

A Functional Perspective for Reef Benthic Communities: Temporal Trends in the Only Atoll in Southern Atlantic

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Abstract

Reef benthic communities provide many important ecosystem functions such as nutrient cycling, carbonate accretion and tridimensional complexity. Yet, reefs worldwide face an uncertain future, being threatened by local and global impacts. As an alternative approach to evaluate communities' changes, functional ecology aims to understand how species shape the environment and how functions conduct ecosystems' dynamics. The aim of this study was to investigate the temporal dynamics (2013–2019) of the reef benthic community in the most pristine reef in Brazil, Rocas Atoll, using a functional diversity approach. We identified 48 organisms grouped into 17 functional entities (according to their traits' combination), considering all sampling years. Benthic community was temporally dominated by functional entities responsible for providing low reef tridimensional complexity (represented mainly by turf algae). This dominance reflected in low values of functional entropy, due to uneven abundances distribution between unique functional entities, those that have unique trait combination. Functional richness oscillated over years, but did not show great changes in functional spaces, maintaining an equity in the number of functional entities and indicating stability of reef functions in Rocas Atoll, even with unequal abundances' distribution. Our study is the first to use a functional approach in temporal scale and represents a baseline for South Atlantic, since it provides the actual state of reef benthic communities using a functional approach, in an environment with no direct anthropic impacts. This can help to predict the effects on some ecosystem functions caused by local and global changes and its consequence for ecosystem services.

Introduction

Despite covering small areas in the oceans (Spalding and Grenfell 1997), reefs are the richest marine ecosystems, being comparable to tropical forests (Connel 1978; Costanza et al. 1997). In reefs, benthic communities deliver many important ecosystem functions (Solan et al. 2004; Brandl et al. 2019), such as nutrient cycling (Costanza et al. 1997), carbonate accretion and tridimensional complexity (Zawada et al. 2019a). Tridimensional complexity is a reef function that directly affects the habitat formation for many species, dictating how organisms interact with the environment and with each other (Zawada et al. 2019a). Yet, reefs worldwide face an uncertain future towards changes in the Anthropocene (Williams and Graham 2019), being threatened by local (e.g. overfishing and pollution) and global (e.g. climate change) impacts (Bellwood et al. 2004; Halpern et al. 2008; Munday et al. 2008; Hughes et al. 2010). Those impacts can compromise reef resilience, leading to phase shifts (Smith et al. 2016) and reef flattening (Alvarez-Filip et al. 2009), threatening the sustainability and stability of ecosystem functions and services (Nyström et al. 2000; Cardinale et al. 2012).

As an alternative approach to evaluate communities' changes (Mouillot et al. 2013), functional ecology aims to understand how species shape the environment and how functions conduct ecosystems' dynamics (Williams and Graham 2019). By using species traits, functional diversity has become increasingly appropriate to evaluate and to monitor communities (Ernst et al. 2006), by accessing spatiotemporal changes in different community's aspects through functional diversity indices (Mouillot et

al. 2013; Biggs et al. 2020). On marine environments, functional approaches have been widely applied for fishes and invertebrates (Bremner et al. 2003, 2006; Halpern and Floeter 2008; Mouillot et al. 2008, 2014; Villegger et al. 2010; Bolam et al. 2016; Gusmao et al. 2016; Bejarano et al. 2017; Richardson et al. 2017; Denis et al. 2019). Nevertheless, for reef benthic communities, studies assessing functional diversity are still scarce and mainly focused on corals (Darling et al. 2012; Madin et al. 2016; Denis et al. 2017; Zawada et al. 2019b; McWilliam et al. 2020). For the Brazilian coast, where turf algae and macroalgae are the main reef components (Aued et al. 2018), only one study has applied functional diversity indices to describe reef benthic communities (Aued et al, *in prep*).

Benthic communities of Brazilian reefs are dominated by turf algae and macroalgae (Aued et al. 2018). These reefs are threatened by many disturbances, as those associated to urban development, coastal runoff, marine tourism and overexploitation of reef organisms, and by ocean warming effects (Leão et al. 2019). Even in oceanic islands, which are relatively isolated from anthropogenic effects, it is possible to observe global scale impacts (Ferreira et al. 2013). For being unique and remote systems, oceanic islands reefs may operate as natural laboratories and as a reference for monitoring how these ecosystems behave through distinct spatiotemporal scales (Knowlton and Jackson 2008; Gatti et al. 2015). Moreover, spatiotemporal studies and monitoring programs support the identification of long-term changes in reef benthic communities as seen in the Caribbean, for example (Gardner et al. 2003; Côté et al. 2005; Alvarez-Filip et al. 2009; Schutte et al. 2010; Contreras-Silva et al. 2020). Still, baselines for these near pristine environments are scarce (Jackson 2001; Knowlton and Jackson 2008). In this context, a long-term ecological research can help to fulfill gaps of knowledge in understanding reef communities' spatiotemporal patterns in the Brazilian oceanic islands. All four Brazilian oceanic island are Marine Protected Areas, nevertheless, some are already impacted by overfishing, tourism (Giglio et al. 2018) and by coral bleaching events associated to thermal anomalies (Ferreira et al. 2013; Gaspar et al. 2021). These phenomena jeopardize reef biodiversity, and ecosystem functions and services (Hughes et al. 2018a; Williams and Graham 2019). However, an understanding of temporal patterns in ecosystem functions of oceanic islands is still lacking. Here, we used the functional approach to investigate the temporal dynamics (2013–2019) of the reef benthic community in the most pristine reef in Brazil, Rocas Atoll. To date, this is the longest publicly available dataset for benthic communities in the Southwestern Atlantic, representing a baseline for future studies of dynamics and functional diversity from reef benthic communities.

Material And Methods

Study area

Rocas Atoll (03°50'S, 33°49'W) is located approximately 267 km off the Brazilian coast (Kikuchi and Leão 1997). It is considered one of the world's smallest atolls, with 3,7 km in E-W directions and 2,5 km in N-S (Soares et al. 2011), and the only atoll in the South Atlantic Ocean (Kikuchi and Leão, 1997). Crustose coralline algae (CCA), vermetid gastropods and foraminiferans are the main shallow reef builders, while

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wer coverage and contribute less to the reef

framework structure (Gherardi 1995; Kikuchi and Leão 1997). Rocas Atoll is the first Brazilian no-take marine reserve, established in 1979. It has controlled anthropic impacts (e.g. very low pollution and fishing) and it is probably the most similar to a pristine reef in Brazil, being a natural laboratory and an important study area (Longo et al. 2015).

Benthic community sampling

Reef benthic community was annually monitored from 2013 to 2019 (May and June). In each year, benthic data was collected by photoquadrat method in four different sites: Âncoras, Cemitério, Falsa Barreta and Podes Crer (Fig. 1). Every year, three 20 m transect were fixed at each site, and a 1 m² quadrat was photographed every 2 m along each transect. In summary, over 838 photoquadrats were taken from the same reef area across seven years (Table 1 in Appendix). Percent cover of each photoquadrat were analyzed with CPCe software (Kohler and Gill 2006), randomly distributing 50 points over each photo. The organisms below each point were identified to the lowest taxonomic level possible.

Table 1
Reef sites and field effort in Rocas Atoll.

		Photoquadrats								
Site	Lat/Long	Depth	2013	2014	2015	2016	2017	2018	2019	Total
Âncoras	03°52'51" S 33°48'16" W	2-3m	28	32	30	33	30	33	31	217
Cemitério	03°52'18" S 33°49'02" W	1-2m	29	33	30	31	29	33	33	218
Falsa Barreta	03°51'64" S 33°49'40" W	1-4m	30	33	30	32	30	33	30	218
Podes Crer	03°52'20" S 33°48'45" W	1-3m	30	32	30	32	30	31	-	185
Total per year			117	130	120	128	119	130	94	838

Functional traits

We selected six traits proposed by Aued et al (*in prep*) for the benthic communities from the Brazilian Province and adapted them to the Rocas Atoll benthic community. We classified the organisms according

to five biological and one life history trait available in the literature (Table 2). Organisms sharing the same traits were grouped into Functional Entities (FE).

Table 2
Traits classification for reef benthic communities adapted from Aued et al (*in prep*).

Trait category	Trait	Trait level	Description
Biological	Maximum body size	Small (< 10cm)	Related directly to substrate cover (Woodward et al. 2005). For colonial morphospecies, we used the maximum size for colony or modular aggregations, and for unitary morphospecies, the individual size.
		Medium (10-50cm)	
		Large (50-400cm)	
		Very large (> 400cm)	
	Growth form	Bushy	The growth form of benthic organisms is related to the tridimensional habitat complexity and use of resources (Richardson et al. 2017).
		Encrusting	
		Encrusting/filamentous	
		Filamentous	
		Massive	
	Trophic type	Autotroph	Trophic type corresponds to food web interactions, competition and nutrient cycling (Wahl et al. 2011).
Autotroph/carnivore			
Carnivore			
Grazer			
Suspension/filter feeder			
Modularity	Solitary	Associated to reproduction type and the organisms' ability to occupy the substrate (Wahl et al. 2011)	
	Modular		
Carbonate accretion	Produce CaCO ₃	Influences the potential for reef structure development and maintenance (Perry and Alvarez-Filip 2018).	
	Do not produce CaCO ₃		
Life history	Reproduction type	Asexual	Can describe the ability to disperse and recover after a disturbance, the persistence and longevity of populations through time (Costello et al. 2015)
		Sexual/asexual	
		Sexual	

Functional diversity indices and data analysis

We measured functional diversity indices (Functional Richness and Functional Entropy – Rao) for each year. Functional Richness (Fric) measures the convex hull volume occupied by functional entities in

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functional space. Fric can show how functional diversity is related to ecosystem function through the gain or loss of functional entities and their traits, without considering their abundances (Cornwell et al. 2006; Villéger et al. 2008). Functional Entropy (Fent) or Rao index represents a combination between species abundances and their functional dissimilarity (Mouillot et al. 2013). It is the sum of pairwise distances between species randomly chosen, weighted by their relative abundances (Botta-Dukát 2005), as defined by the mathematical formula:

$$Q = \sum_i p_i K_i = \sum_i p_i \sum_j p_j \delta_{ij}$$

where p_i ($i = 1, 2, \dots, N$) are species relative abundances in the community composed by N species ($0 < p_i \leq 1$, because all calculations must involve only species with nonzero abundances); δ_{ij} are the elements of the dissimilarity matrix which summarize the pairwise functional dissimilarities between species i and j . $K_i = \sum_j p_j \delta_{ij}$ represents the expected dissimilarity between species i and the randomly chosen species j . When FEnt value approaches to 0, it indicates dissimilar abundances distribution among the most unique functional entities (i.e. those located at functional space vertices). Higher FEnt values near 1 indicate a more even distribution in unique functional entities abundances.

Using a functional trait matrix built with Gower's distance, we plotted the multidimensional trait space for each year based on a Principal Coordinate Analysis (PCoA). The distribution of functional entities (FE) and their abundance were plotted in the functional trait space using the two principal axes. All analysis were made using software R (R Core Team, 2019). Fric was calculated using the function 'multidimFD' from 'FD' package (Laliberté et al. 2015), and for FEnt we used 'uniqueness' function (Ricotta et al. 2016). We used generalized linear models (GLM) with indices results and years as factors to test changes through the time series, and the package 'ggplot2' (Wickham and Winston 2019) for plots.

Results

Community functional structure

We identified 48 organisms grouped into 17 functional entities (those who share the same trait combination), considering the seven years of sampling. Functional entities and their respective ecosystem functions are presented in Fig. 2. Suspension/filter feeders are functional entities composed by sponges or ascidians, responsible for nutrient cycling function. Macroalgae make up primary production and high tridimensional complexity functional entities, while turf algae, cyanobacteria and zoanthids compose low tridimensional complexity functional entities. Corals such as *Siderastrea stellata*, *Porites astreoides* and *Favia gravida* (massive bioconstructors), and crustose coralline algae (encrusting bioconstructors), perform calcium carbonate accretion function, being responsible for reef formation and maintenance. The functional trait space was occupied by 15 functional entities every year, but organism's composition differed, reaching the highest value (36 morphospecies) in 2013 and the lowest (26 morphospecies) in 2019 (Table 3).

Table 3
 Number of morphospecies, functional entities (i.e. morphospecies that share similar traits).

	Morphospecies richness	Functional entities
2013	36	15
2014	31	15
2015	33	15
2016	28	15
2017	30	15
2018	29	15
2019	26	15

Low tridimensional complexity function, represented mainly by turf algae, was dominant every year, with functional entities mean percent cover oscillating from 40.56–59.18% (GLM $p < 0.05$) (Fig. 3). Despite presenting 5.96% cover in 2019, high tridimensional complexity entities oscillated from 16.05–30.28% cover between 2013 and 2018 (GLM $p < 0.05$). Encrusting calcifiers also presented significant variations in percent cover (GLM $p < 0.05$), ranging from 1.96–5.47%, while massive calcifiers did not have clear oscillations through years (GLM $p > 0.05$), with abundances fluctuating between 1.65% and 2.70%. Mean percent cover of suspension/filter-feeders did not exceed 1% nor presented clear oscillation over the years (GLM $p > 0.05$).

Functional diversity dynamics

Overall, Functional Richness (FRic) oscillated over the years (GLM $p < 0.05$) but presented small changes in convex hull volumes over the years (Fig. 4), indicating temporal stability in ecosystem functions provided by functional entities. FRic is shown in the functional space, where axes represent the higher explanation PCoA axis (PC1-PC2). Temporal differences in FRic occurred due to the presence of a massive bioconstructor functional entity (represented by *Favia gravida*) only in 2015 and 2017; and a high tridimensional primary producer functional entity in 2013, 2014 and 2016 (Fig. 4). Despite an almost fulfilled convex hull volume in 2018, due to a new functional entity composed by a globular suspension/filter-feeder, that did not appear in previous years, FRic was lower than 2015 and 2017 because the convex hull volume was less fulfilled in axis 3 and 4 (Fig. 5 in Appendix).

Functional Entropy (FEnt) was low every year, indicating uneven percent cover between functional entities (Fig. 6). Despite significant oscillations in FEnt between years (GLM $p < 0.05$), differences among years occurred in small scales (Fig. 6), showing small variations in percent cover of functional entities with unique trait combination. These fluctuations in FEnt were conducted by low and high tridimensional complexity and encrusting bioconstructors functional entities percent cover, located at functional space

vertices. The highest FEnt was in 2013, representing a well-distributed percent cover of extreme functional entities if compared to other years, while the lowest was in 2019, due to uneven percent cover distribution, when reef benthic community was dominated by low tridimensional complexity functional entities represented mainly by turf algae (59.19% cover; Fig. 3).

Discussion

Our study is the first to use functional approach in a temporal scale for reef benthic communities. Our results show that Rocas Atoll benthic community is temporally dominated by functional entities responsible for providing low reef tridimensional complexity (e.g. turf algae, cyanobacteria and *Zoanthus sociatus*), high tridimensional complexity and primary production (e.g. macroalgae as *Sargassum* spp., *Dictyopteris* spp.), with low contribution of carbonate accretion (e.g. crustose coralline algae and corals as *Siderastrea stellata*, *Porites astreoides* and *Favia gravida*) and nutrient cycling (e.g. sponges and/or ascidians) functional entities. This dominance reflected in low values of functional entropy (FEnt), due to uneven abundances distribution between unique functional entities, that is, those that have unique trait combination and are in functional space vertices. Functional richness (FRic) oscillated over years, but did not show great changes in functional spaces, maintaining an equity in the number of functional entities and indicating stability of reef functions in Rocas Atoll, even with unequal abundances' distribution.

Diversity patterns in Brazilian oceanic islands are well known for reef fishes assemblages and barely known for benthic organisms (Floeter and Gasparini 2000; Floeter et al. 2001, 2008; Pinheiro et al. 2017, Aued et al. 2018). Marine oceanic communities generally present low species richness when compared to coastal communities, specially due to their isolation and different oceanographic conditions (Pinheiro et al. 2017), and functional richness (FRic) usually responds to species richness pattern (Whittaker et al. 2014; Jacquet et al. 2017; Wong et al. 2018). Our results indicate that organisms' richness did not affect the number of functional entities and FRic values, which presented small variations through the years. In 2013, when we identified 36 morphospecies, and in 2019 - the lowest morphospecies richness -, FRic was the same in our temporal series. If compared to other regions in the Brazilian province - mainly those located at mid-latitudes, but also with Fernando de Noronha Archipelago, other oceanic island located less than 100 miles from Rocas Atoll -, the number of taxa and FRic are both low (Aued et al. 2018; Aued et al. *in prep*).

Low tridimensional complexity functional entities are composed by benthic organisms from different groups, such as epilithic algal matrix, articulate coralline algae, cyanobacteria and zoanths. Different from entities that are bioconstructors or provide high tridimensional complexity, they form widespread patches and occupy larger areas on the substrate, with small vertical growth. Epilithic algal matrix (EAM or turf algae) is the main component of reef benthic communities among Brazilian reefs, including Rocas Atoll (Longo et al. 2015; Aued et al. 2018). Our results showed higher abundances of low tridimensional complexity functional entities every year, indicating that the community is also dominated temporally by turf. On EAM composition, it is possible to find a variety of algal groups (e.g. diatoms, cyanobacteria, Chlorophyta, Rhodophyta), associated crustaceans and sediment (Connell et al. 2014). Therefore, EAM

contribute to sediment trap, primary productivity, and provide habitat and food for other marine organisms (Vroom et al. 2006; Dijkstra et al. 2017), but offer smaller tridimensional complexity. Therefore, due to its high percent cover, the functional entities composed by EAM are also the main responsible for primary production in Rocas Atoll.

High tridimensional complexity in marine environments, such as tropical forests in terrestrial environments, provides habitat for many marine species, promotes interactions between species and the environment (Marx and Herrkind 1985; Williams et al. 2002; Graham and Nash 2013; Richardson et al. 2017; Fulton et al. 2019; Lamy et al. 2020), and also influences reef fish recruitment and development (Evans et al. 2014; Fontoura et al. 2019). This function is generally associated to branching corals in the Caribbean and Indo-Pacific sites (Alvarez-Filip et al. 2011; McWilliam et al. 2018; Richardson et al. 2020), but for Rocas Atoll, due to the absence of branching bioconstructors, the 'high tridimensional complexity' is associated to macroalgae. Opposed to massive corals, like *Siderastrea stellata*, or benthic organisms that form widespread patches, like EAM and zoanths, macroalgae can act as refuge from larger predators and affect the local diversity (Ware et al. 2019). Besides providing local tridimensional complexity, primary production is also a function performed by macroalgae and EAM (Brandl et al. 2019; Fulton et al. 2019). Primary producers usually dominate populated atolls and regions with high human disturbances (Sandin et al. 2008). Conversely, for Rocas Atoll, where anthropic impacts are controlled, primary production is associated to ten of the 17 functional entities found in our study. Entities associated to low and high tridimensional complexity occupy together around 80% of the substrate in every sampling year. Due to their dominance over the community and to their extreme trait combination, FEnt was low at Rocas Atoll every year, but still the small oscillations in FEnt occurred as a function of the oscillations of functional entities percent cover, indicating that these functional entities are substantially contributing to ecosystem functioning (D'Agata et al. 2016).

Both carbonate accretion (bioconstructors) and nutrient cycling (suspension/filter feeders) functional entities, have low percent cover at Brazilian Province when compared to the other groups (Aued et al. 2018), and our results showed that this has been a consistent pattern at Rocas Atoll through time. The distribution and abundance of bioconstructors can create habitat heterogeneity and provide the main framework of reef ecosystems (Perry and Alvarez-Filip 2018). FRic revealed four functional entities responsible by calcium carbonate accretion across time, but due to its unique trait combination and low percent cover, they might be considered as vulnerable functional entities. Crustose coralline algae (CCA) is the main reef builder in Rocas Atoll (Kikuchi and Leão 1997), but during the years of sampling it presented low and oscillating percent cover. This pattern may be related to a potential limitation of the photoquadrat method used (Preskitt et al. 2004). The same occurred to the functional entities composed by corals that act as massive bioconstructors. Still, the maintenance of massive bioconstructors percent cover indicates that calcium carbonate accretion function is stable over the years. Sponges and/or ascidians (suspension/filter feeder functional entities) are the main responsible by nutrient uptake and cycling, and bioerosion in reef ecosystems (Bell 2008; Brandl et al. 2019). Although suspension/filter feeders were persistent, their percent cover was extremely low. Even providing important functional roles in the

ecosystem (Bell 2008; De Goeij et al. 2013), due to its low percent cover, suspension/filter feeders might not be considerably influencing the nutrient cycling in Rocas Atoll shallow reefs.

Functional richness and functional entropy are indices that represent the actual state of communities functional structure (Galland et al. 2020). Therefore, applying them in temporal scales might act as a baseline for future studies. Our results indicated a temporal stability in Rocas Atoll benthic communities, in the opposite way of many places around the world, where not just benthic, but also fish communities, are eroding (Jackson 2001; Gardner et al. 2003; Schutte et al. 2010; Alvarez-Filip et al. 2011; Cruz et al. 2015a; Smith et al. 2016; de Bakker et al. 2017; Leggat et al. 2019; Muñiz-Castillo et al. 2019). Changes in FRic over the years occurred when two specific functional entities, a massive bioconstructor and a suspension/filter feeder, were found in our analysis. Higher FRic values were in 2015 and 2017, when the massive bioconstructors functional entity appeared in one photoquadrat in both years, while in 2018 – the second higher FRic -, the suspension/filter feeder was detected. In the other years, when both functional entities were not found in our analysis, FRic in Rocas Atoll presented the lowest values, but no ecosystem function was lost.

FEnt was low every year due to uneven abundances distribution between functional entities with unique trait combination (i.e. those located at functional space vertices). The uneven abundance distribution over the years is conducted mainly by the dominance of functional entities responsible for low and high tridimensional complexity, and low percent cover of other groups as bioconstructors and suspension/filter-feeders, a pattern already observed for Brazilian Province and Rocas Atoll (Longo et al. 2015; Aued et al. 2018). Oscillations in FEnt are, therefore, related to these dominant groups and their ephemeral oscillations, given that they are groups that respond faster to different environmental conditions (Cheroske et al. 2000; Vroom et al. 2006). By using both FRic and FEnt, it is possible to have a notion of communities functional redundancy (Galland et al. 2020). Functional redundancy buffers ecosystems functions loss against species loss in a community, ensuring stability and resilience to communities structures and functions (Bender et al. 2017; Biggs et al. 2020). FEnt low values and high FRic over the years might be indicating low functional redundancy, that is, there are many functional entities with unique trait combination with low percent cover in Rocas Atoll benthic community. If somehow these functional entities and morphospecies go extinct locally, considering all impacts that might happen with climate change over benthic communities (i.e. phase shifts, reef flattening) (Alvarez-Filip et al. 2011; de Bakker et al. 2017; McWilliam et al. 2020), there will be no other functional entities able to substitute the same function in the functional space and, consequentially, there will be erosion in ecosystems functions (Wong et al. 2018).

Species occurrence and abundances can vary in different ways in a community, depending on natural changes of environmental conditions such as light penetration, temperature and sediment (Putman and Wratten 1984; Perry and Alvarez-Filip 2018). Consequently, changes on environmental conditions can cause impacts in species traits and abundances and, therefore, in ecosystem functions (Wong et al. 2018; Zawada et al. 2019a). Being an oceanic island, Rocas Atoll is a very dynamic system (Longo et al. 2015), with intense water circulation and wave action that can influence the availability and sediment dynamics

(Hearn et al. 2001). For example, depending on the quantity of sediment, it can cause shading and hence, affect primary production (Riul et al. 2008), also it can promote the temporal burrowing and smothering of coral colonies (Brown et al. 2002). This probably explains differences in percent cover of massive bioconstructors functional entities. The intense hydrodynamic at shallow tide pools can also favor the presence of more resistant functional entities (Steneck and Dethier 1994; Cheroske et al. 2000), such as the ones composed by epilithic algal matrix, macroalgae and crustose coralline algae.

Considering the more common and frequent global impacts caused by ocean warming and thermal anomalies, and other emerging impacts of the Anthropocene (Hughes et al. 2017, 2018b; Lough et al. 2018; Perry and Alvarez-Filip 2018; Williams et al. 2019), there is a chance of Rocas Atoll be impacted either. In view of these changes around the world, it is more than necessary to enhance our knowledge of ecosystems actual state to serve as baselines for future studies (Christensen et al. 1996; Sandin et al. 2008; Downs et al. 2011; Gatti et al. 2015; Chollett and Robertson 2020), as well as to keep monitoring these communities structures and functions (Alvarez-Filip et al. 2011; Cruz et al. 2015b; Heron et al. 2016; Smith et al. 2016; de Bakker et al. 2017). Our study, inserted in Long Term Ecological Research of Brazilian Oceanic Islands, therefore acts as a baseline for Brazilian Province, since it provides the actual state of reef benthic communities using a functional approach, in an environment with no direct anthropic impacts.

Wilderness areas as Rocas Atoll support unique ecological values, different from the ones near the coast, due to well-managed efforts and limited human pressure, being the only environment considered as near pristine in Brazil (Longo et al. 2015). In our research, due to the maintenance in number of functional entities, small oscillations in FRic and FEnt, ecosystem functions do not seem to vary substantially, indicating a stable state dominated by primary producers and tridimensional complexity functional entities over the years. However, we speculate that the changes in the Anthropocene may result in gains in some functions (*e.g.* low complexity) and loss of other functions (*e.g.* carbonate accretion), and hence cause erosions in FRic and even smaller FEnt values. Indeed, a strong bleaching event has stricken Rocas Atoll bioconstructors recently (Gaspar et al. 2021). Therefore, reef communities are expected to show changes in the next years. Although COVID-19 pandemic and political dismantling of science and institutions in Brazil are impairing our monitoring, the continuity of temporal sampling is needed to understand how local and global variables are affecting benthic ecosystem functions even at pristine places, like Rocas Atoll. This can help to predict the effects on some ecosystem function (*e.g.* complexity) caused by global changes and it's consequence for the ecosystem services.

Declarations

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Conflicts of interest

The authors declare that they have no conflict of interest.

Availability of data and material

All data generated and analyzed during this study are available from the corresponding author. The LTER program will publish all data on a global database soon.

Code availability

The code used for the analysis are available from the corresponding author.

Author’s contributions

VAPP, AWA and BS: substantial contribution to the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to the manuscript’s preparation.

JBZ and LCPMS: contribution to data analysis; contribution to the manuscript’s preparation.

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Figures

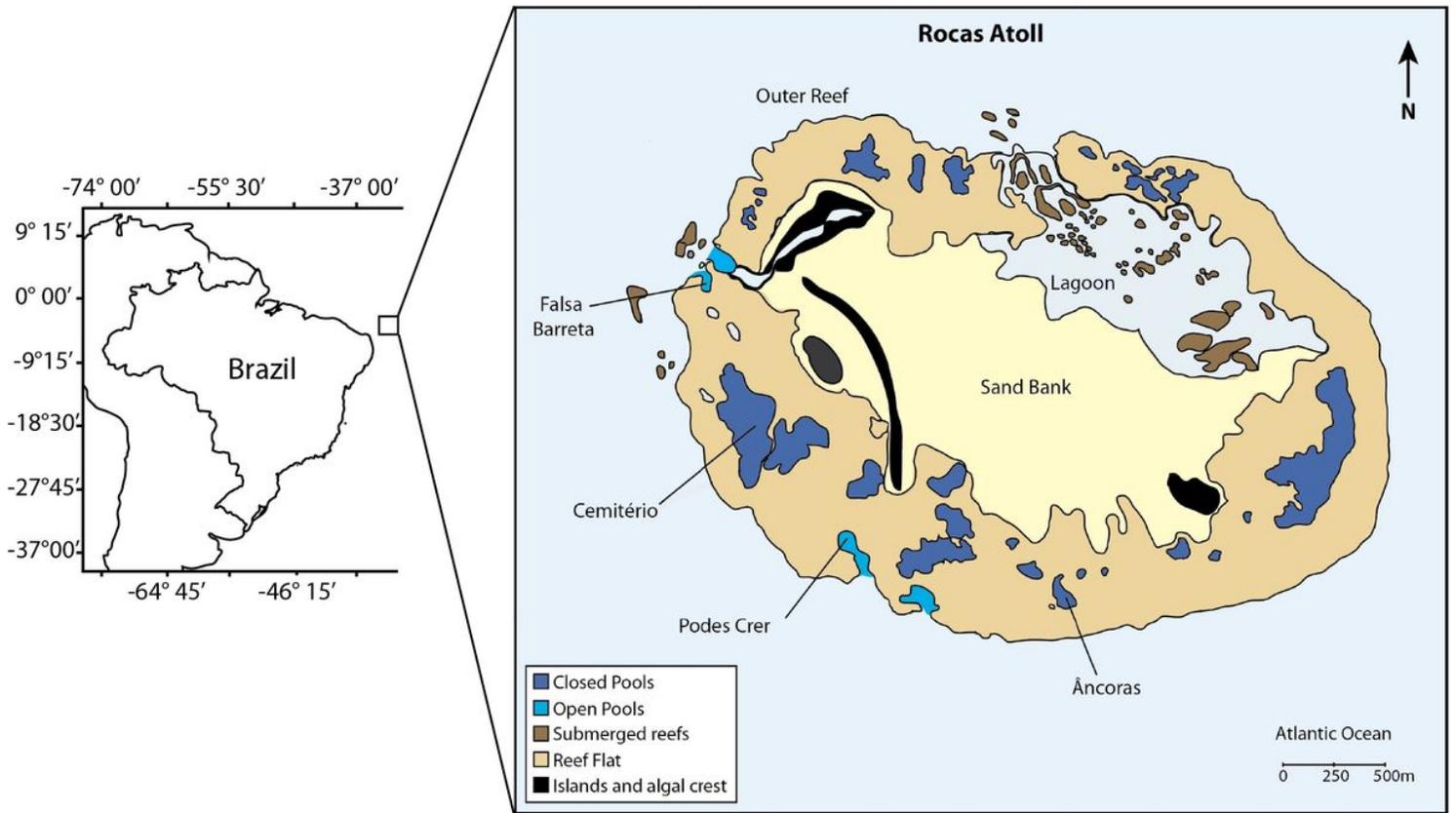


Figure 1

Location of Rocas Atoll and sampling sites during the seven years of monitoring indicated by arrows. Adapted from Longo et al. (2015).

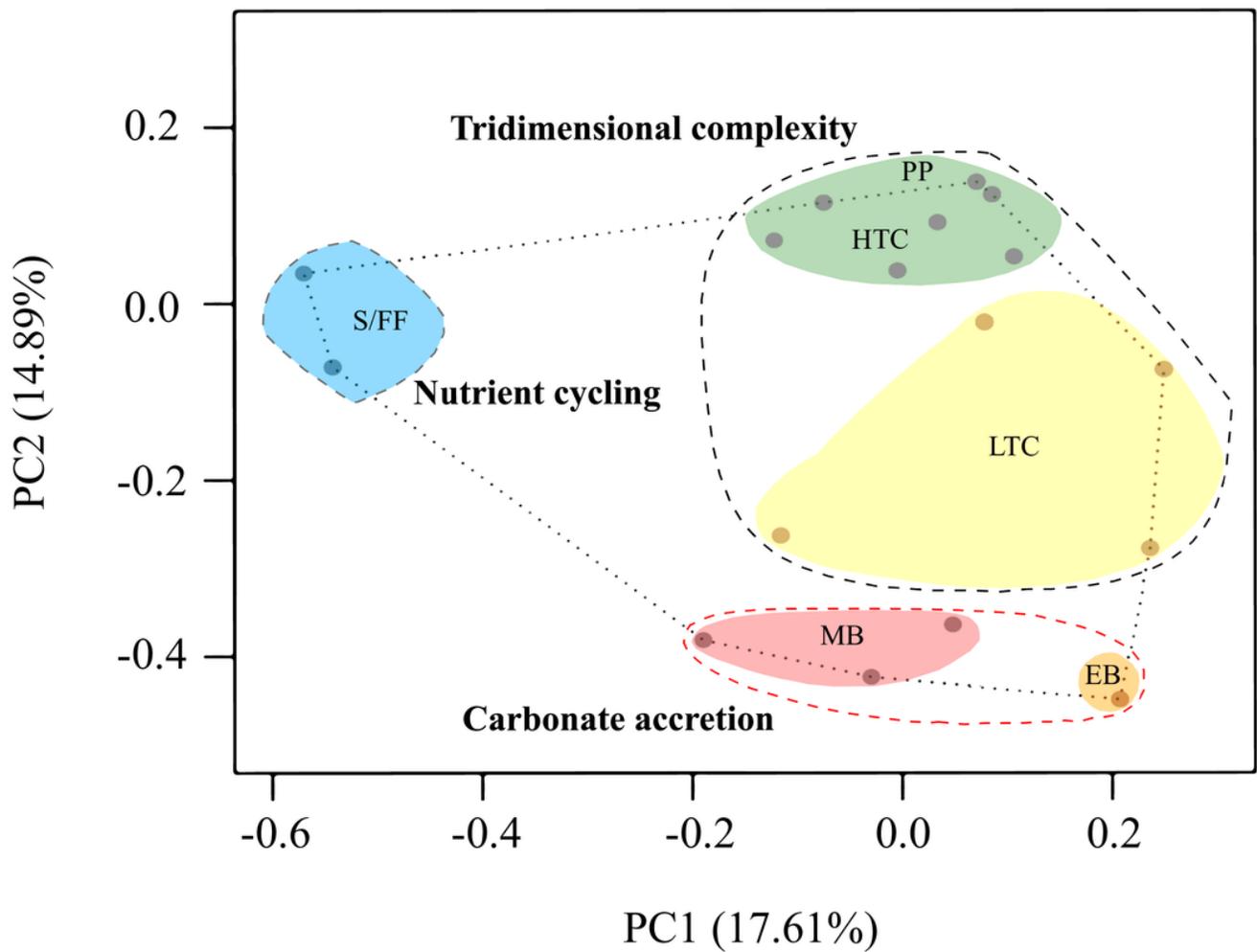


Figure 2

Position of functional entities (circles) in the multidimensional trait space considering all monitoring years. Dotted polygons represent the major ecosystem function performed by functional entities (tridimensional complexity, carbonate accretion and nutrient cycling). Filled polygons are groups of functional entities within specific ecosystem functions. PP: primary producers; HTC: high tridimensional complexity; LTC: low tridimensional complexity; EB: encrusting bioconstructors; MB: massive bioconstructors; S/FF: suspension/filter feeders.

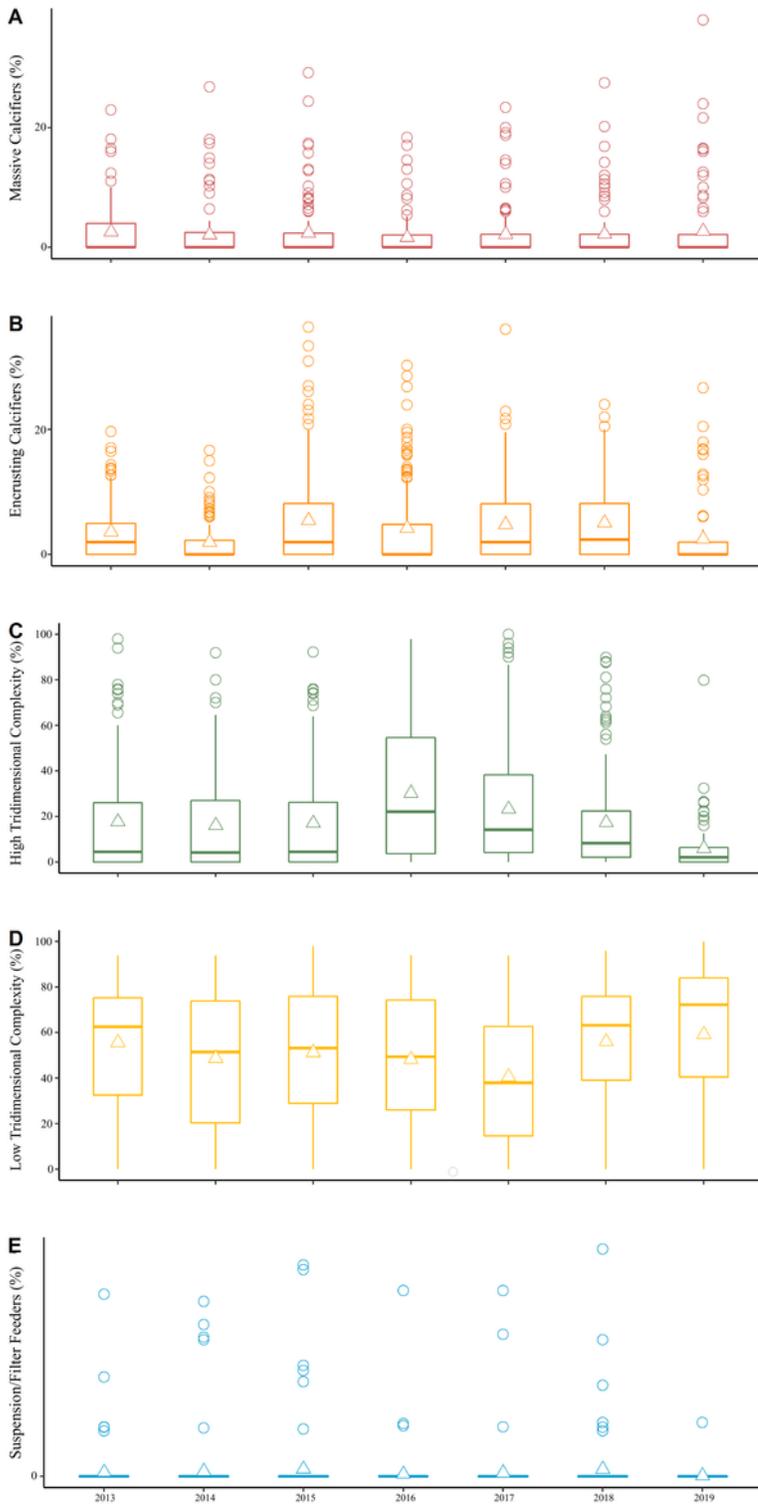


Figure 3

Percent cover dynamics from ecosystem functions (considering functional entities abundances), showing dominance of low tridimensional complexity function during our time series. Triangles represent mean percent cover and circles the outlier values. Mind the scale. (A) Massive calcifiers (e.g. corals as *Siderastrea stellata*) mean percent cover oscillated between 1.65-2.70% (GLM $p > 0.05$); (B) Encrusting calcifiers (e.g. *Porolithothamnion*) mean percent cover between 1.96-5.47% (GLM $p < 0.05$); (C) High

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tridimensional complexity (e.g. big macroalgae as *Sargassum* spp.) mean percent cover between 5.96-30.28% (GLM $p < 0.05$); (D) Low tridimensional complexity (e.g. turf algae) mean percent cover between 40.56-59.18% (GLM $p < 0.05$); and (E) Suspension/Filter-feeders (e.g. sponges and/or ascidians) mean percent cover lower than 1% (GLM $p > 0.05$).

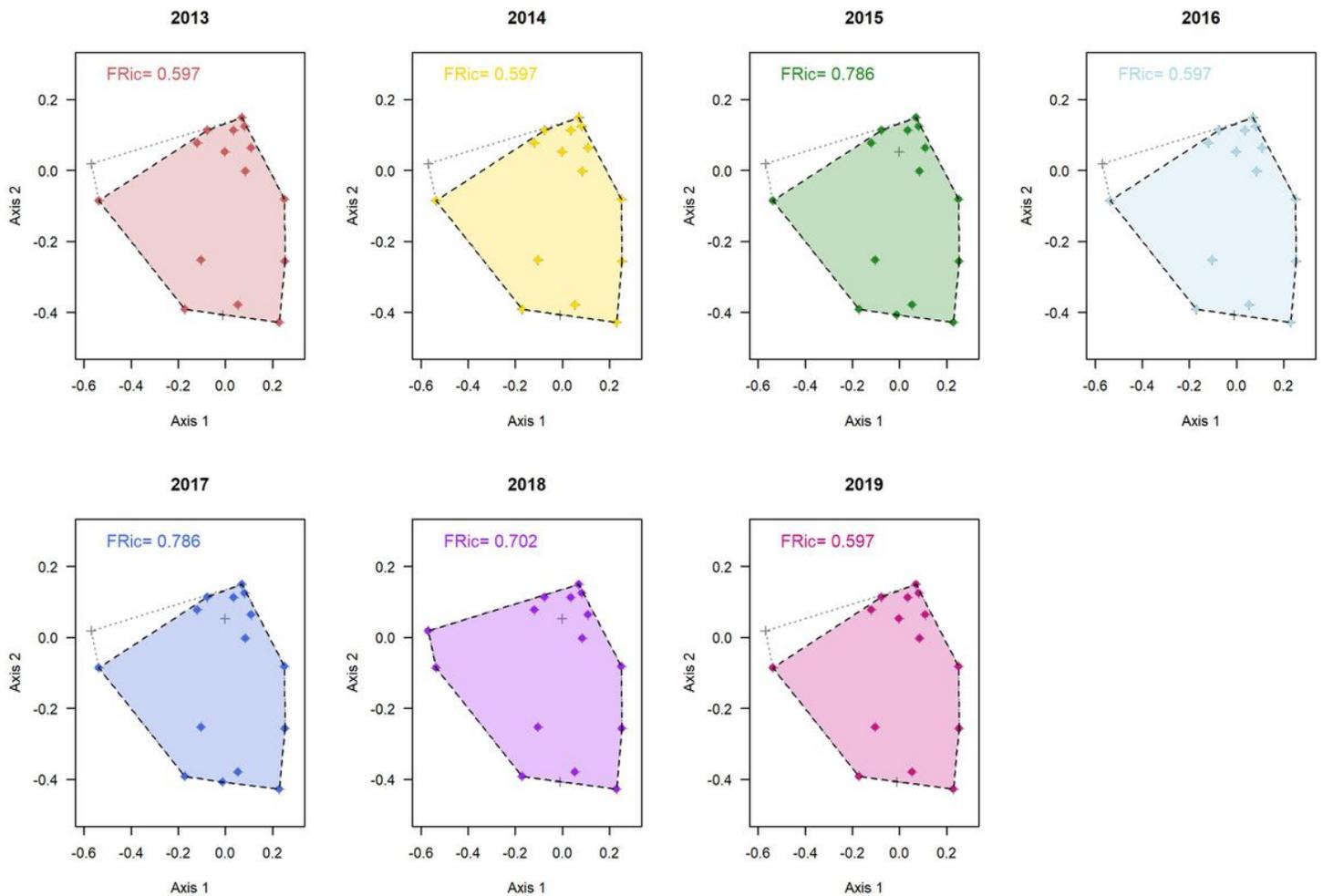


Figure 4

Volume occupied (Functional richness) in the functional space through years considering PCoA Axis 1 and 2. The total multidimensional trait space for all benthic morphospecies is presented in grey, with annual trait space overlaid in color. Dots denote the presence of functional entities, while crosses represent absent functional entities.

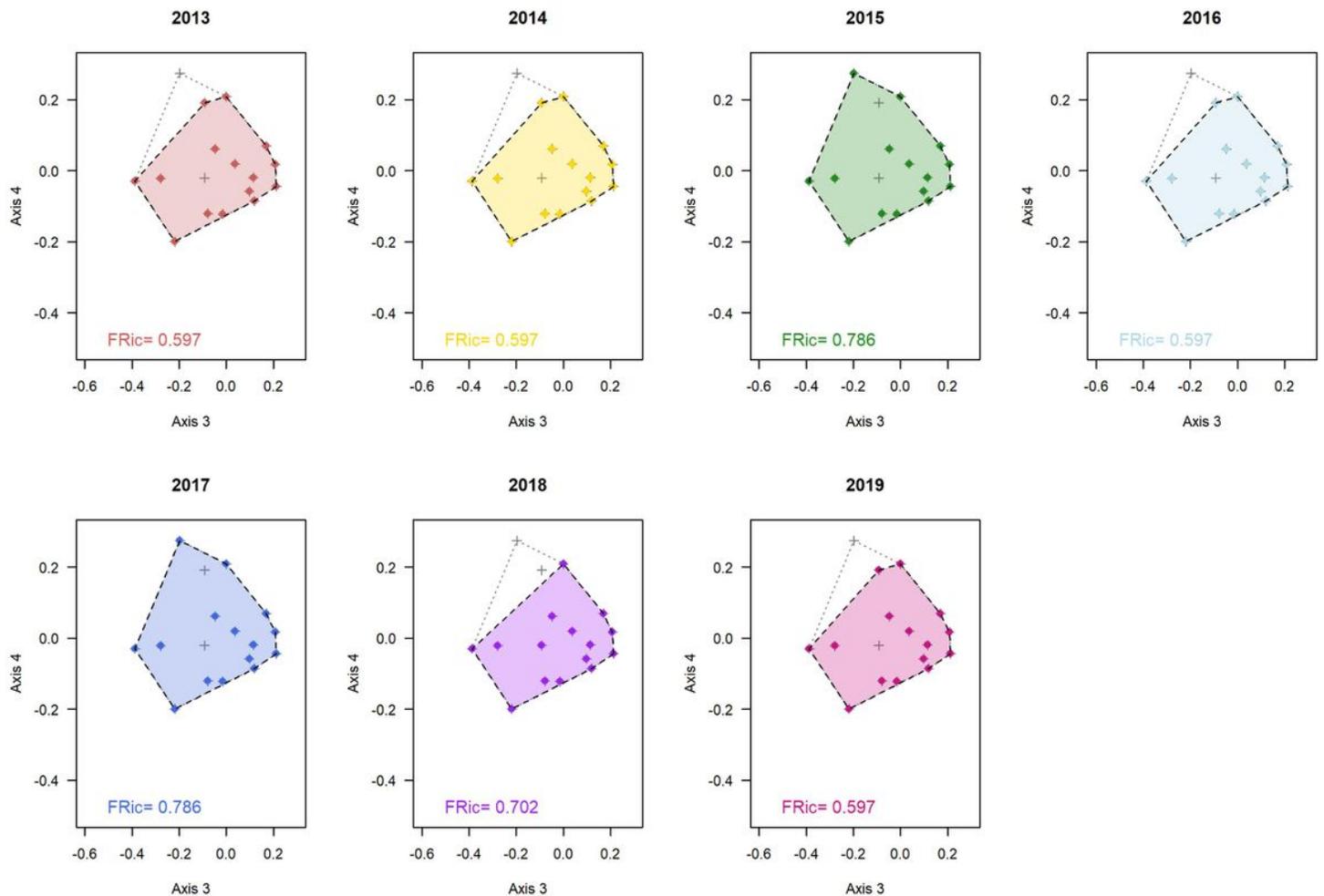


Figure 5

Volume occupied (Functional richness) in the functional space through years considering PCoA Axis 3 and 4. The total multidimensional trait space for all benthic morphospecies is presented in grey, with annual trait space overlaid in color. Dots denote the presence of functional entities, while crosses represent absent functional entities.

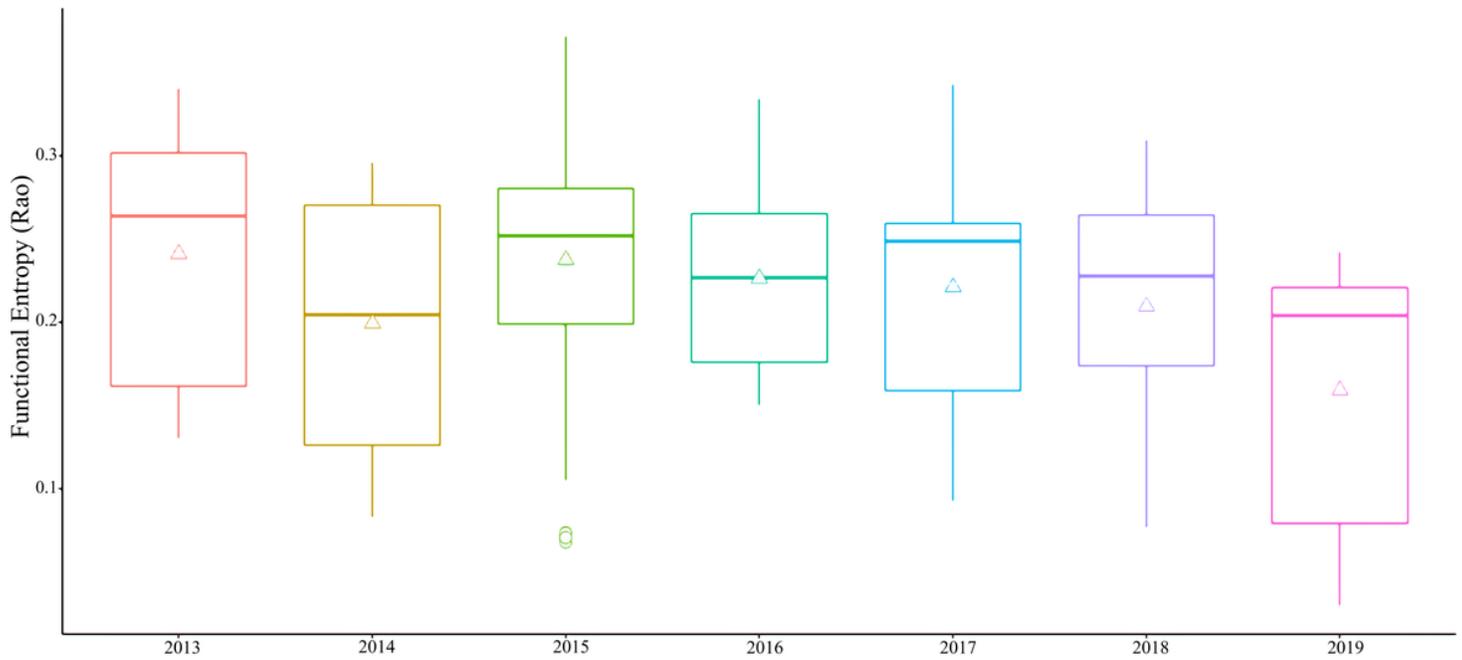


Figure 6

Functional entropy (FEnt) dynamics, indicating the evenness distribution of percent cover between functional entities with unique trait combination, that is, those located at functional space vertices. Higher FEnt values indicate a more even abundance distribution, while lower FEnt an uneven distribution. For Rocas Atoll, FEnt was generally low, showing dominance of some functional entities over others. Triangles represent mean FEnt values. Bars represent median values and circles the outliers.