1.66
Leptuca cumulanta	7.33 ± 1.66	8.77 ± 1.2
Minuca sp.	12.88 ± 1.23	4.11 ± 1.57
Pachygrapsus gracilis (Saussure, 1858)	1.88 ± 1.87	0.77 ± 1.32
Callinectes bocourti A. Milne-Edwards, 1879	0.11 ± 1	1.11 ± 1.44
Acantholobulus bermudensis (Benedict & Rathbun, 1891)	0.33 ± 1	0

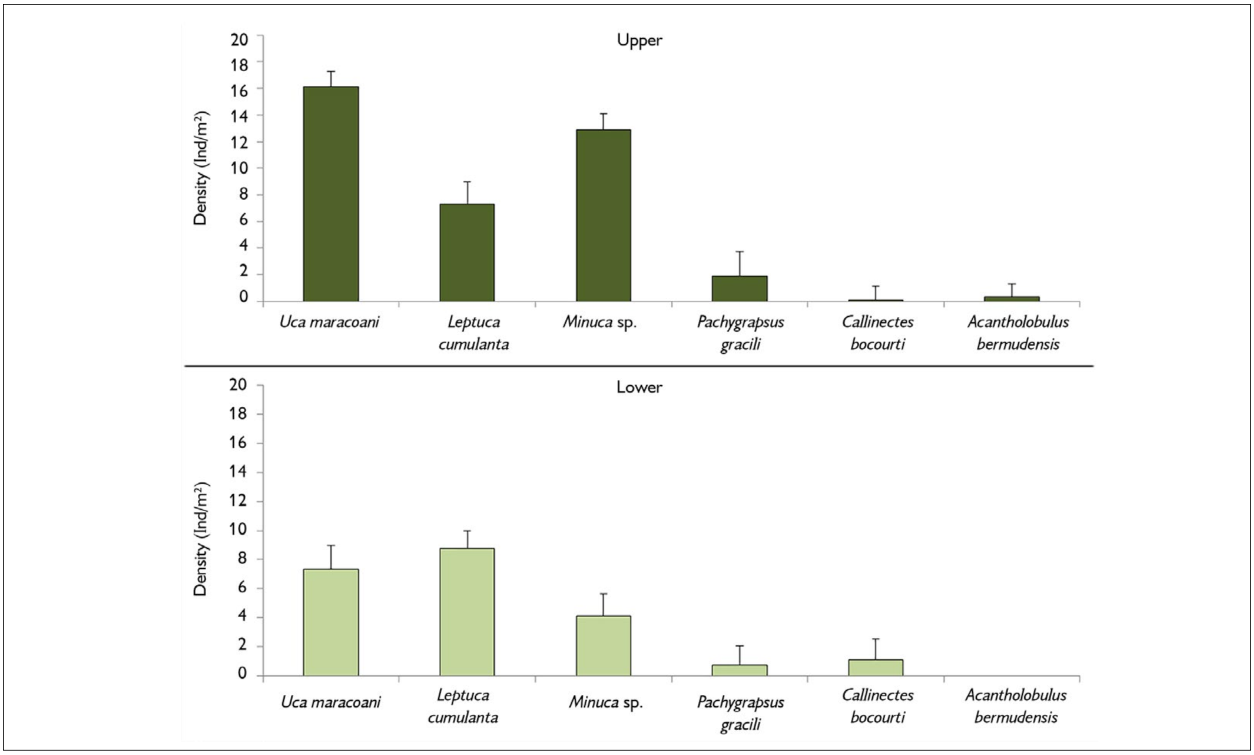

Figure 3. Density (ind/25 cm^2) of the most abundant crab species across Upper and Lower intertidal areas at Maçarico beach (Pará, northern Brazil).

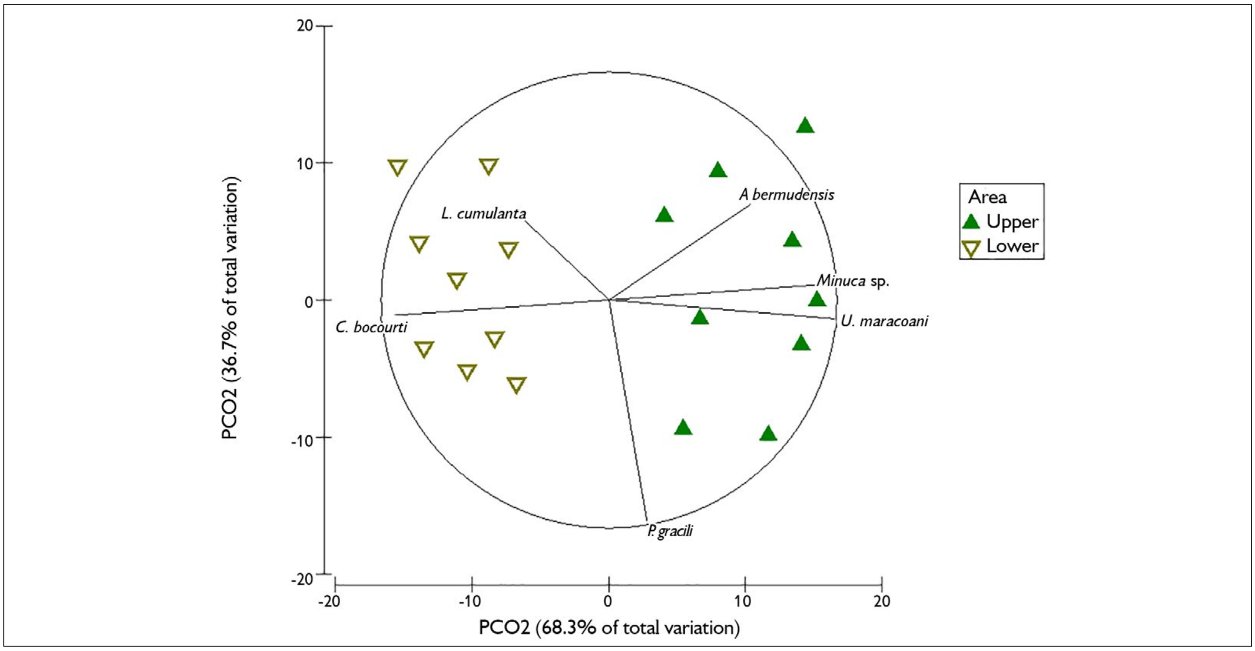

Figure 4. Principal Coordinates Analysis (PCO) of brachyuran assemblages in Upper and Lower intertidal areas based on Bray–Curtis similarity of square-root transformed data.

PERMANOVA results showed significant differences in spatial between study areas (*pseudo*-F = 3.76; $p_{(perm)} = 0.01$; $p_{(Monte\ Carlo)} = 0.001$). SIMPER analysis indicated a mean dissimilarity of 94.36% between areas, with *C. bocourti* and *A. bermudensis* being the main contributors to this dissimilarity. Within each area, similarity was largely explained by the dominance of *U. maracoani*, *Minuca* sp., *A. bermudensis* and *P. gracilis* in the Upper area (90.95% cumulative contribution), and by *C. bocourti* and *L. cumulanta* in the Lower area (92.5%).

BIO-ENV analysis indicated that the root length, above- and belowground biomass, and organic matter content were the best match with the structure of the brachyuran community ($r = 0.586$; $p < 0.05$). Linear regression analyses revealed significant positive correlations between crab abundance and several vegetation parameters, particularly belowground biomass ($R^2 = 0.68$, $p < 0.01$), aboveground organic matter ($R^2 = 0.62$, $p < 0.05$), and stem height ($R^2 = 0.55$, $p < 0.05$). Burrow density was also strongly correlated with root biomass ($R^2 = 0.73$, $p < 0.01$). Species-specific analyses further indicated that *C. bocourti*, *P. gracilis*, *A. bermudensis*, *L. cumulanta*, *U. maracoani*, and *Minuca* sp. all exhibited significant relationships with vegetation variables such as stem height and aboveground organic matter content (Table 3).

DISCUSSION

The results of this study demonstrate that the structural attributes of *Spartina alterniflora* vegetation exert a strong influence on the abundance, richness, and spatial distribution of brachyuran assemblages in Amazonian saltmarshes. Structurally complex areas, characterized by taller stems, greater above- and belowground biomass, and higher organic matter content, supported more abundant and diverse crab communities, as well as higher burrow density. These findings reinforce the role of vegetation complexity as a primary ecological filter in intertidal systems, shaping faunal communities through modifications of sediment stability, hydrodynamics, and microhabitat availability.

Table 3. Pearson correlation coefficients (r values) for linear regression between marsh variables and crab species between the intertidal areas (upper and Lower) (X = absence of specimen; * $p < 0.05$).

Plant variable	Area	*Uca maracoani*	*Leptuca cumulanta*	*Minuca* sp.	*Pachygrapsus gracili*	*Callinectes bocourti*	*Acantholobulus bermudensis*
Stem length	Upper	-0.1107	-0.0195*	-0.0351*	-0.1414	0.0636	-0.1427
	Lower	0.1342	0.0519	0.3523	-0.0105*	0.0445*	X
Root length	Upper	-0.1411	0.0027*	0.2326	-0.1396	-0.1342	0.0513
	Lower	0.1647	0.0083*	0.2543	0.1532	0.0680	X
Marsh density	Upper	-0.1260	-0.1132	0.0290*	0.1431	0.0767	-0.1307
	Lower	0.1753	-0.0568	0.0594	0.2061	-0.0487*	X
Steam H_2O content	Upper	-0.0975	-0.1420	0.0664	-0.0737	-0.1379	-0.0944
	Lower	-0.0434*	0.4958	0.0739	0.0983	0.3240	X
Root H_2O content	Upper	0.3095	-0.1002	-0.1184	-0.1199	0.5502	0.1355
	Lower	0.3142	0.3368	0.0804	-0.1356	-0.0671	X
Stem OM	Upper	0.0350*	-0.1426	0.0290*	-0.0979	0.0148*	-0.1034
	Lower	-0.1257	-0.1396	0.0729	0.1848	0.1478	X
Root OM	Upper	-0.1023	0.1016	0.1752	-0.0136*	0.1627	-0.1405
	Lower	0.4143	-0.1375	0.1353	0.1687	0.0221*	X

Amazonian coastal environments are highly dynamic due to macrotidal regimes, strong hydrodynamic forcing, and intense seasonal freshwater inputs (Dittmar & Lara, 2001; Souza-Filho et al., 2009; Santos et al., 2026). As a result, saltmarshes along this coastline are subjected to marked variability in environmental drivers such as sediment moisture, organic matter accumulation, inundation frequency, and oxygen penetration into porewaters (Levin & Talley, 2000). These abiotic factors play a major role in shaping benthic invertebrate communities, modulating habitat suitability for both burrowing and mobile crab species.

In the present study, the environmental contrasts between the Upper and Lower intertidal zones reflect the influence of key abiotic gradients that characterize Amazonian macrotidal systems (Dittmar & Lara, 2001; Souza-Filho et al., 2009). The Lower zone, positioned near the tidal edge, exhibited higher stem and root water content, indicating prolonged inundation and reduced sediment drainage, conditions typical of more exposed environments that result in softer and more saturated substrates (Levin & Talley, 2000). In contrast, the Upper zone, subjected to shorter inundation periods, displayed greater above- and belowground biomass, taller stems, and higher aboveground organic matter content, characteristics consistent with more stable and better-drained sediments that favor detritus retention and accumulation (Braga et al., 2009, 2011, 2013, 2024).

Although vegetation density did not differ significantly between zones, the higher organic matter content in stems and the greater biomass recorded in the Upper zone suggest that differences in sediment stability and hydrodynamic energy, rather than density alone, drive the spatial distribution of organic matter. This interpretation aligns with the well-established influence of hydrodynamic conditions on the deposition and retention of fine sediments and detrital material in saltmarsh systems (Adam, 1990; Davy & Costa, 1992). In more energetic areas, such as the Lower zone, stronger currents and wave action likely limit long-term organic matter accumulation despite the presence of *Spartina* (Santos et al., 2020). Conversely, the relatively sheltered conditions of the Upper zone favor detritus deposition, a pattern similarly documented in other Amazonian estuarine environments (Braga et al., 2011; Santos et al., 2025).

Overall, these findings indicate that the environmental heterogeneity observed between Upper and Lower intertidal marshes at Maçarico is shaped principally by hydrodynamic exposure, inundation regime, and sediment moisture, factors that in turn influence vegetation structure and the spatial distribution of brachyuran crabs. As reported for other regions, saltmarshes act as plastic coastal features whose sediment and vegetation characteristics are tightly linked to local hydrodynamics (Isacch et al., 2006; Braga et al., 2011, 2013). In our system, these abiotic gradients mediate habitat suitability and contribute directly to the observed patterns of species distribution, abundance, and burrow density.

The crab assemblage recorded included representatives of Ocypodidae (*U. maracoani*, *Minuca* sp., *L. cumulanta*), Grapsidae (*P. gracilis*), Panopeidae (*A. bermudensis*), and Portunidae (*C. bocourti*). This composition is common in Brazilian saltmarshes (Checon et al., 2023) and this taxonomic diversity illustrates the functional mosaic of Amazonian saltmarshes. Ocypodids dominated the community, as expected, since they are recognized as ecosystem engineers whose burrowing activity directly affects sediment structure and nutrient cycling (Bertness, 1985; Bortolus & Iribarne, 1999). The predominance of *U. maracoani*, a large-bodied fiddler crab, has also been reported in other regional studies (Braga et al., 2009, 2011; Santos et al., 2020), and is related to its strong burrowing capacity and tolerance to tidal inundation (Szura et al., 2017). Their dominance in vegetated areas suggests positive feedback between vegetation and crab activity: denser *Spartina* stands provide food and shelter, while crab burrows improve sediment conditions and organic matter turnover, ultimately favoring plant productivity (Bertness, 1991; Raposa et al., 2018).

Smaller-bodied fiddler crabs species such as *Minuca* sp. and *L. cumulanta* also reached high abundances, reflecting their ecological plasticity and ability to exploit both vegetated and more exposed intertidal zones (Iribarne et al., 1997). Similar patterns have been observed in subtropical saltmarshes of southern Brazil (Bonnet et al., 1994; Netto & Lana, 1997) and in South Atlantic marshes (Iribarne et al., 1997). Less abundant species, including *A. bermudensis* and *P. gracilis*, add to the functional heterogeneity of saltmarsh assemblages, with the former associated with fine, organic-rich sediments and the latter showing generalist habits and mobility across substrates (Melo, 1996). The presence of *C. bocourti* in higher densities in the lower area is particularly relevant, as portunid crabs are usually associated with sandy/muddy or open substrates (Wolff et al., 2000). Their occurrence in saltmarshes suggests the use of these habitats as feeding or nursery grounds, as also reported in Amazonian estuaries (Braga et al., 2009).

Patterns of species distribution across areas provide evidence of niche partitioning mediated by vegetation structure. While *U. maracoani* and *Minuca* sp. were more abundant in densely vegetated zones (upper area), *C. bocourti* and *P. gracilis* showed a stronger association with less vegetated areas (lower area). Such spatial segregation is consistent with global studies reflecting the ability of vegetation to regulate crab assemblages by altering food availability, predation risk, and sediment properties (Bertness, 1985; Whitcraft & Levin, 2007).

The positive relationship observed between belowground biomass and burrow density confirms the central role of root systems in modifying sediment properties and providing suitable microhabitats for burrowing (Levin & Talley, 2000). Similar trends have been described in temperate marshes of the United States, where fiddler crab activity enhances sediment aeration and nitrogen availability, increasing *Spartina* productivity (Bertness, 1991). In European marshes dominated by *Spartina. maritima* (Curtis) Fernald, 1916 and *Spartina anglica* C.E. Hubbard, 1968, higher vegetation complexity promoted organic matter retention and favored macrofaunal assemblages (Lillebø et al., 1999). In South American marshes, particularly in Argentina and Uruguay, studies with *Leptuca uruguayensis* (Nobili, 1901) revealed reciprocal effects, where crab burrows influenced sediment drainage and plant growth (Iribarne et al., 1997; Bortolus & Iribarne, 1999). These global comparisons reinforce that the plant–crab relationship is an ecological pattern consistently observed across biogeographic regions.

Despite these similarities, Amazonian saltmarshes present unique features that distinguish them from temperate and subtropical systems (Braga et al., 2011; Santos et al., 2020, 2025). Macrotidal influence, marked rainfall seasonality, and close interaction with extensive mangroves shape local sediment and vegetation dynamics (Santos et al., 2025). While temperature seasonality regulates benthic patterns in southern Brazil and in the North Atlantic (Netto & Lana, 1997; Flynn et al., 1996), rainfall and fluvial input appear to be more determinant in Amazonian marshes (Santos et al., 2025). These regional singularities highlight the need for local studies to complement global frameworks.

Overall, our findings demonstrate that Amazonian saltmarshes support diverse and functionally important crab assemblages, strongly mediated by vegetation complexity. By integrating local results with and global studies, we reinforce that conserving *Spartina alterniflora* marshes is crucial not only for maintaining brachyuran biodiversity, but also for sustaining ecological processes such as sediment bioturbation, nutrient cycling, reproduction, and nursery functions that are vital at local and global scales.

Limitations of the present study must be acknowledged. Because sampling was conducted only once and under a single set of tidal and meteorological conditions, our dataset represents a snapshot of a highly dynamic saltmarsh system. As such, temporal variability in crab activity, vegetation structure, and sediment properties could not be assessed, and causality cannot be inferred from the patterns observed. In addition, several potentially important environmental drivers were not measured in this study, including microtopography, sediment granulometry, salinity gradients, human disturbance, and predator presence. These factors may also influence crab assemblages and could contribute to the spatial patterns observed here.

Nevertheless, the spatially structured sampling design and the integration of multiple vegetation metrics with faunal data provide a robust basis for identifying consistent associations within the study area. We recommend that future studies incorporate temporal replication across seasons and tidal phases to strengthen the generality and mechanistic interpretation of vegetation–faunal interactions in Amazonian saltmarshes.

CONCLUSIONS

This study provides an exploratory evaluation of spatial patterns linking vegetation structure and brachyuran assemblages within an Amazonian saltmarsh. Although based on a single sampling event, the results reveal consistent associations between inundation gradients, sediment conditions, and *Spartina alterniflora* attributes, particularly belowground biomass and organic matter content which correspond to differences in crab abundance, species richness, and burrow density. These patterns suggest that local vegetation architecture and environmental conditions may act as important correlates of crab habitat use, supporting the idea that structurally complex saltmarsh zones can serve as favorable areas for foraging, refuge, and occupation by multiple brachyuran species.

Because the study relies on a single-time survey, the relationships identified here should be interpreted as indicative rather than mechanistic. Nevertheless, the dataset contributes valuable baseline information for a region where saltmarshes remain severely understudied and highlights the potential role of *S. alterniflora* marshes in supporting faunal assemblages and sediment-related processes in tropical estuarine environments. Future research incorporating temporal replication, expanded environmental measurements, and experimental approaches will be essential to clarify underlying mechanisms and to strengthen ecological inferences regarding vegetation–faunal interactions in Amazonian saltmarshes.

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AUTHORS' CONTRIBUTION

S. de B. Neves Neto contributed with formal analysis, methodology, investigation, and writing (original draft); C. F. Braga contributed with project administration, conceptualization, data curation, supervision, and writing (review and editing); and T. M. T. dos Santos contributed with supervision, validation, visualization, and writing (review and editing).