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 assessed using Rao's Quadratic Entropy (Rao's Q) and RLQ analysis. Corticated algae species hosted more functionally dissimilar annelid assemblages than foliose ones. Moreover, macroalgal morphological traits 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, Geometric complexity.

Introduction

The critical role of habitat structure in shaping community diversity has long been recognized in the 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; Loke & Chisholm, 2022; 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).

Accordingly, the complexity component of habitat structure comprises complementary dimensions, with Loke & Chisholm (2022) presenting a framework that classifies them into two main groups: informational and geometric. Informational complexity captures the diversity, variability, and spatial organisation of system elements (e.g., entropy), whereas geometric complexity describes the physical structure of habitats in two or three dimensions (e.g., rugosity, modularity, fractal dimensions). 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, especially from a geometric perspective (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). Among them, 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 macroalgal morphology and play key roles in the assembly of epifaunal communities by buffering the effects of environmental stressors, such as hydrodynamics, and negative biological interactions, including predation and resource competition (Dean & Connell, 1987; Christie et al., 2009). Hence, favouring the current assembly theory perspective that macroalgae hosts act as “habitat templates" for their epifauna by imposing selective filters towards colonization (Southwood, 1977; HilleRisLambers et al., 2012).

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 these studies 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 also 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 epifaunal communities. By varying experimental designs, focal species, and geographic regions, such research would enable broader generalizations about 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 beachrock reef formation called Enseada dos Corais (South Atlantic, NE Brazil). The region is characterized by a seasonal dynamic driven by wind reversals, which define a rainy season with increased rainfall and hydrodynamic stress, and a drier, thus, more hydrodynamically stable season (Domingues et al., 2017). In this system, host macroalgal species exhibited morphological trait changes over time in response to seasonal variation, thereby affecting the taxonomic diversity of their associated epifaunal assemblages (Craveiro & Rosa-Filho, 2024). Indeed, these variations related to abiotic stress are well known to drive macroalgae eco-morphological and eco-physiological responses (Clark et al., 2018; Craveiro & Rosa-Filho, 2024). Thus, building on the well-documented role of macroalgal architecture in providing protection, filtering, and shelter for associated fauna (Dean & Connell, 1987; Christie et al., 2009), we hypothesize that macroalgal morphological traits effectively capture the geometric complexity of habitat structure that they provide in phytal ecosystems, thereby influencing the trait diversity of associated annelid epifaunal assemblages (Fig. 1).

Body size, feeding, and reproductive behaviours are key functional response traits directly related to the life history strategies adopted by species to couple with: environmental gradients, distinct patterns of resource fluctuation, and biotic interactions (Beauchard et al., 2017; Medeiros et al., 2021; Beauchard et al., 2022). For example, in marine systems, harsher conditions tend to impose trait convergence toward r-selected traits, such as smaller body sizes, opportunistic feeding, and reproductive behaviours (Medeiros et al., 2021; Beauchard et al., 2022; Mendes et al., 2025). On the other hand, environmental stability tends to promote trait divergence towards K-selected functional traits, such as larger body sizes, active macrophagic behaviours, and diverse reproductive strategies (Medeiros et al., 2021; Beauchard et al., 2022; Mendes et al., 2025). Specifically, we expect that more complex corticated morphologies can buffer against environmental severity, particularly during the rainy season, thereby supporting annelid assemblages with a broader range of body sizes, feeding strategies, and reproductive traits than structurally simpler foliose macroalgae. In contrast, foliose forms are expected to promote narrower trait configurations due to greater exposure to external conditions and a reduced capacity to retain nutrients on their fronds (Fig. 1).

By examining the interplay among macroalgal structural complexity, local seasonal dynamics, and the functional-trait diversity of associated annelid assemblages, this study aims to advance our understanding of how habitat complexity shapes community structure in marine ecosystems. In this sense, we adopt a functional trait–based perspective to explore the mechanisms by which habitat-forming macroalgae mediate environmental conditions, influence species filtering, and ultimately determine patterns of functional diversity within epifaunal communities.

Material and methods

Data collection

Samples of two corticated macroalgae, *Gelidiella acerosa* (Forsskål) Feldmann & Hamel, 1934, and *Palisada perforata* (Bory) K.W. Nam, 2007, and two foliose macroalgae, *Padina gymnospora* (Kützing) Sonder, 1871, and *Ulva lactuca* Linnaeus, 1753b, 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. 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 monsoon climate according to

Köppen–Geiger classification (Peel et al., 2007), with two distinct seasons: a dry season from September to February and a rainy season from March to August (Domingues et al., 2017; Craveiro & Rosa-Filho, 2024). So, samples collected in December and February correspond to the dry season, whereas those collected in April and June correspond to the rainy season. 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).

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 ImageJ to measure the Interstitial Spatial Index (ISI), height (cm), fractal dimension of the area (Da), and perimeter (Dp) (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: $ISI = \frac{fh}{lh} + \frac{fv}{lv}$, 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 the 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-counting algorithm in ImageJ (Craveiro & Rosa-Filho, 2024).

Functional traits

A functional trait matrix was constructed using fuzzy-coding of body size, feeding strategy, and reproductive traits of annelid epifaunal genera (Table 1). The scores were 0 (no affinity), 1 (low affinity), 2 (high affinity), and 3 (absolute affinity, i.e., when all other modalities were 0-scored), following the Oug et al. (2012) coding criteria. Annelid size was assessed using the body-length trait modalities of Jumars et al. (2015), with coding based on a generic-level literature review. 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 complete dataset of functional traits fuzzy scores and the references supporting the assignment are available at the following GitHub repository: https://github.com/samuelmendes-polychaeta?tab=repositories.

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 conducted to assess 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").

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 from the fuzzy-coded traits of annelid genera. 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; Pavoine, 2026).

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 (macroalgal trait) and estimate their average effects, we selected all models with ΔAICc < 2 units relative to 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 fourth-corner 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 correlation structures between environmental gradients (in our case, macroalgal traits) and annelid functional traits, mediated by annelid genera abundances (Dray et al., 2014). The fourth-corner analysis complements this approach by assessing the significance of bivariate associations between annelid and macroalgal traits (Dray et al., 2014). In this sense, the two analyses complement the patterns revealed by Rao's Q modelling by explicitly disentangling how individual functional traits contribute to overall functional diversity and how their dispersion varies along gradients of macroalgal morphological complexity (Wouters et al., 2018; Beauchard et al., 2022; Mendes et al., 2025). By examining trait-specific responses, this approach provides a more mechanistic interpretation of the observed patterns of functional diversity, allowing us to identify which traits are most responsive and how macroalgal morphological complexity shapes the functional space occupied by associated annelid assemblages.

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 49.999 repetitions within model 6, was implemented to assess the significance of correlations between macroalgae traits and annelid traits following the abovementioned fourth-corner approach, controlling for p-values using the false discovery rate (FDR) method (Benjamini & Hochberg, 1995; Dray et al., 2014). All analyses were performed in R using RStudio (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 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 associated with Rao's Q, whereas Da and Height were negatively associated.

The RLQ analysis demonstrated an evident covariation 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%), only model 2 permutation test was significant (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 distinct topological group from those of the other months, a pattern that was more pronounced 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 predation (Table 4). In contrast, body size and larval development strategies were weakly correlated with RLQ axes 1 and 2 and did not contribute significantly to the observed multivariate pattern (Table 4). Importantly, fourth-corner analysis revealed no significant bivariate correlations between annelid and macroalgal traits.

The macroalgal traits ISI and height were positively related to the first axis, whereas Da and Dp were negatively related (Fig. 4b). Specifically, Da and height were more strongly correlated with this axis than Dp and ISI, which were more closely associated with axis 2 (Table S3). Herbivore and facultative suspension-feeding nereidids, such as *Platynereis* Kinberg, 1865, and *Pseudonereis* Kinberg, 1865, were the dominant genera, showing a negative association with the first axis (Fig. 4c-d). In contrast, predatory genera, mostly syllids, were positively related (Fig. 4c-d). Moreover, the first axis distinguished some foliose algae observations in June from the others, occupying its negative extreme (Fig. 4a). The second axis was negatively correlated with all macroalgae traits, and distinguished some samples collected in June from others, as some observations of corticated algae exhibited high ISI and height values, clearly separating them from their foliose counterparts (Fig. 4a-b). The higher ISI and height associated with the June observations on the second axis were consistent with the opportunistic/scavenging and deposit-feeding strategies of epifaunal annelids (Fig. 4c).

Discussion

It was hypothesized that the two distinct macroalgal functional groups would differ from each other and across months, providing contrasting habitats for their associated annelid assemblages and thereby favouring distinct epifaunal trait configurations. Our findings showed that Rao's Q varied significantly between the two macroalgal functional groups, reflecting differences in morphological complexity. However, the expected seasonal pattern was controversial, as Rao’s Q test did not yield a significant difference across the months assessed. In addition, as demonstrated by the RLQ analysis, corticated and foliose macroalgae showed distinct affinities for annelid traits and genera, corroborating the initial expectations. Finally, the assessed macroalgal morphological traits, as predictors of Rao’s Q for annelid assemblages, captured relevant aspects of the assembly process at the frond scale and exerted non-negligible effects on the trait diversity of associated epifauna.

On the relationship between macroalgae and their associated epifauna

Among the measured macroalgal traits, Da, ISI, and height were selected in the best-fitting model, with Da and ISI having higher importance 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; thus, higher values of Da indicate structurally simpler fronds (McAbendroth et al., 2005). On the other hand, ISI quantifies the degree to which macroalgal fronds are subdivided, with higher ISI values indicating 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 trade-off in epifaunal trait combinations in 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 body sizes (Dean & Connell, 1987; Gee & Warwick, 1994), these assemblages displayed higher ISI and lower Da values, suggesting more dissimilar feeding trait configurations rather than 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 on 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 pattern was observed in previous studies on feeding strategies and body-size traits, with complex macroalgae supporting higher functional diversity in mollusc 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).

The observed influence of macroalgal morphology on epifaunal trait dissimilarity is also consistent with previous findings on the evolutionary aspects of epibiotic interactions, in which coevolution between hosts and associated fauna has important consequences for community structure and ecosystem processes (Thornber et al., 2016). The eco-evolutionary relevance of these interactions often reveals reciprocal morphological adaptations between partners and broad-scale diversity gradients (Thornber et al., 2016; Gross et al., 2022). Moreover, these relationships may be negative, positive, or “neutral,” depending on the ecological context and the biology of the species involved, with illustrative examples arising from interacting systems composed of marine annelids and macroalgae (Woodin, 1977; Kollars et al., 2016; Álvarez-Campos & Verdes, 2017; Rossbach et al., 2021; Cronau et al., 2023).

Commensalistic and facilitative interactions between annelids and macroalgae are widespread in benthic systems, often providing benefits to one or both partners by facilitating colonization and protection, whereas negative effects are mostly attributed to herbivory and overgrowth (Thornber et al., 2016; Kollars et al., 2016; Álvarez-Campos & Verdes, 2017; Rossbach et al., 2021). For instance, serpulid polychaetes living as epiphytes on red algal thalli exemplify commensalism, as the calcareous tubes of these species attach to algal mats, using the thalli as a substrate, with minimal impact on the host under normal conditions (Rossbach et al., 2021). Similarly, syllid polychaetes inhabiting kelp holdfasts exploit the complex three-dimensional cavities generated by holdfast morphology for shelter and foraging, benefiting from protection from predators and access to food resources without apparent harm to the kelp (Álvarez-Campos & Verdes, 2017). In the beachrock phytal system studied here, polychaetes may likewise benefit from the interstitial spaces provided by corticated macroalgae, which likely function as refuges offering protection and, consequently, favor a more diverse set of trait configurations.

Beyond one-directional benefits for epifauna, annelids can also facilitate macroalgal colonization and persistence. For example, serpulid worms form biogenic structures that enhance macroalgal persistence in high-intertidal zones, as their calcareous tubes create microhabitats that retain moisture, protect algal spores, and supply nutrients through excretions (Liversage, 2018). Another illustrative case involves annelid “gardening” behaviour, in which species, particularly from the genus *Platynereis*, actively seize macroalgal fronds and exhibit selective grazing that allows algal fragments to persist and even grow (Woodin, 1977). Similarly, onuphid annelids can anchor the red alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967 to their tubes in substrate-poor soft sediments, while the seaweed, in turn, enhances prey availability by attracting amphipods (Kollars et al., 2016).

The presence of associated epifauna from other phyla can generate trophic cascades that shape community structure, particularly involving molluscs and crustaceans that commonly coexist with marine annelids in phytal systems, where they may function as competitors for space and food, as well as predators and/or prey (Kollars et al., 2016; Thornber et al., 2016; Cronau et al., 2023). For instance, epiphytic algae growing on host macroalgae, or the host macroalgae themselves, may serve as nursery habitats and food sources for juvenile crustaceans, which in turn can be preyed upon by carnivorous polychaetes (Kollars et al., 2016). This configuration results in a multi-step facilitation cascade in which macroalgae support epiphytes, epiphytes support crustaceans, and crustaceans support polychaetes. Interestingly, the interaction among the annelid *Platynereis*, the gastropod *Littorina* Férussac, 1822, and the macrophyte *Zostera* Linnaeus, 1753a provides a clear example of such complex trophic cascades (Cronau et al., 2023). In this system, *Platynereis* negatively affects *Zostera* by promoting epiphyte growth, whereas *Littorina* mitigates this effect by grazing on epiphytes and consuming *Platynereis* tubes. This three-way interaction highlights that the net effect of annelids on macrophytes can depend on the presence and abundance of associated invertebrate epifauna (Cronau et al., 2023).

Together, these examples highlight the complex and multidirectional nature of interactions between epifauna and their hosts, mediated by habitat structure and eco-evolutionary processes (Thornber et al., 2016; Gross et al., 2022; Cronau et al., 2023). In this context, research aimed at disentangling the ecological responses and effects of epibiotic relationships in marine ecosystems is of paramount importance, particularly in the context of current climate change and increasing anthropogenic pressures.

The seasonal change controversy

On the Pernambuco coast, winds are mainly driven by the semi-permanent high-pressure system over the South Atlantic Ocean, and control rainfall and hydrodynamics (Lira et al., 2010; Domingues et al., 2017). Winds are predominantly 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 and algae

(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, in which macroalgal morphological complexity and biomass were higher in more hydrodynamically stable months during the dry season.

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, suggesting that local conditions shape the assembly process by filtering species with similar traits, consistent with the "habitat templet" hypothesis (Southwood, 1977; HilleRisLambers et al., 2012). Another possible explanation lies in the connection 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; Pavoine, 2026).

In June, the multivariate distinction between algae morpho-functional groups and annelid 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 is attributed to the presence of large herbivores and tube-building nereidids, which secrete mucus within their tubes to capture suspended material from the water column for later ingestion (Daly, 1973; Toba & Sato, 2013).

Taken together, the structural complexity of macroalgal hosts can be used to evaluate the assembly process of their epifauna through the lens of the filtering metaphor, particularly 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 filters for associated epifaunal traits, mediating this process at the frond scale. They significantly affected the mean trait dissimilarity among 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 mitigate the effects of negative interspecific interactions and buffer environmental stress, thereby creating complex habitats that sustain high biodiversity at both taxonomic and functional levels.

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 R.L.N and S.L.D.D.M originally formulated the idea. S.L.D.D.M analyzed the data and wrote the first manuscript draft under the supervision of R.L.N and P.C.P Both R.L.N and 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 trait data will be made available after the review process at the S.L.D.D.M. GitHub repository (https://github.com/samuelmendes-polychaeta?tab=repositories).

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Table 1. Epifaunal marine annelid functional traits and their respective definitions.

Trait	Modality (Abbreviation)	Definition	Response mechanism
Body length (Growth)	Small (Lgs)	Less than 20mm	Energy requirements and species vulnerability (Jumars et al., 2015; Beauchard et al., 2017)
	Medium (Lgm)	From 20 to 200mm	
	Large (Lgl)	More than 200mm	
Feeding strategy (Survival)	Deposit feeder (Fsdf)	Feeds on organic matter accumulated on deposits from any kind of surface	Resource acquisition strategy (Rouse & Pleijel, 2001; Jumars et al., 2015)
	Suspension feeder (Fssf)	Feeds on water-suspended particles	
	Opportunist/scavenger (Fso)	Feeds on decaying matter	
	Herbivore (Fsh)	Feeds on living algae and/or plants	
	Predator (Fsp)	Feeds on other animals	
Larval development (Reproduction)	Direct development (Ddir)	Eggs are brooded until develop in young benthic juveniles, culminating in higher parental care investment and juvenile survival per reproductive event	Recruitment survival investment (Rouse, 2000; Beauchard et al., 2017; Rouse et al., 2022)
	Lecitotrophic larvae (Dlc)	Eggs develop as lecitotrophic larvae that remains in the water column by consuming yolk reserves	
	Planktotrophic larvae (Dpl)	Eggs are spawned as planktotrophic larvae, feeding on water column until settlement, which is associated with rapid colonization but higher juvenile mortality	

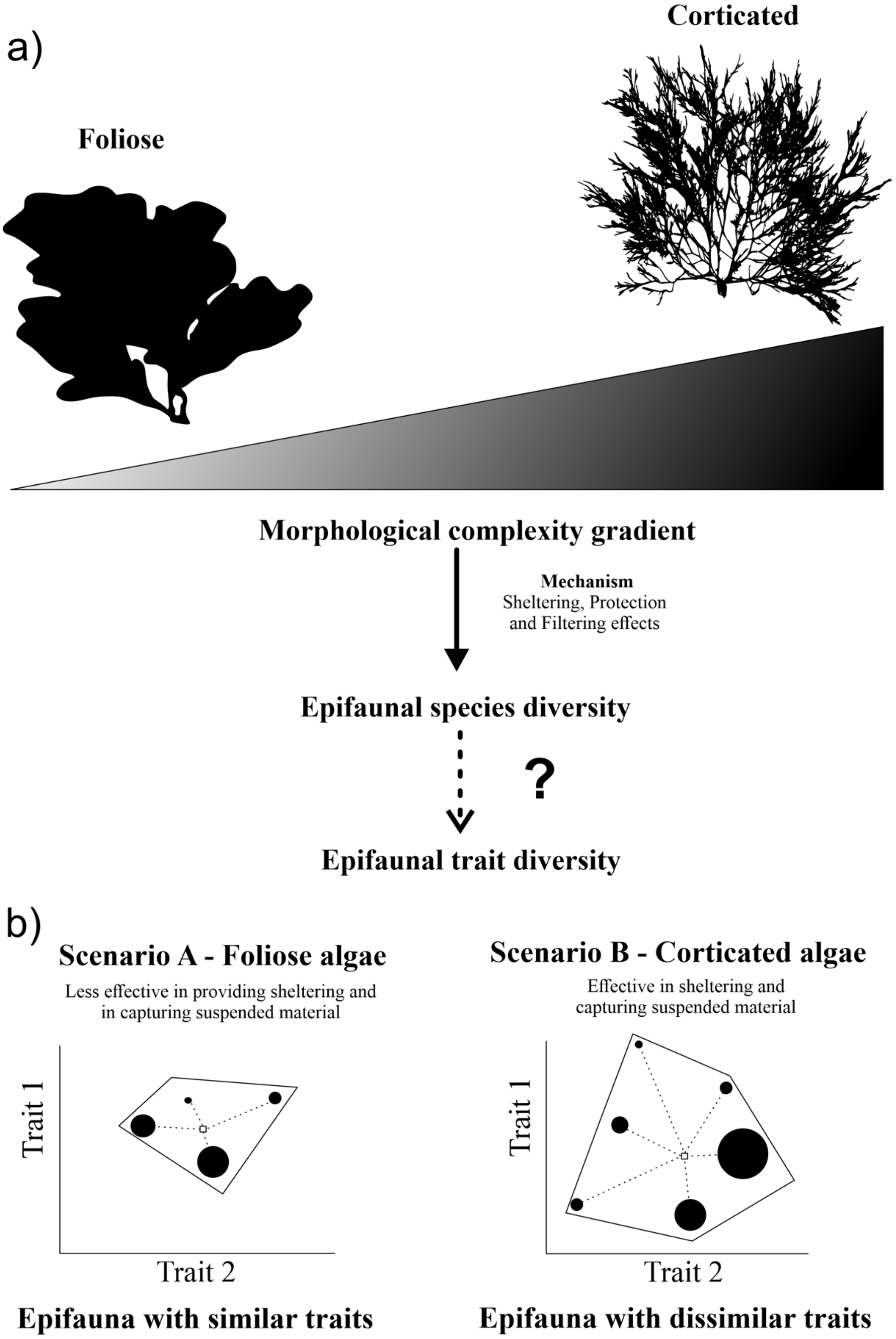

a)
Foliose
Corticated
Morphological complexity gradient
Mechanism
Sheltering, Protection
and Filtering effects
Epifaunal species diversity
?
Epifaunal trait diversity
b)
Scenario A - Foliose algae
Less effective in providing sheltering and
in capturing suspended material
Trait 1
Trait 2
Epifauna with similar traits
Scenario B - Corticated algae
Effective in sheltering and
capturing suspended material
Trait 1
Trait 2
Epifauna with dissimilar traits

Figure1.

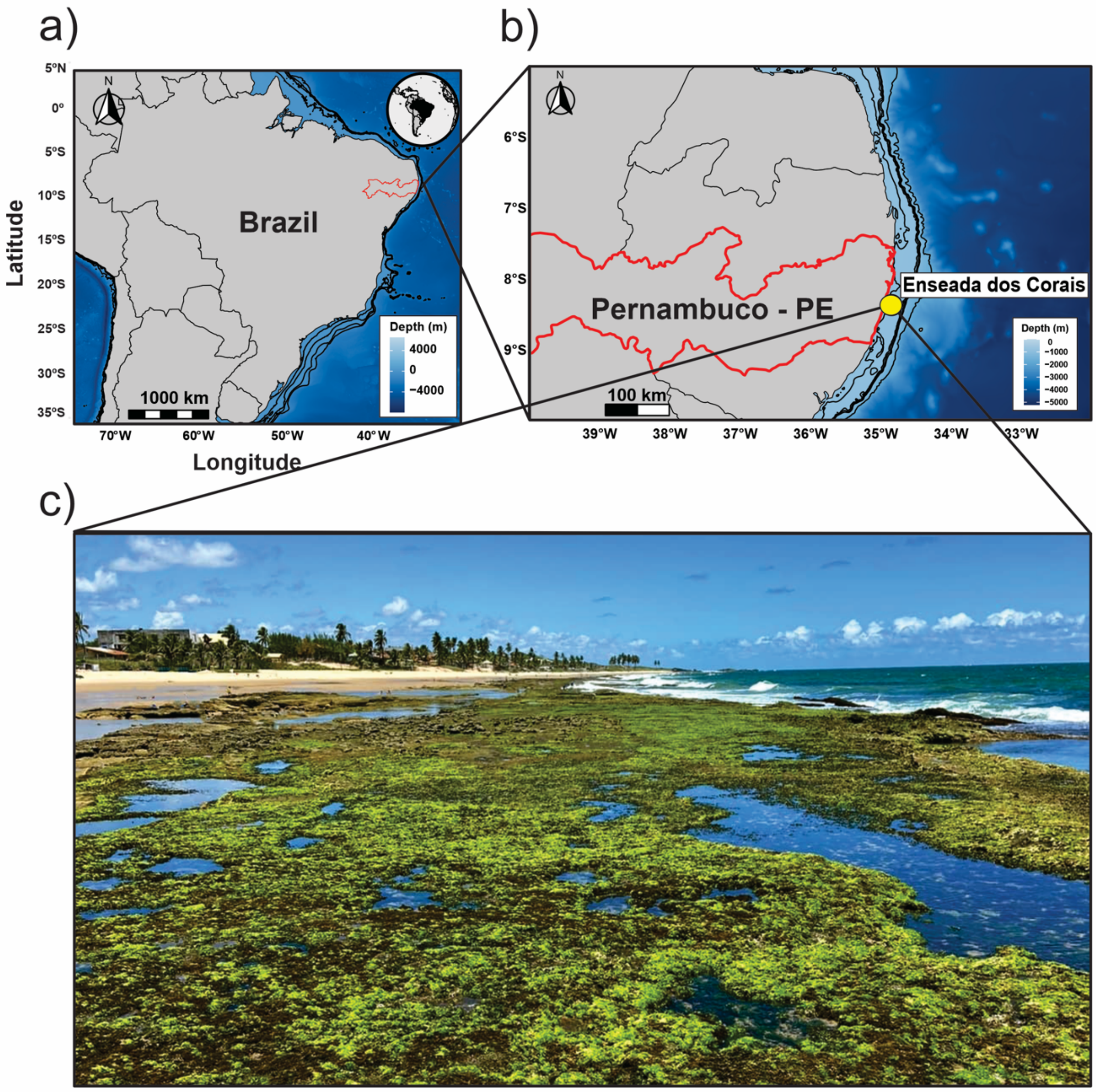

a)
b)
c)
5ºN
0º
5ºS
10ºS
15ºS
20ºS
25ºS
30ºS
35ºS
Latitude
Brazil
1000 km
Depth (m)
4000
0
−4000
70°W
60°W
50°W
40°W
Longitude
N
6°S
7°S
8°S
9°S
Pernambuco - PE
Enseada dos Corais
100 km
Depth (m)
0
−1000
−2000
−3000
−4000
−5000
39°W
38°W
37°W
36°W
35°W
34°W
33°W

Figure 2

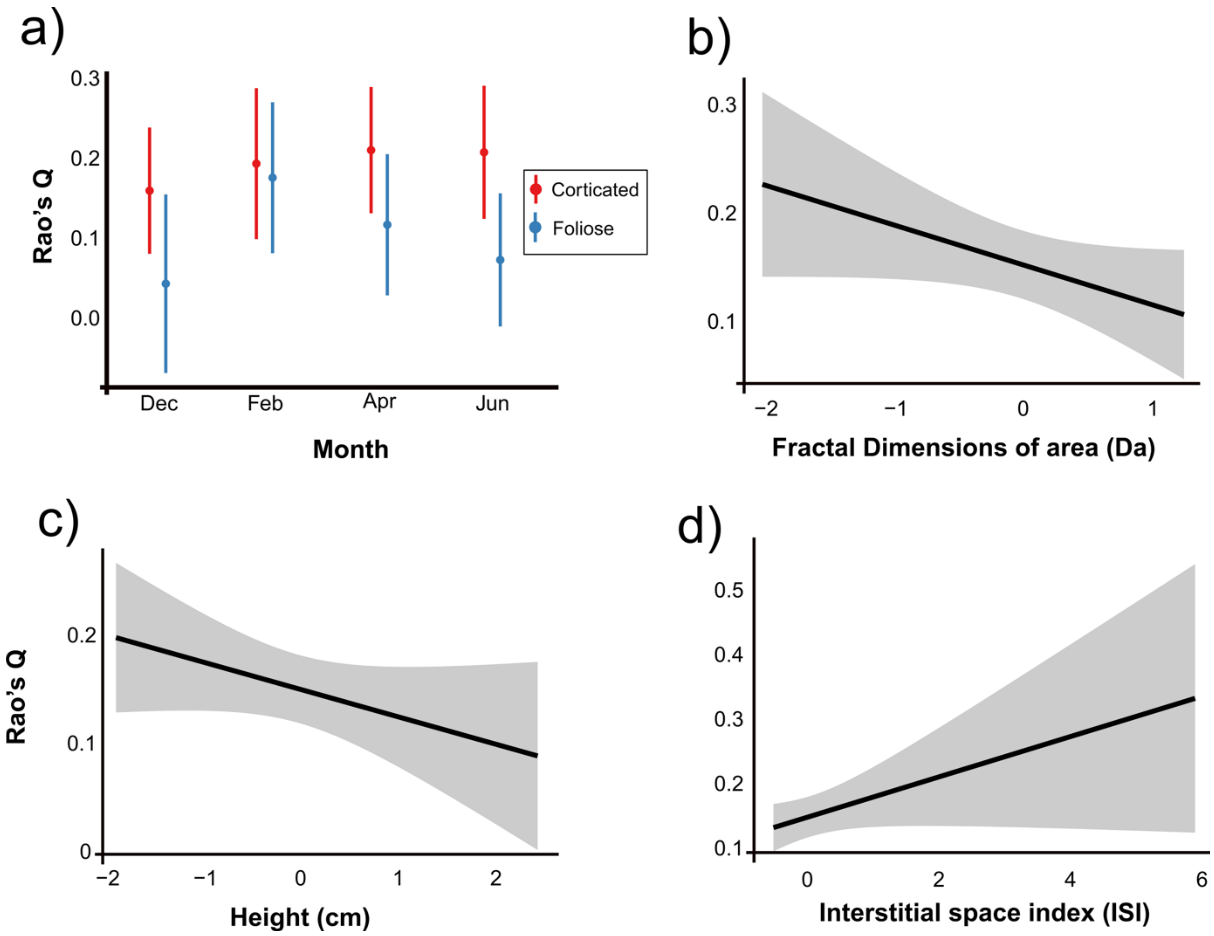

a)
Rao's Q
0.3
0.2
0.1
0.0
Dec
Feb
Apr
Jun
Month
● Corticated
● Foliose
b)
0.3
0.2
0.1
−2
−1
0
1
Fractal Dimensions of area (Da)
c)
Rao's Q
0.2
0.1
0
−2
−1
0
1
2
Height (cm)
d)
0.5
0.4
0.3
0.2
0.1
0
2
4
6
Interstitial space index (ISI)

Figure 3.

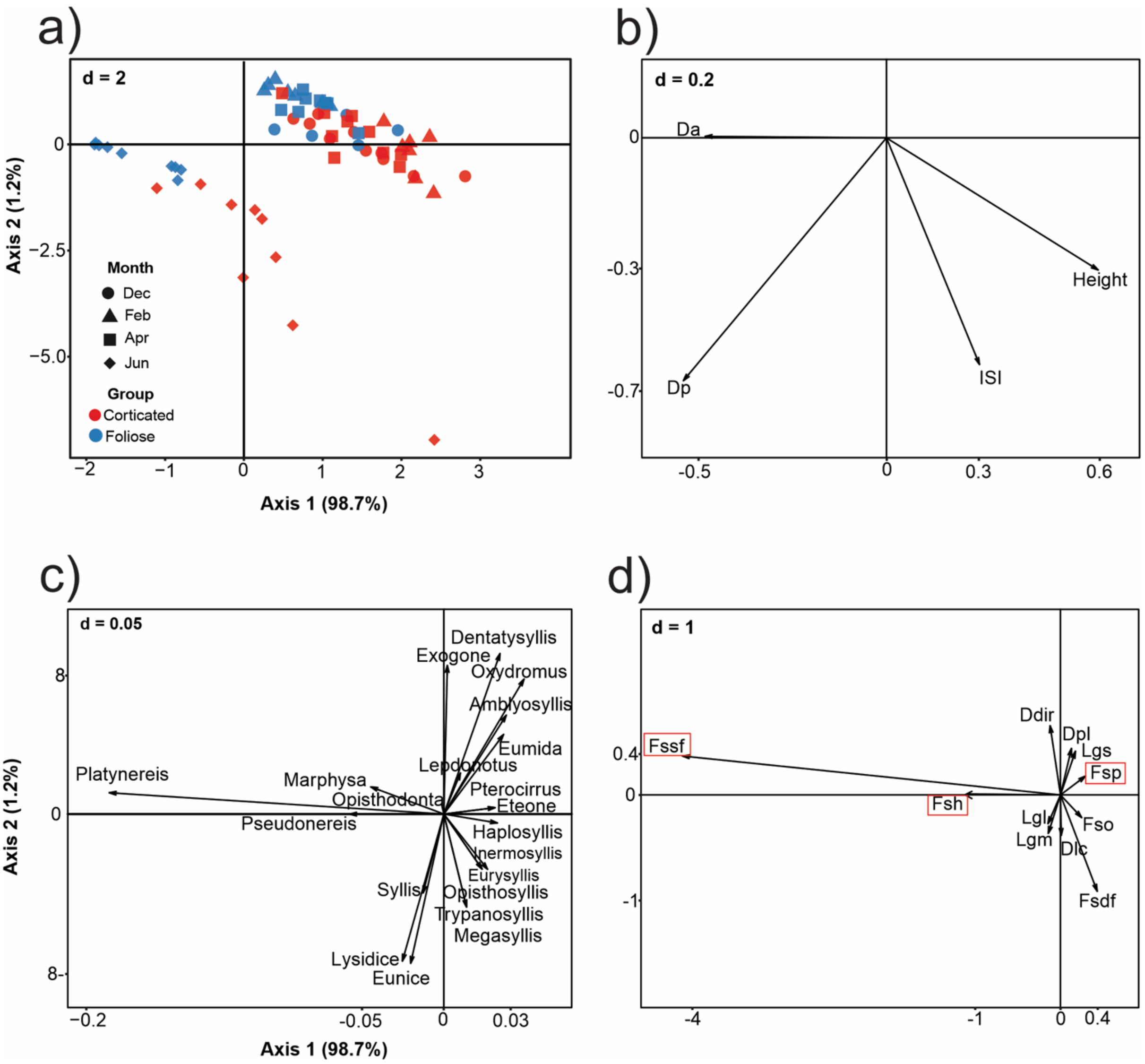
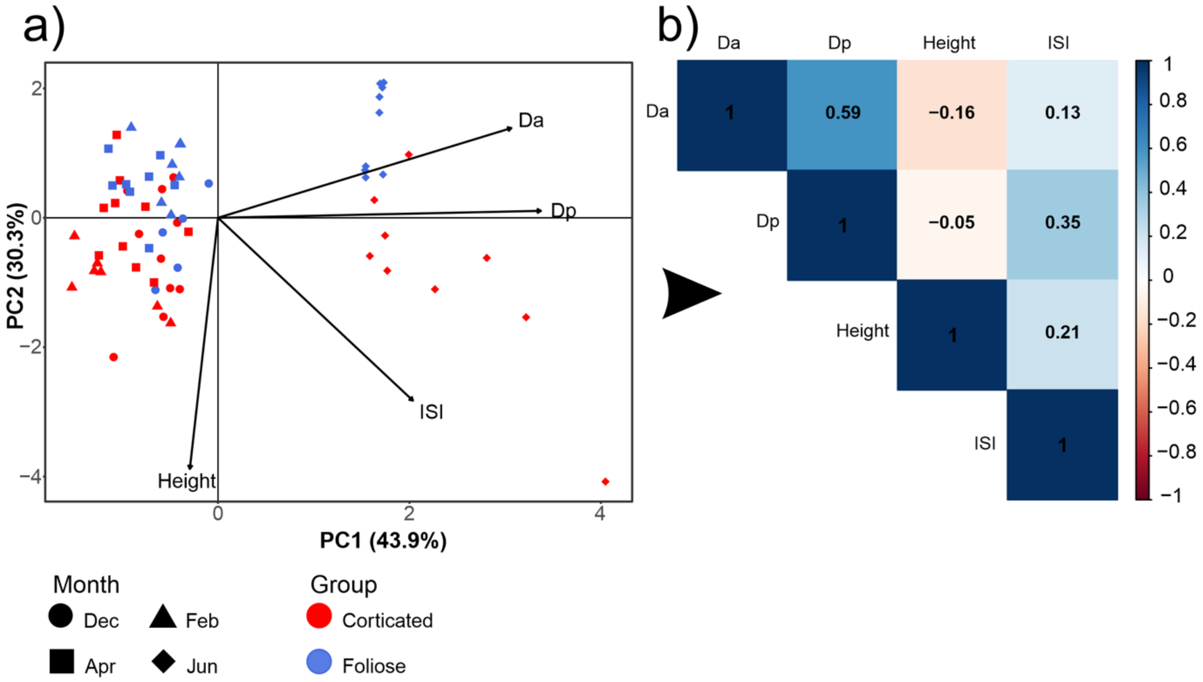

a)
d = 2
Axis 2 (1.2%)
Axis 1 (98.7%)
0
−2.5
−5.0
−2
−1
0
1
2
3
Month
Dec
Feb
Apr
Jun
Group
Corticated
Foliose
b)
d = 0.2
Da
Dp
ISI
Height
0
-0.3
-0.7
-0.5
0
0.3
0.6
c)
d = 0.05
Axis 2 (1.2%)
Axis 1 (98.7%)
8
0
8
-0.2
-0.05
0
0.03
Dentatysyllis
Exogone
Oxydromus
Amblyosyllis
Eumida
Lepidonotus
Platynereis
Marphysa
Opisthodonta
Pterocirrus
Eteone
Pseudonereis
Haplosyllis
Inermosyllis
Eurysyllis
Syllis
Opisthosyllis
Trypanosyllis
Megasyllis
Lysidice
Eunice
d)
d = 1
Ddir
Dpl
Lgs
Fssf
Fsp
Fsh
Lgl
Lgm
Fso
Dlc
Fsdf
0.4
0
-1
-4
-1
0
0.4

Figure 4.



	Da	Dp	Height	ISI
Da	1	0.59	−0.16	0.13
Dp		1	−0.05	0.35
Height			1	0.21
ISI				1

Figure S1.

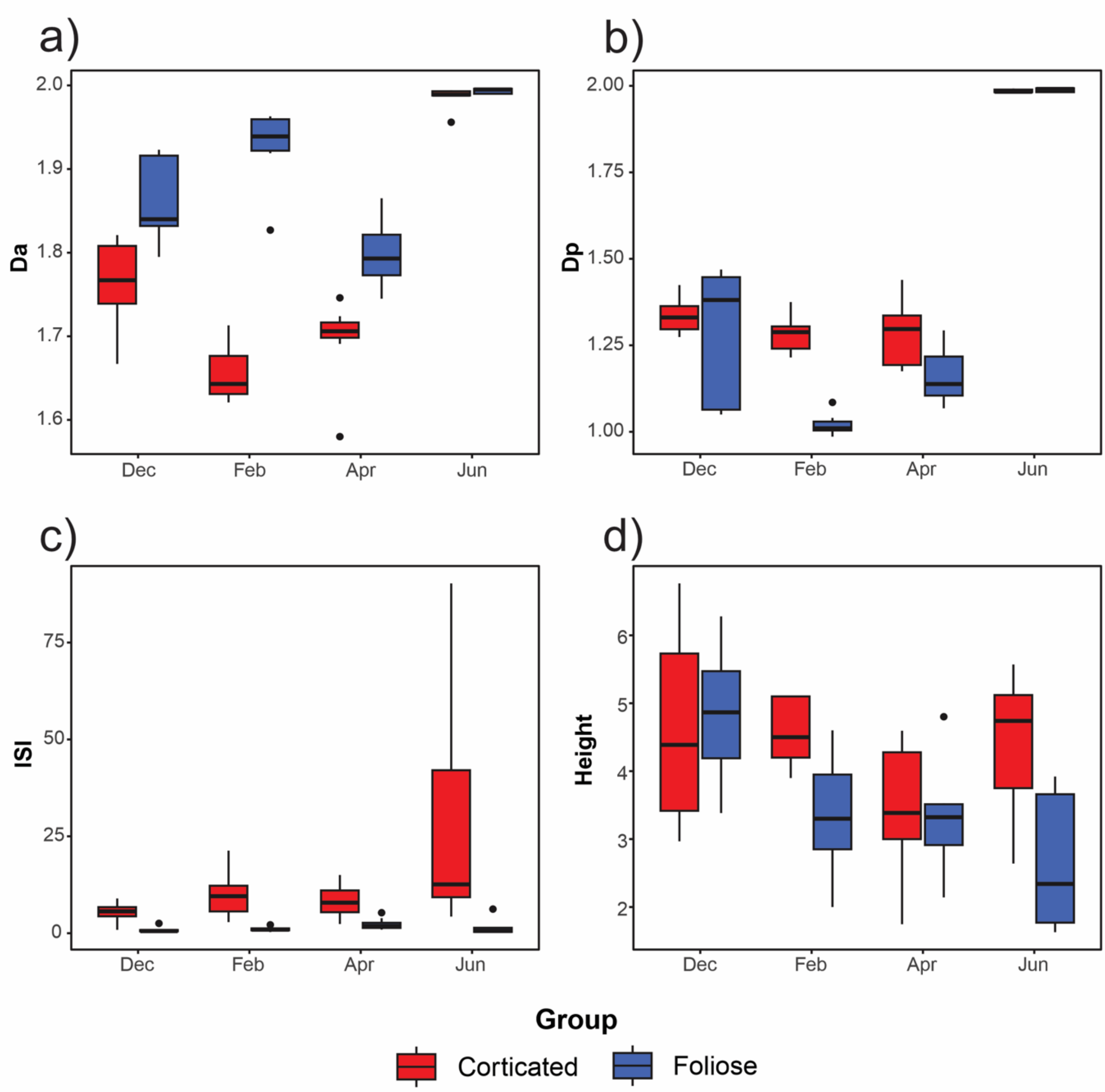

a)
Da
2.0
1.9
1.8
1.7
1.6
Dec
Feb
Apr
Jun
b)
Dp
2.00
1.75
1.50
1.25
1.00
Dec
Feb
Apr
Jun
c)
ISI
75
50
25
0
Dec
Feb
Apr
Jun
d)
Height
6
5
4
3
2
Dec
Feb
Apr
Jun
Group
Corticated
Foliose

Figure S2.

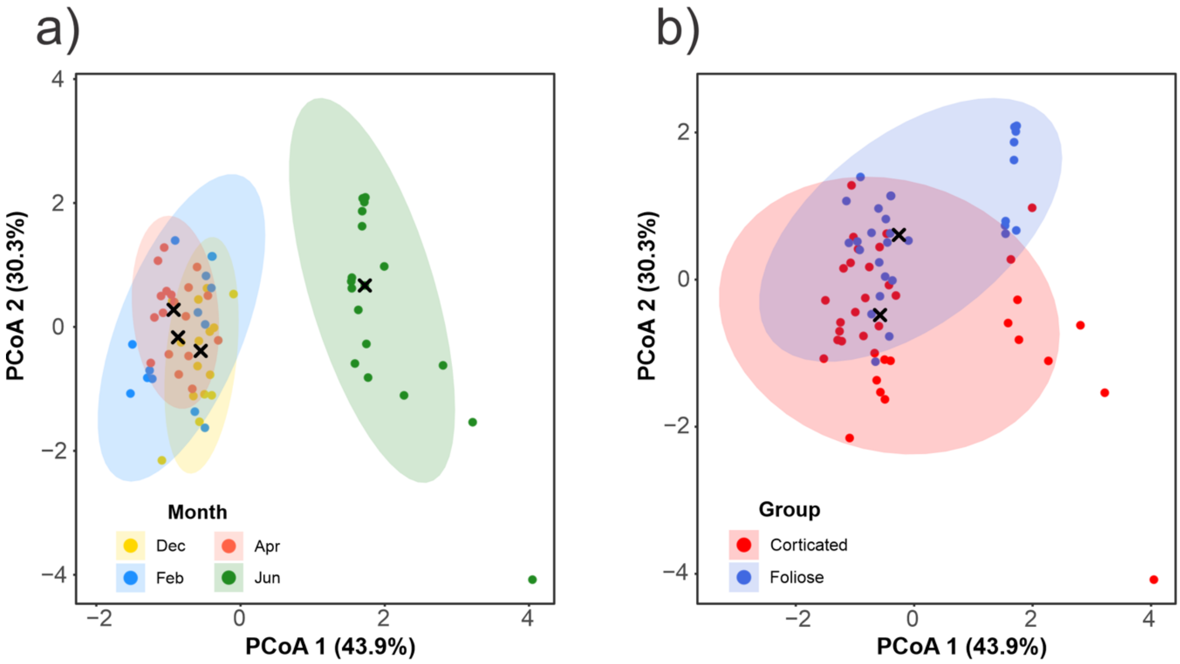

a)
PCoA 2 (30.3%)
PCoA 1 (43.9%)
4
2
0
−2
−4
−2
0
2
4
Month
Dec
Apr
Feb
Jun
b)
PCoA 2 (30.3%)
PCoA 1 (43.9%)
2
0
−2
−4
−2
0
2
4
Group
Corticated
Foliose

Figure S3.