Macroalgae morphological complexity affects the functional diversity of epifaunal annelid assemblages

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Abstract

Host structural complexity influences the diversity of associated epifaunal species, but its role in shaping functional trait diversity remains underexplored. We developed a trait-based framework to assess whether macroalgal structural complexity significantly influences the functional assembly of marine annelid epifauna in a sandstone reef system at Enseada dos Corais Beach (NE Brazil). Sampling was conducted in December 2018, February 2019, April 2019, and June 2019. Ten fronds from each of four macroalgal species—*Gelidiella acerosa* and *Palisada perforata* (corticated), *Padina gymnospora* and *Ulva lactuca* (foliose)—were collected to describe the associated annelid fauna. Structural complexity was quantified using the interstitial space index (ISI), height, and the fractal dimensions of frond area (Da) and perimeter (Dp). Based on body length, feeding strategy, and larval development, the functional trait diversity of annelid assemblages was analyzed using Rao's Quadratic Entropy (Rao's Q) and RLQ analysis. Corticated algae species hosted more functionally dissimilar annelid assemblages than foliose ones. Moreover, morphological traits of macroalgae influenced epifaunal functional trait composition, particularly during the rainy season, when hydrodynamics are more intense. Our findings thus supported the hypothesis that increased habitat complexity positively influences functional trait diversity in marine macroalgal phytal communities.

Keywords: Trait-Based Approach, Benthos, Polychaeta, Habitat complexity.

Introduction

The critical role of habitat structure in shaping community diversity has been recognized for a long time in ecological literature (Tokeshi & Araraki, 2012; Carvalho & Barros, 2017). This concept encompasses both the qualitative and quantitative aspects of spatial structuring, following the paradigm that greater habitat complexity provides more microhabitats and ecological niches, ultimately supporting higher biodiversity (Tokeshi & Araraki, 2012; Stein et al., 2014; Carvalho & Barros, 2017; LaRue et al., 2023). Habitat structure is typically described in terms of three key components: scale, heterogeneity, and complexity (Carvalho & Barros, 2017; LaRue et al., 2023). Complexity refers to the multidimensional variation in structural attributes within an environment, while heterogeneity represents a single facet of habitat complexity (Carvalho & Barros, 2017; LaRue et al., 2023). Numerous studies, especially from marine and freshwater systems, have quantified the influence of habitat complexity and heterogeneity on species diversity at local scales, consistently revealing a strong positive effect (Dean & Connel, 1987; Christie et al., 2009; Stein et al., 2014; Carvalho & Barros, 2017; Torres-Pulliza et al., 2020).

Phytal ecosystems, characterized by dense assemblages of macroalgae and macrophytes in shallow coastal waters, play a crucial role in sustaining high ecological productivity and biodiversity (Christie et al., 2009; Stagnol et al., 2013). However, they are increasingly threatened by climate change and various human-induced impacts (Stagnol et al., 2013). These vegetated habitats provide shelter and resources for multiple animal species, acting as natural architects of habitat structure (Gee & Warwick, 1994; Christie et al., 2009). Such habitat engineers might exhibit a wide variety of morphologies, which can be summarized into distinct functional groups based on their chemical, reproductive, and morphological traits (Gee & Warwick, 1994; Steneck & Dethier, 1994; Balata et al., 2011; Gan et al., 2019). Two recurrent architectural groups have been recognized based on macroalgae frond morphology: (i) foliose species, with broad blades with none to few branching (Fig. 1a), and (ii) corticated species, with stiff, highly ramified thalli (Fig. 1a). Corticated forms supply a more intricate three-dimensional matrix than their foliose counterparts (Fig. 1a) (Steneck & Dethier, 1994; McAbendroth, 2005; Dibble & Thomas, 2006; Gan et al., 2019; Craveiro & Rosa-Filho, 2024).

Dean and Connell (1987) proposed three non-exclusive mechanisms by which increasing algal complexity (Fig. 1a) can raise the diversity of resident epifauna: (i) the protection effect – complex fronds block visual or tactile detection by predators, reducing predation-induced mortality; (ii) the sheltering effect – interstices dampen physical stressors such as wave action; (iii) the filtering effect – intricate matrices slow water flow, trapping larvae or suspended food particles and enhancing colonization. These mechanisms are linked to macroalgae morphology, playing key roles in the assembly process of epifaunal communities, as they can buffer the effects of environmental severity, such as hydrodynamics, and negative biological interactions, including predation and resource competition (Dean & Connell, 1987; Christie et al., 2009).

Previous studies have shown that higher structural complexity of host macroalgae supports greater epifaunal abundance, diversity, and biomass (Gee & Warwick 1994; Veiga et al. 2014; Pérez-García et al. 2015; Gan et al. 2019; Waren et al. 2019; Duarte et al. 2020a, b; Craveiro & Rosa-Filho 2024). However, only a few investigations have tested this prediction using a functional trait–based approach, and those indicate that host complexity positively influences epifaunal functional diversity (Barbosa et al., 2019; Duarte et al., 2020a; Katsiaras et al., 2022). Moreover, this relationship may exhibit important nuances because a more complex corticated architecture can impose spatial constraints on larger-bodied adult epifaunal species (Dean & Connell, 1987; Gee & Warwick, 1994). Therefore, a well-designed study employing specific functional traits linked to hypotheses about the role of structural complexity could enhance our understanding of how macroalgal morphology influences the assembly of associated communities. By varying experimental designs, focal species, and geographic regions, such research would allow broader generalization of patterns in this critical component of coastal marine ecosystems.

Marine annelids, particularly polychaetes, are among the most diverse groups inhabiting the ocean floor, performing many ecological functions and exhibiting a remarkable array of forms and life strategies (Rouse et al., 2022). Notably, these animals are prevalent in macroalgal epifaunal communities (Bailey-Brock et al., 1980; Rossbach et al., 2021). Their functional traits - defined as morphological, phenological, and physiological traits indirectly or directly related to fitness (Violle et al., 2007) - have

been employed to discern ecological patterns across various environmental gradients, contributing to the overall understanding of the assembly process in coastal systems (Wouters et al., 2018; Morais et al., 2019; Nogueira et al., 2023; Medeiros et al., 2021; Katsiaras et al., 2022; Mendes et al., 2025).

We analyzed a dataset of epifaunal annelid assemblages associated with four distinct macroalgal species from a tropical phytal ecosystem in a bedrock reef formation called Enseada dos Corais (South Atlantic, NE Brazil). Building upon the well-documented roles of macroalgae architecture in providing “protection”, “filtering”, and “sheltering” to their associated fauna (Dean & Connell, 1987; Christie et al., 2009). We hypothesize that macroalgae complexity will favour a more diverse set of epifaunal functional traits configurations (Fig. 1). Specifically, we anticipate that structurally complex corticated macroalgae will support annelid assemblages exhibiting a broader range of sizes, feeding strategies, and reproductive traits when compared to the structurally simple foliose macroalgae, which we expect to favour narrower trait configurations related to the greater exposure to the external environment and the weaker capacity in retaining nutrients on their fronds (Fig. 1b). Hence, by examining the relationship between the structural complexity of macroalgae and the functional trait diversity of associated annelid assemblages, our study aims to contribute a

deeper understanding of how habitat complexity influences community structure in marine ecosystems from a functional trait perspective.

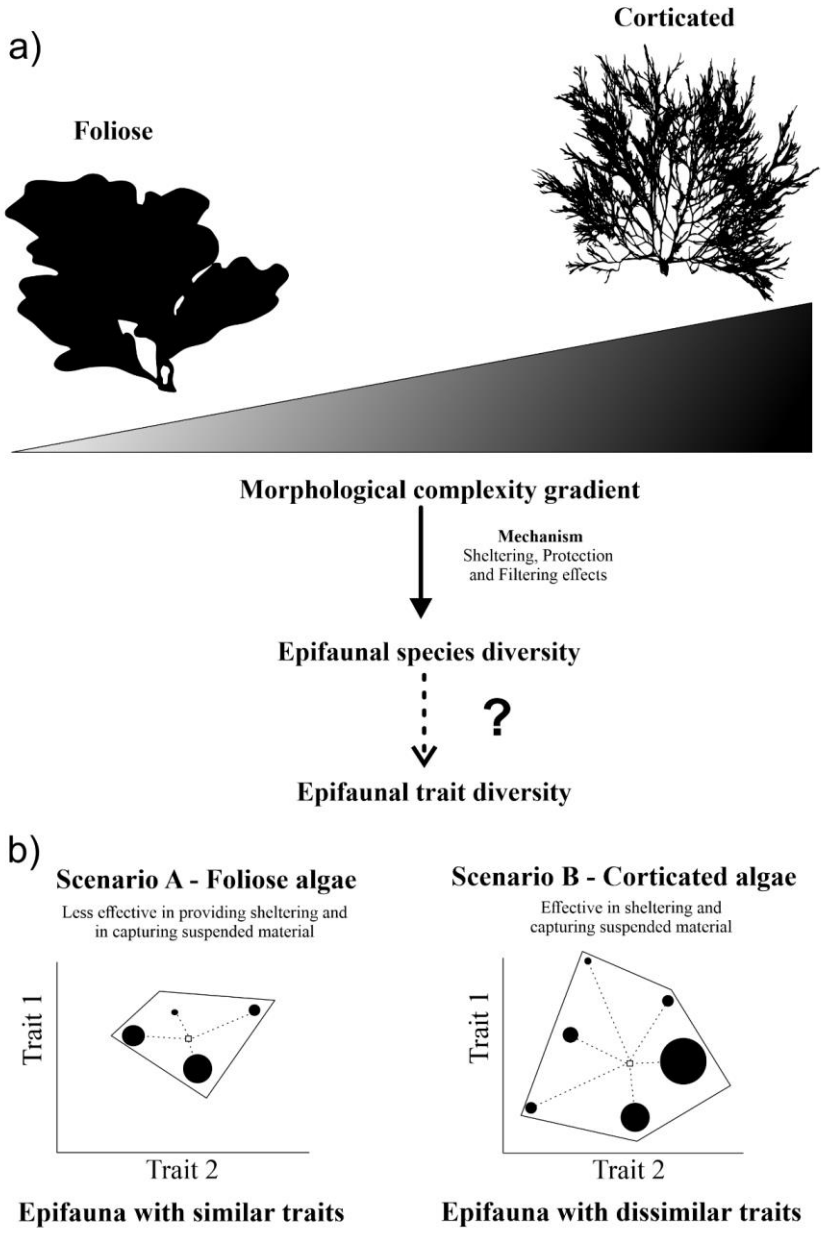

Figure 1 The morphological characteristics of corticated and foliose macroalgae represent two extremes of a gradient of complexity and fractality, with significant implications for the taxonomic diversity of associated epifaunal communities. Corticated algae, with their more intricate and structurally complex features, support a more diverse array of epifauna. This raises the question of whether a similar relationship exists when viewed from the perspective of functional traits (a). We expect that the functional trait diversity of marine annelids associated with corticated macroalgae should display greater dissimilarity, as foliose algae offer fewer resources and protection when compared to corticated counterparts (b)

Material and methods

Data collection

Samples of two corticated macroalgae, *Gelidiella acerosa* and *Palisada perforata*, and two foliose macroalgae, *Padina gymnospora* and *Ulva lactuca*, were randomly collected during four sampling periods: December 2018, February, April, and June 2019. Collections were conducted at Enseada dos Corais (8°19′09.6″ S, 34°56′53.7″ W) in northeastern Brazil (Fig. 2). This site is a 3-km-long coastal area characterized by sandstone (beachrock) reefs parallel to the shoreline (Vasconcelos et al., 2013). The region has a tropical climate with two distinct seasons: a dry season from September to February and a rainy season from March to August. Environmental

conditions include a mean water temperature of 27 °C, salinity levels around 36, high dissolved oxygen concentrations, and low turbidity (Domingues et al., 2017).

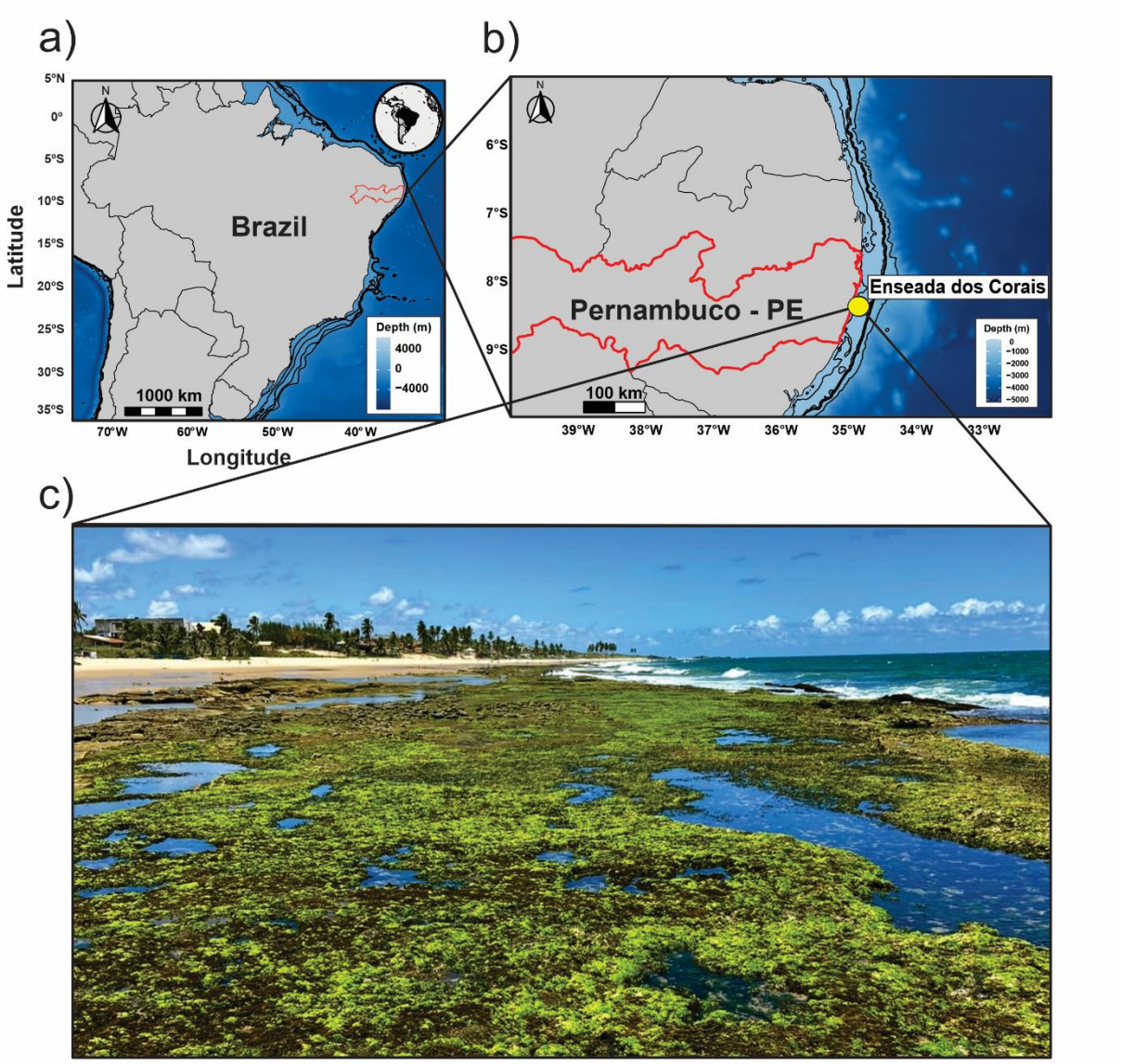

Figure 2 Study area map. (a) Overview of South America highlighting the location of Pernambuco State in northeastern Brazil. (b) Detailed map of Pernambuco showing the Enseada dos Corais sampling site (c), indicated by the yellow point where macroalgal fronds were collected

At each sampling time, ten fronds from each macroalgae species were collected. Before detaching the algae from the substrate, fronds were enclosed in a plastic bag to prevent the escape of the motile fauna. The specimens were then preserved in 4% saline formalin buffered with sodium tetraborate. In the laboratory, the samples were rinsed in fresh water and shaken multiple times to dislodge associated organisms. The resulting water was passed through a 0.3 mm mesh sieve

to capture the epifaunal annelids. The fronds were then placed on a sheet of white paper, spread out to their full extent, and pressed. The fronds were subsequently dried in an oven at 60 °C for 72 hours. After drying, each frond was removed from the botanical press and photographed using a Nikon Coolpix AW100 digital camera. The photographs were analyzed using the ImageJ software to measure the Interstitial Spatial Index (ISI), height (cm), fractal dimensions of the area (Da) and perimeter (Dp) on Image J software (Scheider et al., 2012).

The Interstitial Space Index (ISI) was calculated following the Dibble and Thomaz (2006) method. Briefly, two vertical black dashed lines, one orange dotted line, and three horizontal black dashed lines were superimposed on each image to delineate the upper, middle, and lower sections of the frond, and the interstitial spaces within the macroalgae were quantified along these lines (Craveiro & Rosa-Filho, 2024). Specifically, the index was calculated using the formula: ISI = fh/lh + fv/lv, where fh is the average frequency of interstices intercepted per centimeter along the horizontal axis, lh is the average length of interstices along the horizontal axis, fv is the average frequency of interstices intercepted per centimeter along the vertical axis, and lv is the average length of interstices along the vertical axis (Dibble & Thomas, 2006; Craveiro & Rosa-Filho, 2024).

Macroalgae height was calculated by setting a central line (base to apex) on each image (Craveiro & Rosa-Filho, 2024). Finally, regarding the fractal dimensions, Da represents the measure of the area covered by the macroalgae, which is an estimate of area occupancy of its fronds, while Dp indicates the perimeter area of the macroalgae, which means the degree of dissection of its fronds (Haley et al., 2004; McAbendroth et al., 2005). Fractal dimensions were calculated following the methods of McAbendroth et al. (2005) and Kovalenko et al. (2009), using the box-count algorithm from Image J (Craveiro & Rosa-Filho, 2024).

Functional traits

A functional trait matrix was constructed through fuzzy-coding of body size, feeding strategy, and reproduction traits of annelid epifaunal genera (Table 1). The scores varied from 0 (no affinity), 1 (low affinity), 2 (high affinity), and 3 (absolute affinity, i.e., when all other modalities are 0 scored), following Oug et al. (2012) coding criteria. Annelid size was assessed following Jumars et al. (2015) body length trait

modalities, coded after a generic-level literature consult. Regarding the feeding strategy trait, we follow the guidelines of Jumars et al. (2015) and Wouters et al. (2018). Feeding trait modalities, whenever possible, were also coded based on the generic-level literature. When diet information was unavailable at a generic level, family-level literature was consulted for additional information. Larval development was assessed based on Rouse (2000) and updated family- and genus-level literature (Rouse et al., 2022).

The fuzzy-scores for each trait were calculated using the *prep.fuzzy* function from the ade4 R package (Dray & Dufour, 2007). Then, a Gower distance matrix was calculated based on annelid genera's fuzzy-coded traits. This matrix, alongside the abundance of each genus per macroalgae frond matrix, was used to calculate Rao's Quadratic Entropy (Rao's Q) index of each epifaunal assemblage using the "melodic" function (de Bello et al., 2016). Rao's Q measures trait dispersion by quantifying the mean dissimilarity among epifaunal genera in each assemblage, summarizing the expected differences between randomly selected species pairs with replacement (Ricotta & Moretti, 2011; de Bello et al., 2016).

Data analysis

The macroalgae traits were compared between morpho-functional groups (corticated vs foliose) and among months ("December/18", "February/19", "April/19", and "June/19") using a Permutational Analysis of Variance (Permanova). Moreover, for the linear modelling step described below, a Principal Component Analysis (PCA) of scaled macroalgae traits and a Pearson correlation test were implemented to check for multicollinearity. The Rao's Q of epifaunal communities was modelled against the interaction between macroalgae functional groups (fixed factor with two levels: "corticated" and "foliose") and months (fixed factor with four levels: "December/18", "February/19", "April/19" and "June/19").

Macroalgae traits related to their morphological complexity (Da, Dp, Height, and ISI) were fitted as predictors of Rao's Q in a global model. A multimodel inference approach, combining model selection and model averaging, was applied to determine which macroalgae traits were included in the best-fitting models for explaining variation in epifaunal Rao's Q values, using the MuMIn package in R (Burnham & Anderson, 2002; Bartoń, 2024). The model with the lowest Akaike Information Criterion corrected

for small sample sizes (AICc) was considered the best approximating model for predicting Rao's Q variation (Burnham & Anderson, 2002). To evaluate the importance of each predictor (macroalgae trait) and estimate their averaged effects, we selected all models within ΔAICc < 2 units of the first-ranked model (Burnham & Anderson, 2002; Symonds & Moussalli, 2011; Tredennick et al., 2021). The importance of a given predictor was quantified as the sum of Akaike weights (AICw) across all models in which it appeared, representing the probability that the predictor is part of the best approximating model (Burnham & Anderson, 2002; Galipaud et al., 2013). Each model weight (AICwi) was calculated as the relative likelihood of the model "i" divided by the sum of the likelihoods across all selected models (Burnham & Anderson, 2002; Galipaud et al., 2013).

Separately, to investigate specific correlations between annelid and macroalgae traits, RLQ and fourth-corner analysis were employed. RLQ and fourthcorner analyses were conducted using the ade4 package to investigate potential associations between functional traits and macroalgae traits (Dray et al., 2014). The RLQ analysis integrates three matrices: R (scaled macroalgae traits), L (genera abundances), and Q (fuzzy-coded functional traits), enabling the identification of multivariate relationships between environmental gradients (in our case macroalgae traits) and annelid functional traits, mediated by annelid genera abundances (Dray et al., 2014). The fourthcorner analysis complements this approach by testing the significance of bivariate associations between annelid traits and macroalgae traits (Dray et al., 2014). Each matrix was individually processed using appropriate multivariate analyses. The Q matrix was analyzed using a Fuzzy Correspondence Analysis (FCA), while the R and L matrices were subjected to Principal Component Analysis (PCA) and Correspondence Analysis (CA), respectively. Finally, a Monte Carlo permutation test, with 49999 repetitions within model 6, was implemented to assess the significance of correlations between macroalgae traits and annelid traits with RLQ axes, controlling for p values using the false discovery rate (FDR) method (Benjamini & Hochberg, 1995; Dray et al., 2014). All analyses were performed in R with R Studio (R Core Team, 2023).

Results

Most morphological complexity traits of macroalgae (Da, Dp, Height, and ISI) differed significantly between the two morpho-functional groups (Table S1; Figs. S1–S2) and also among months (Table S1; Fig. S3), with particularly marked differences in June (Fig. S3). In most months, corticated and foliose macroalgae had distinct values of Da and Dp, except in June, when both groups had maximum values and no longer differed (Fig. S2a-b). ISI values remained relatively consistent throughout the year, although the ISI of corticated macroalgae notably increased in June, becoming more subdivided than in previous months (Fig. S2c). Corticated and foliose algae had similar height throughout most of the year, except in June, when corticated algae were taller while foliose algae were shorter (Fig. S2d).

The two morpho-functional groups of macroalgae supported polychaete epifaunal assemblages with distinct patterns of trait dissimilarity (Table 2, Fig. 3a). Corticated algae generally hosted a more diverse set of epifaunal annelids traits than the foliose ones (Fig. 3a). The mean trait dissimilarity of the epifaunal assemblages did not vary significantly among months (Table 2, Fig. 3a). In addition, model selection indicated Da, ISI, and Height as predictors of Rao's Q in the best approximating model (Table 3). The ISI was positively related to Rao’s Q, whereas Da and Height were negatively related.

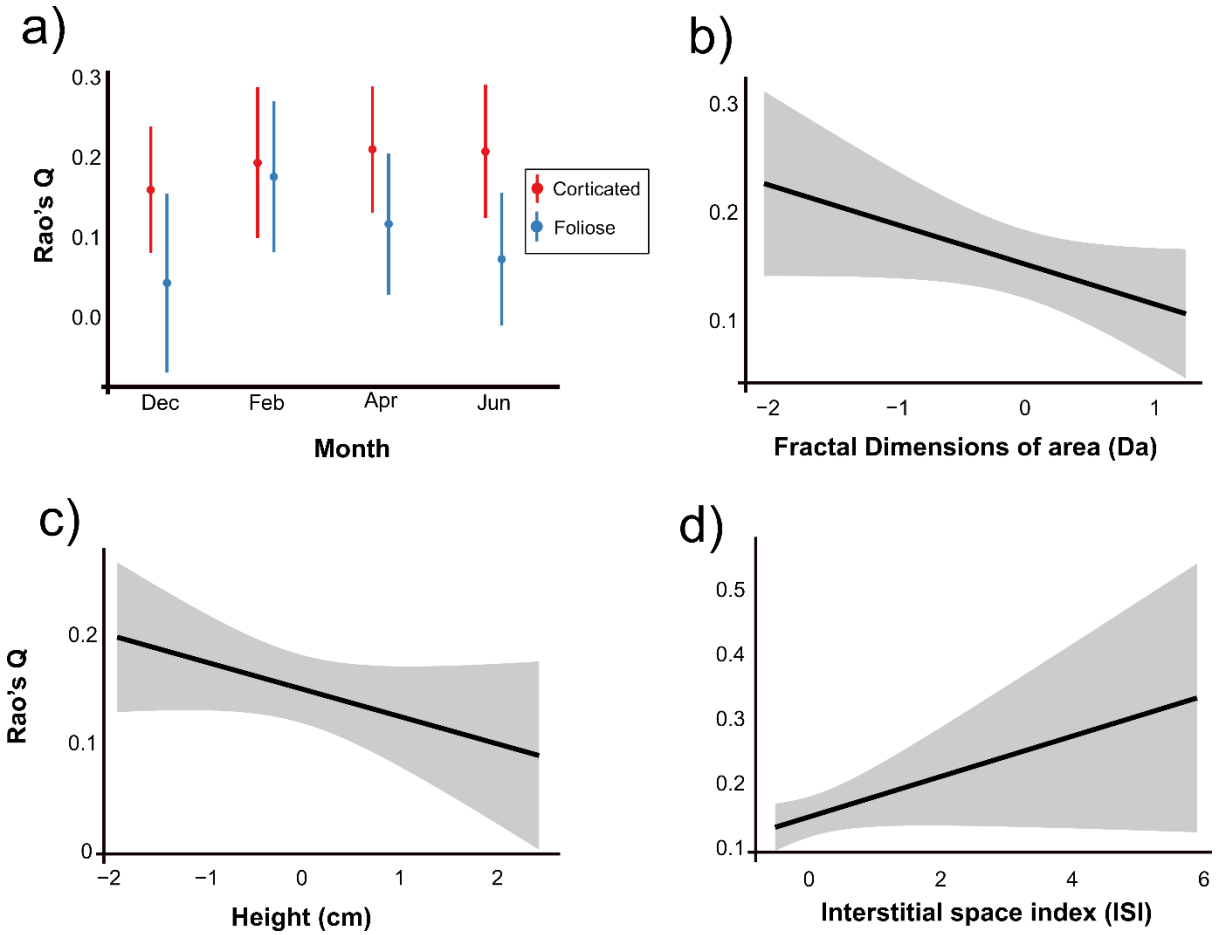

Figure 3 Predicted values (95% Confidence Interval) of mean functional trait dissimilarity of epifaunal annelid assemblages. Corticated algae supported more dissimilar epifaunal assemblages than foliose algae (a). However, the mean trait dissimilarity of epifaunal annelids did not vary significantly across months (a). The macroalgal traits predictors present in the first-ranked model were Da, Height, and ISI (b-d). Da and Height showed a negative relationship with Rao's Q, while ISI was positively associated with it, suggesting that the greater structural complexity of macroalgae influences the trait diversity of its epifauna

The RLQ analysis demonstrated an evident influence of macroalgae functional groups on the traits of epifaunal annelids, with corticated and foliose algae being distinctly separated from each other (Fig. 4a). The first two axes accounted for 99,8% of the variation (axis 1: 98.7%, axis 2: 1.7%) (Table S2). Axis one distinguished corticated macroalgae (mostly positively associated) from foliose macroalgae (primarily negatively associated), but with both groups exhibiting some degree of overlap over time (L correlation = 0.435). However, observations from June (Fig. 4a) formed a topological group apart from those of other months, a pattern more evident along the second axis (L correlation = 0.24). Epifaunal annelid traits were significantly associated only with the first RLQ axis, particularly suspension feeding, herbivory, and

306 predation (Table 4). In contrast, body size and larval development strategies were
307 weakly correlated with RLQ axes 1 and 2 and did not contribute significantly to the
308 observed multivariate pattern (Table 4). Importantly, fourth-corner analysis revealed
309 no significant bivariate correlations between annelid and macroalgal traits.
310 The macroalgal traits ISI and height were positively related to the first axis,
311 whereas Da and Dp were negatively related (Fig. 4b). Specifically, Da and height were
312 more strongly correlated with this axis than Dp and ISI, which were more closely
313 associated with axis 2 (Table S3). Herbivore and facultative suspension-feeding
314 nereidids, such as *Platynereis* Kinberg, 1865, and *Pseudonereis* Kinberg, 1865, were
315 the dominant genera, showing a negative association with the first axis (Fig. 4c-d). In
316 contrast, predatory genera, mostly syllids, were positively related (Fig. 4c-d).
317 Moreover, the first axis distinguished some foliose algae observations in June from
318 the others, occupying its negative extreme (Fig. 4a). The second axis was negatively
319 correlated with all macroalgae traits, and also distinguished some samples collected
320 in June from others, as some observations of corticated algae exhibited high ISI and
321 height values, clearly separating them from their foliose counterparts (Fig. 4a-b). The
322 higher ISI and height associated with the June observations on the second axis
323 coincided with the opportunistic/scavenger and deposit-feeding strategies of epifaunal
324 annelids (Fig. 4c).

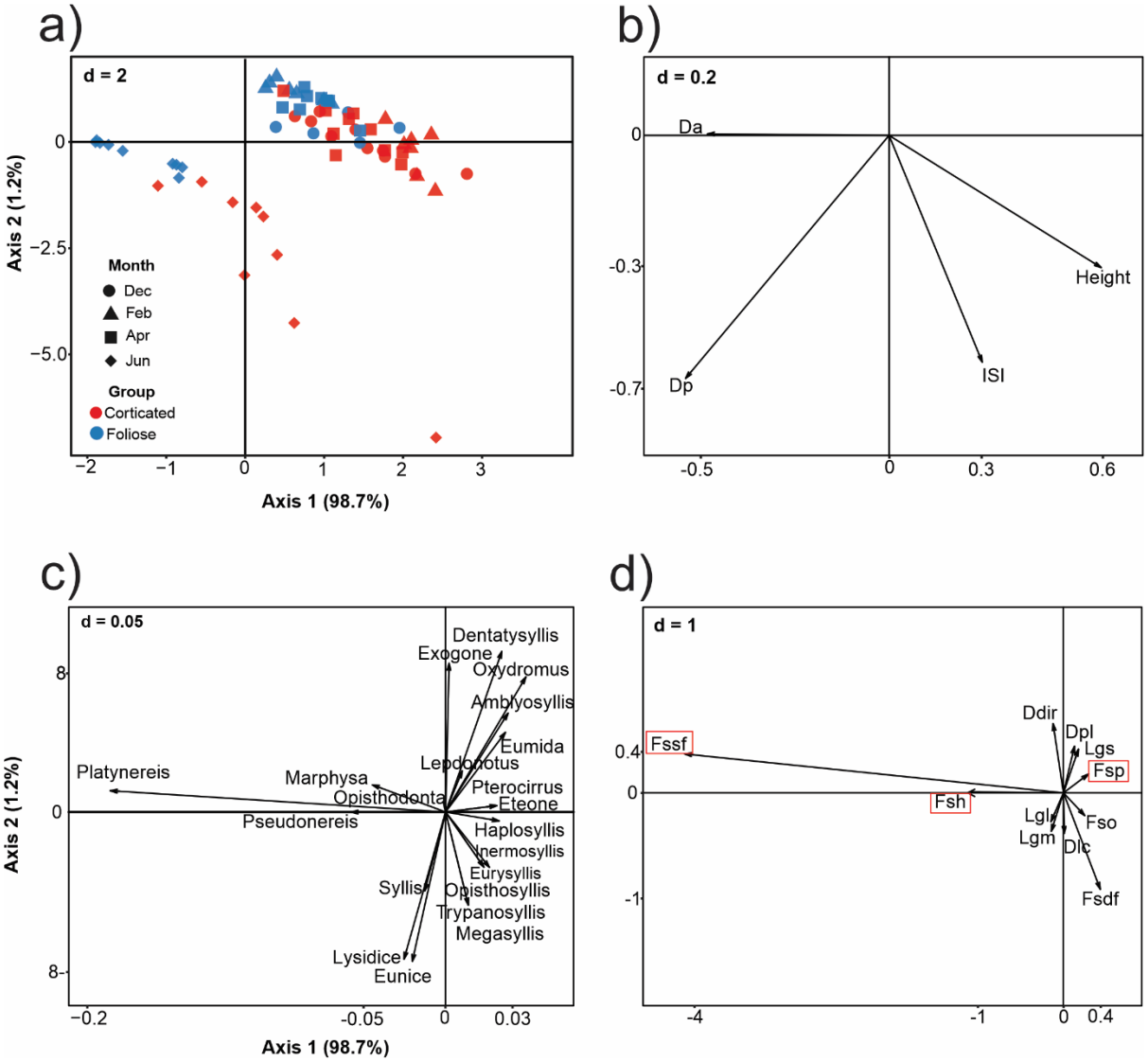

Figure 4 RLQ ordinations illustrating changes in epifaunal assemblages associated with corticated and foliose macroalgae (a), as revealed by the correlation of macroalgal morphological traits (b) with the abundance and functional traits of epifaunal annelid genera (c–d). Functional traits of epifaunal annelids that showed significant correlations with RLQ axis 1 are highlighted in red. Abbreviations = Ddir: Direct development; Dlc: Development through lecithotrophic larval stage; Dpl = Development through planktotrophic larval stage; Fso = Opportunist/scavenger feeding strategy; Fsp = Predatory feeding strategy; Fsh = Herbivore feeding strategy; Fssf = Suspension-feeding strategy; Lgl = Large body length; Lgm = medium body length; Lgs = small body length

Discussion

It was hypothesized that the two distinct macroalgal functional groups would provide contrasting habitats for their associated annelid assemblages, favouring

distinct epifaunal trait configurations. Our findings indeed showed that Rao's Q varied significantly between the two macroalgal functional groups, responding to differences in their morphological complexity. In addition, as demonstrated by the RLQ analysis, corticated and foliose macroalgae presented separate affinities to annelid traits and genera, corroborating the initial expectations, as well. The assessed macroalgae morphological traits as predictors of Rao's Q of annelid assemblages captured relevant aspects of the assembly process at the frond scale. Among the measured traits of macroalgae, Da, ISI, and height were selected in the best approximating model, with Da and ISI presenting higher importances than height.

Since Da represents a measure of fractality, expressed as total frond occupancy area, fronds with higher Da values are less subdivided than those with lower Da values (McAbendroth et al., 2005). On the other hand, ISI represents how much macroalgae's fronds are subdivided, with higher ISI values representing fronds with numerous interstitial spaces (Dibble & Thomas, 2006). Thus, the structural complexity of macroalgae influenced the trait dispersion of their annelid assemblages, and this finding is consistent with the well-documented role of morphological complexity of hosts in shaping epifaunal taxonomic diversity in freshwater and marine ecosystems (Dean & Connell, 1987; Gee & Warwick, 1994; Chemello & Milazzo, 2002; Hansen et al., 2010; Hansen et al., 2011; Veiga et al., 2014; Gan et al., 2019; Fraser et al., 2020; Duarte et al., 2020a,b; Craveiro & Rosa-Filho, 2024).

Under this paradigm, the combination of the RLQ approach with Rao's Q modelling demonstrates an interesting tradeoff of epifaunal trait combinations as a response to the fractal nature of host macroalgae. Although the more complex corticated architecture is expected to impose spatial restrictions on adult epifaunal species with larger bodies (Dean & Connel, 1987; Gee & Warwick, 1994), by displaying higher ISI and lower Da values, they presented assemblages with more dissimilar feeding trait configurations, and not necessarily smaller body length. As for foliose species, the lower Rao's Q values agree with prior expectations, as they do not impose size restrictions to their epifauna, but are less effective in capturing suspended material and in providing protection (Dean & Connel, 1987; Gee & Warwick, 1994), ultimately leading to the observed narrower set of feeding trait affinities. A similar situation was also observed in previous studies, relating to feeding strategies and body size traits, with complex macroalgae presenting higher functional diversity of mollusk assemblages (Barbosa et al., 2019; Duarte et al., 2020a).

Such pattern is expected because of the positive effects of macroalgae and macrophytes structural complexity on the diversity of their epifaunal communities, which act by influencing the space availability for foraging, colonization, and refuge (Gregg & Rose, 1982; Dean & Connell, 1987; Hacker & Steneck, 1990; Gee & Warwick, 1994; Christie et al., 2009; Barbosa et al., 2019; Ware et al., 2019; Duarte et al., 2020a). More structurally complex hosts are effective at accumulating organic matter, facilitating the settlement and persistence of small-sized, detritivorous, and opportunistic species (Christie et al., 2009; Panyawai et al., 2019; Barbosa et al., 2019; Duarte et al., 2020a), while also enhancing protection against predation and hydrodynamics as interstitial spaces serve as refuges (Barbosa et al., 2019; Ware et al., 2019).

Although Rao's Q did not vary significantly among months, the RLQ analysis indicated a monthly affinity of both macroalgae and annelid traits in relation to June observations. This apparent discrepancy between the mean dissimilarity of annelid traits, as quantified by Rao's Q, and the RLQ output also contrasts with the findings of Craveiro & Rosa-Filho (2024), who documented a monthly shift in epifaunal species composition in response to changes in macroalgal morphological traits. Such changes affected the dominance patterns of polychaetes within the same phytal system. A possible explanation lies in the strong correlation between Rao's Q and taxonomic diversity, which reduces the index's sensitivity to changes driven by species relative abundances in low-richness systems, where the dissimilarity matrix is "small" (de Bello et al., 2016).

On the Pernambuco coast, winds, mainly driven by the semi-permanent high-pressure system over the South Atlantic Ocean, control rainfall and hydrodynamics (Lira et al., 2010; Domingues et al., 2017). Winds tend to be predominant from the east in austral summer and shift to the southeast in austral winter (Lira et al., 2010). This seasonal inversion in wind direction affects rainfall and hydrodynamics, effectively dividing the year into two distinct climatic periods: a rainy season (March to August) and a dry season (September to February) (Macêdo et al., 2004; Lira et al., 2010; Vasconcelos et al., 2013; Domingues et al., 2017). In the rainy season, high rainfall, hydrodynamics, and turbidity stress intertidal marine plants (Domingues et al., 2017; Bérgamo et al., 2022; Bérgamo et al., 2024). Macroalgae may respond to such stressful conditions by altering their morphological traits, growth rates, and flexibility (Madsen et al., 2001; Hurd, 2000). This pattern was observed by Craveiro & Rosa-

Filho (2024) in the studied system, where macroalgae morphological complexity and biomass were higher in more hydrodynamically stable months during the dry season.

In June, the multivariate distinction between algae morpho-functional groups and polychaete assemblages traits was influenced by the affinity of opportunistic/scavenger and deposit-feeding annelid trait modalities with corticated algae observations positioned along the negative extremes of the second RLQ axis, and herbivore and facultative suspension-feeding modalities with foliose species observations positioned along the negative extremes of the first RLQ axis. As corticated macroalgae can retain suspended material more efficiently (Dean et al., 1987), the superposition of deposit-feeding and opportunistic/scavenger annelid genera with observations from corticated algae is expected. In contrast, the suspension-feeding correlation with foliose algae observations is attributed to the incidence of large herbivores and tube-building nereidids, which can secrete mucus within their tubes to capture the suspended material from the water column to be later ingested (Daly, 1973; Toba & Sato, 2013).

Putting things together, the structural complexity of macroalgae hosts can be interpreted to evaluate the assembly process of their epifauna through the lens of the filtering metaphor, especially in a niche selection context (Dean & Connell, 1987; HilleRisLambers et al., 2012; Locke & Chisholm, 2023). Briefly, assembly theory predicts that at fine spatial scales, biotic interactions exert a more decisive influence than abiotic environmental filtering in modulating functional trait diversity within local communities (Mayfield & Levine, 2010; Kraft et al., 2015; Boet et al., 2022; Gross et al., 2022). The morphological traits of macroalgae can be considered as filters for the traits of associated epifauna by mediating this process at the frond scale, as they significantly affected the mean trait dissimilarity of annelid genera, leading to distinct epifaunal trait affinities between the two host morpho-functional groups. For these reasons, the assembly of epifaunal communities on macroalgae is a multifaceted ecological process mediated by host structural traits that can mitigate the effects of negative interspecific interactions and buffer environmental severity, thereby creating complex habitats that sustain their high biodiversity from both taxonomic and functional perspectives.

Conclusion

The relationship between habitat structure and functional trait diversity was examined, revealing that increased macroalgal architectural complexity positively influences the trait dispersion of associated epifaunal assemblages. However, the strength and nature of this relationship varied depending on the specific traits considered, as different traits capture distinct dimensions of species' ecological niches (Spasojevic et al., 2012; Kraft et al., 2015). All annelid genera inhabiting macroalgae were errant polychaetes, characterized by a shared set of morphological traits linked to an epifaunal lifestyle and high mobility, typical of the Errantia clade (Rouse et al., 2022). Nonetheless, their traits varied primarily in body size, reproductive modes, and feeding strategies, with the latter contributing most significantly to the observed multivariate patterns of trait distribution across macroalgal morpho-functional groups and months.

Finally, a major limitation to the advancement of more robust trait-based approaches is the current paucity of information on the life-history traits of marine invertebrates—a knowledge gap known as the Raunkiaeran shortfall (Hortal et al., 2015; Gonçalves-Souza et al., 2023; Luza et al., 2023). To overcome this constraint, future research should prioritize the characterization of functional traits in epifaunal species, with particular emphasis on updating and expanding trait data for tropical taxa. It is also important to recognize that macroalgae interact with both their environment and associated fauna not only through morphological traits, but also via chemical and reproductive characteristics. Future research should place greater emphasis on elucidating their role in shaping the functional, phylogenetic, and taxonomic diversity of epifaunal assemblages. Such efforts may reveal a highly multidimensional structure of epifaunal biodiversity, underscoring the need for an integrative, cross-taxa framework that encompasses multiple facets of biological diversity. This comprehensive approach will be crucial for advancing our understanding of how climate change and anthropogenic pressures impact marine phytal ecosystems.

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Author contributions S.L.D.D.M. originally formulated the idea, analyzed the data and wrote the first manuscript draft under the supervision of R.L.N.. P.C.P. contributed to the statistical analysis routine supervision, data modelling insights, and theoretical refinement. J.S.R.F. and N.C. formulated the sampling design, conducted the fieldwork and provided the taxonomic identifications. All authors reviewed and edited the final text.

Data availability The R script with the coding routines will become publicly available after the reviewing process at S.L.D.D.M. github repository (https://github.com/samuelmendes-polychaeta?tab=repositories).

Confict of interest We have no conflict of interest to declare.

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