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Reef fish community structure across an ecological transition zone

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ABSTRACT

Transition zones exhibit a unique combination of abiotic characteristics derived from the merging of two distinct areas, hosting communities with different thermal tolerance and distribution ranges. Given these characteristics, these zones are key to unmasking the effects of climate change on biodiversity since rapid changes in the sea temperature can favor some populations more than others. This study aimed to investigate the community structure of reef fish in seven islands of the southwestern Atlantic in a transition zone. Our results revealed distinct patterns of thermal affinity separating reef fish communities from the north to south islands, indicating a higher tolerance for species experiencing colder and seasonal temperatures. We also found that the abundance distribution pattern corresponds to the presence of many rare and few dominant species. The northern islands exhibited greater species richness, density, and biomass compared to the southern islands, potentially due to differences in the oceanographic conditions of the region and protection status. Our findings underscore the importance of understanding how communities differ or shift in space, which is crucial for predicting the consequences of environmental changes on biodiversity and ecosystem functioning.

1. Introduction

One of the primary challenges in ecology is to identify general patterns and processes determining the distribution, composition and diversity of communities (Lawton, 1999; McGill et al., 2006; Simberloff, 2004). Species distribution patterns can be shaped by environmental conditions and ecological interactions (Chase and Leibold, 2003; Hubbell, 2001). Some environmental conditions that determine marine species distribution and biodiversity patterns at large include temperature, depth, and habitat complexity, whereas competition and predation are some ecological interactions that can modulate natural communities on a local scale (MacNeil et al., 2009; Samoilys et al., 2019). Additionally, anthropogenic activities are important factors affecting biodiversity (Bongaarts, 2019), since activities such as fishing, pollution, and the introduction of non-native species can alter the structure and composition of communities and consequently impact ecosystem functioning (McGill et al., 2015). Therefore, identifying how communities are spatially structured and how these can respond to environmental and human disturbances are the first steps to understanding biodiversity changes in the Anthropocene.

Biodiversity patterns at local scales have traditionally been described using species richness, taxonomic composition, and abundance (Levin, 2001). While useful for tracking population trends and community diversity, these metrics overlook species differences and their roles in ecosystem functioning (McGill et al., 2006). Thus, incorporating functional metrics that account for species traits (e.g., diet, body size) is key to revealing biodiversity patterns (Bacheler et al., 2017; McGill et al., 2006; Petchey and Gaston, 2002; Violle et al., 2007). For instance, analyzing traits related to thermal range tolerance can reveal species' responses to temperature fluctuations and variations in their range distributions (Sommer et al., 2017; Vergés et al., 2019). Additionally, classifying species within trophic groups could provide extra tools to evaluate community structure due to their close associations with environmental conditions, such as turbidity, benthic composition, wave exposure, and temperature (Floeter et al., 2007; Maia et al., 2018). Hence, to gain a complete understanding of emergent community patterns, it is essential to combine different metrics that provide a comprehensive perspective on these communities.

Transition zones offer unique opportunities to investigate and analyze patterns and changes in community structure along pronounced environmental gradients (Horta E Costa et al., 2014; Williams, 1996). In marine ecosystems, temperature transition zones are biogeographical

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areas where warmer and colder species overlap (Horta E Costa et al., 2014). This overlap can largely be attributed to the species' niche and ability to tolerate a wider range of temperatures, making them well-suited for the cyclic oscillations of oceanographic conditions in these zones (Bernhardt and Leslie, 2013). Studying these zones is an excellent opportunity to understand the spatial patterns of community structure since species distribution are linked to the individual ecological niche and are projected to shift in response to environmental change (Sexton et al., 2009).

Here, we compiled 1837 underwater visual censuses of reef fish communities to investigate the community structure of reef fishes in seven islands along the (sub)tropical-warm temperate transition zone of the Southwestern Atlantic. Specifically, we aim to address the following research questions: (i) Is there a gradient of thermal tolerance among fish communities across the islands? (ii) How do fish communities vary in assemblage metrics (species richness, density, and biomass) across islands along a temperature gradient? (iii) Are the most abundant species also the most frequently occurring across different islands? (iv) Do trophic groups differ among the islands in terms of species richness, density, and biomass? Considering that global warming is promoting the expansion of species with tropical affinity into subtropical areas (Pinsky et al., 2020), we expect differences in the species' thermal tolerances between the northern and southern islands due to a clear temperature gradient (Anderson et al., 2015, 2020; Silva et al., 2025). Furthermore, the Southwestern Atlantic region is recognized as the southernmost limit of distribution for several reef fishes, resulting in a relatively low species richness when compared to the tropics (Anderson et al., 2015, 2020). We anticipate differences in the islands' abundance, biomass, and trophic groups due to local oceanographic conditions. Warm-affinity species are likely to be more abundant and contribute to higher biomass estimates on the northern islands, influenced by the warmer temperatures that affect their physiology and growth rates. For instance, we expect a greater abundance of herbivores in the northern islands due to temperature influence on feeding rates (Bosch et al., 2022; Longo et al., 2014; Vergés et al., 2018). The opposite is hypothesized for the cold-affinity species, which will tend to be more abundant and have higher biomass in the southern islands of the study region.

2. Material and methods

2.1. Study area

We sampled reef fish assemblages in seven coastal islands located in the subtropical-warm temperate transition zone of the Southwestern Atlantic (Fig. 1). The northern islands: Galé, Arvoredo, and Deserta, experience higher mean temperatures, and the southern islands: Aranhas, Xavier, Campeche and Moleques do Sul generally have cooler conditions (Silva et al., 2023). Furthermore, Galé, Arvoredo, Deserta are located inside the Arvoredo Marine Protected Area (MPA), while Aranhas, Xavier, Campeche and Moleques do Sul are located outside the MPA and are therefore exposed to higher human pressures, including both artisanal and recreational fishing. The reefs in all islands are characterized by hard substrates (i.e., rocky), mainly covered by algal turfs, erect macroalgae, and zoanthids (Aued et al., 2018).

2.2. Underwater visual censuses survey data

Reef fish species occurrences and abundance were obtained from 1837 Underwater Visual Censuses (UVCs) carried out during the austral summers from 2008 to 2022 (Fig. S1). The data is freely available in (Quimbayo et al., 2023). The UVC method involves the identification and counting of all ray-finned fish species found within a transect of 40 m^2 (20 × 2 m). During each survey, the diver visually identifies, counts, and estimates the total length (rounded to the nearest centimeter) of all species present in the water column while unwinding a measuring tape. Then, while retracting the tape, the diver applies the same procedure to smaller and cryptic species, typically found near the bottom (Floeter et al., 2007; Morais et al., 2017). The UVC surveys were conducted at shallow depths ranging from 3 to 15 m below the surface.

2.3. Calculation of fish diversity metrics

To evaluate changes in community structure, we estimated thermal tolerance, species richness, density, and biomass. Additionally, we classified all species observed in UVCs into trophic groups for each island. Due to the heterogeneity in sampling effort, rarefaction technique was used to standardize the number of surveys across locations ensuring comparable representations of the underlying communities (Magurran and McGill, 2011; Quimbayo et al., 2019; Silva et al., 2023). We first identified the minimal number of UVCs (280 m^2, corresponding to 7 UVCs) for each island and year and then fixed this number for all other locations and years as the smallest area sampled. Thereafter, we randomly re-sampled 999 times (with replacement) the fixed number of UVCs for each island. In each permutation, we calculated the diversity metrics per island and derived the mean values and associated standard deviations across all iterations. To ensure comparability with other studies, species richness per island was calculated per transect (UVC), while biomass and density were estimated per m^2. The mean values were

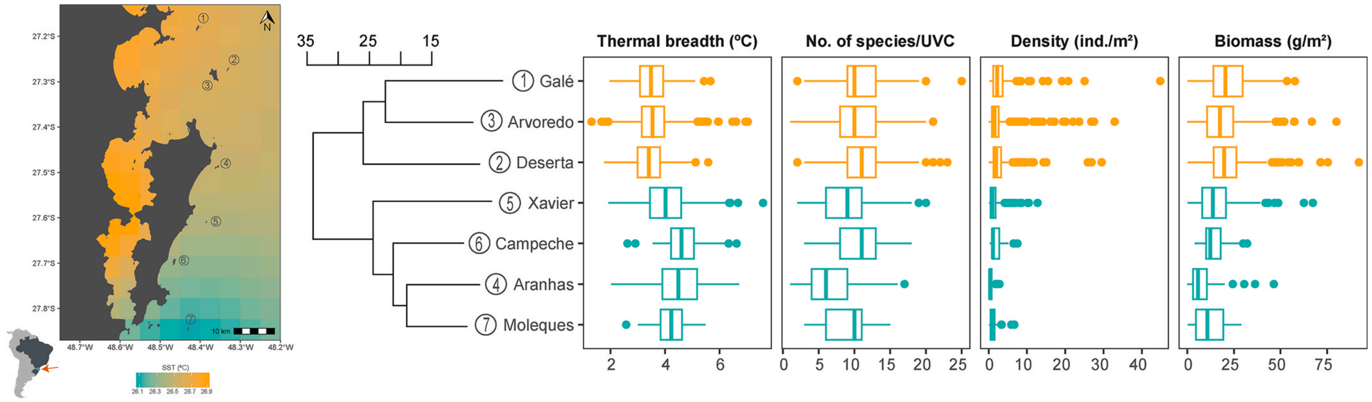

Fig. 1. Map of the study area, including the seven sampled islands across the transition zone. The color range represents the Sea Surface Temperature (SST°C) gradient during one day of the austral summer, serving as an example of differential thermal conditions across the study area. Galé (1), Arvoredo (2), Deserta (3), Aranhas (4), Xavier (5), Campeche (6), and Moleques do Sul (7). The boxplots show the variation in thermal breadth, number of species per UVC, densitity of individuals and biomass of communities per m^2 in each island. All values were obtained from each of the 999 permutations. The cluster analysis for thermal breadth on the right side of the map reveal an overall separation of the islands between the northern and southern regions, indicated by the yellow and blue color boxplots, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

used as input for the graphs, models and tables.

Thermal tolerance of communities was represented by the thermal breadth, a metric representing how many degrees of temperature the species are able to support and therefore providing a measure of response to temperature variations (Schuster et al., 2022). First, we compiled the realized thermal range of all species recorded in the seven islands of our study based on global occurrence data available in the Global Biodiversity Information Facility (GBIF: http://www.gbif.org). We collected data on the full geographic range coverage of each species and matched the geographical coordinate of species presence with the respective monthly sea surface temperature in the occurrence location from Global Ocean Data Assimilation System (GODAS) - NOAA (1980–2020, 0.33 × 1° grid resolution). Species thermal breadth was then calculated as the subtraction of the lower and upper percentile (5th and 95th percentile) of the temperature distribution experienced across a species geographic range to avoid extremes and rare values.

Fish biomass was calculated using the following equation: $W = a * TL^b$, where W is the weight in grams, *a* and *b* represent species-specific constants for length-weight relationships, and TL represents the total length estimated in the UVCs. Length–weight constants were obtained for each species from Quimbayo et al. (2021) and (2023). When coefficients were unavailable, we used the values of congeneric species that are phylogenetically closely related and morphologically similar. Density and biomass values were transformed by $\text{Log}_e (x + 1)$ to stabilize variance and improve the assumptions of linearity.

Community structure was evaluated in terms of linear relationships between occurrence frequency and density/biomass, and by trophic groups. All observed fishes were classified following the trophic groups described by Quimbayo et al. (2021) and (2023): herbivore−detritivore (feed on the epilithic algal matrix), macroalgivore (feed on macroalgae >1 cm high or seagrass), macrocarnivore (feed on fishes and cephalopods), mobile invertebrates (feed on crustaceans, annelids, echinoderms, mollusks), omnivore (feed on animal and plant and/or detrital material), planktivore (feed on zooplankton, coelenterates, detrital aggregates on the water column, etc.), and sessile invertebrate feeder (feed corals, sponges, ascidians). Number of species, density and biomass were calculated for each trophic group per island.

2.4. *Data analysis*

To visualize whether the thermal breadth of species differed between islands, we performed a cluster analysis using a continuous distance matrix based on Euclidean distances and Ward's method as grouping criterion. To obtain a community-level value, we selected the species present on each island in each permutation, retaining their respective thermal tolerances. A dissimilarity matrix was then constructed for each iteration, with species as columns and islands as rows, using the *vegdist* function from the "vegan" R package (Oksanen et al., 2016). The average distance values per island across all iterations were then used to build the final cluster. Subsequently, Linear Mixed Models (LMMs) were used to test significant differences in thermal breadths, species richness, density, and biomass among islands following the formula: metric ∼ island + depth + (1|year). Survey depth was included as a predictor in the model because UVCs were conducted at different depths, and we aimed to test whether the metrics varied accordingly. Furthermore, we considered "Year" as a random factor to account for a possible temporal effect on the community structure. The models were constructed using the function "lmer" within the "lme4" R package (Bates et al., 2015). Validations of the models are shown in Fig. S2–S5.

Additionally, we used linear regressions to assess the relationship between species rarity and dominance, modeling density and biomass as functions of occurrence frequency (i.e., density ∼ occ. frequency and biomass ∼ occ. frequency). Here, occurrence frequency represents species rarity, while density and biomass serve as measures of dominance. By obtaining a separate slope for each island, we were able to compare the observed trends. Regarding trophic groups, we evaluated potential differences among islands through two approaches. The first was based on three-way analysis of variance (ANOVA) to assess whether the number of species, density, and biomass within trophic groups differed among islands (location) and with depth. Significant effects were determined at α = 0.05. The three-way ANOVAS were performed using the average of the metrics per trophic group (richness, density, and biomass) after the permutations considering the minimal sampled area. The second method was based on Non-Metric Multidimensional Scaling (NMDS) to graphically explore the patterns emerged from the above analysis. All analyses were conducted in the R environment (R Core Team, 2020).

3. Results

3.1. *Thermal tolerance*

Our study revealed a clear separation among the studied islands based on species' thermal tolerances. Fish communities in the northern islands (Galé, Deserta, and Arvoredo) presented a lower mean thermal breadth (3.5 °C) and a narrower thermal breadth range, indicating a lower tolerance to temperature fluctuations (i.e., more tropical species). In contrast, the southern islands (Aranhas, Xavier, Campeche, and Moleques) had a higher mean thermal breadth (4.3 °C) and a broader thermal breadth range, suggesting a higher capacity to withstand temperature variations (Fig. 1). These findings were further supported by both the cluster analysis and the models employed, which clearly showed a distinct separation between the islands situated at different latitudes (Table 1). This separation was evident in the form of two distinct branches in the analysis, highlighting the contrasting thermal characteristics of these island groups. The LMM for thermal breadth revealed statistically significant differences between Aranhas Island and the other islands (Table 1). Notably, the differences were smaller between Aranhas and the southern islands than the northern ones,

Table 1

Mean effects of islands as factors and depth on the fish assemblage metrics (thermal breadth, species richness, density, and biomass). Significant values ($p < 0.05$) are highlighted in bold.

Island	Parameter	Thermal breadth	Species richness	Density	Biomass
Intercept (Aranhas)	Estimate	4.387	8.898	1.04	14.152
	t	30.275	13.508	8.554	6.235
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Galé	Estimate	−1.056	3.781	0.782	16.264
	t	−9.954	7.409	8.751	9.615
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Deserta	Estimate	−1.207	4.733	0.78	18.048
	t	−10.992	8.972	8.441	10.313
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Arvoredo	Estimate	−0.93	3.287	0.49	13.116
	t	−8.883	6.529	5.554	7.857
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Xavier	Estimate	−0.476	1.943	0.287	11.492
	t	−4.452	3.784	3.197	6.748
	p	**<0.001**	**<0.001**	**0.002**	**<0.001**
Campeche	Estimate	0.083	2.163	0.559	7.992
	t	0.634	3.457	5.094	3.848
	p	0.526	**<0.001**	**<0.001**	**<0.001**
Moleques	Estimate	−0.667	0.676	0.212	6.312
	t	−3.782	0.798	1.43	2.245
	p	**<0.001**	0.425	0.153	**0.025**
Depth	Estimate	0.022	−0.281	−0.057	−1.268
	t	1.818	−4.773	−5.48	−6.483
	p	0.07	**<0.001**	**<0.001**	**<0.001**
Year (Random effect SD)	Estimate	0.337	1.625	0.284	5.374

reinforcing the latitudinal gradient in thermal breadth. Transect depth did not have a significant influence on thermal breadth.

3.2. Fish diversity metrics

A total of 142 species belonging to 47 families were observed in the seven islands throughout the study period. On average, ten species were observed per transect considering all islands, and varied from 1 to 25 among them (Fig. 1). The northern islands (Galé, Deserta and Arvoredo) presented an average of 10.7 ± 3.6 species per UVC and 2.8 ± 3.6 individuals per m^2 meaning higher species richness and density compared to the south (Aranhas, Xavier, Campeche, and Moleques do Sul), which presented an average 8.9 ± 3.5 species and 1.5 ± 1.6 individuals per m^2 (Fig. 1). Fish biomass showed the same patterns where northern islands display higher values (20.6 ± 11.4 g/m^2), while southern the lowest (14.4 ± 9.7 g/m^2). Aranhas displayed the lowest density and biomass among all islands (mean 0.7 ± 0.7 individuals per m^2; 8.9 ± 9.9 g per m^2), revealing a predominance of smaller individuals. The models for these three response variables (species richness, density, and biomass) showed significant differences among islands, specifically in comparison to Aranhas (used as the reference level in the intercept). Since the models account for variation in depth and year, the estimated values do not correspond directly to the raw averages but rather represent how much higher or lower each island is relative to the estimated intercept. Our results also showed that depth had a negative effect on species richness, density, and biomass (Table 1), indicating that these metrics tend to decrease in deeper transects.

3.3. Community structure

We found no relationship between species occurrence frequency and their density or biomass in the northern islands. In contrast, some positive relationships were observed in the south (Fig. 2). Xavier and Moleques do Sul were the only islands that showed significant positive correlations for density ($R^2 = 0.15$, $p < 0.01$ and $R^2 = 0.44$, $p < 0.01$, respectively; Fig. S6), while only Moleques do Sul exhibited a positive trend for biomass ($R^2 = 0.29$, $p < 0.01$; Fig. S7). The most frequent species were *Haemulon aurolineatum, Orthopristis ruber, Diplodus argenteus, Abudefduf saxatilis*, and *Kyphosus* spp., which also exhibited high or moderate density. Their density can influence overall biomass, although they are not particularly large species (Fig. 2). In contrast, despite their common occurrence in the transects, the species *Stegastes fuscus, Coryphopterus glaucofraenum, Parablennius marmoreus,* and *P. pilicornis*, did not demonstrate high density or biomass.

Several species with higher density or biomass values were found to be rare in terms of occurrence in most reefs of the islands, including *Pempheris schomburgkii* (high density)*, Epinephelus marginatus, Mugil curema,* and *Caranx crysos* (moderate biomass). Finally, examples of rare species both in terms of occurrence frequency and density/biomass included the tropical surgeonfish *Acanthurus bahianus* and the small parrotfish *Sparisoma radians*. The individual regressions and their respective parameters are shown in the supplementary material (Fig. S6 and S7).

3.4. Trophic groups

Overall, mobile invertebrate feeders (e.g., genus *Haemulon*) were numerically dominant in terms of their richness (accounting for ∼50 % of the total species across all islands), density (∼39 % of the total individuals), and biomass (∼33 % of the total biomass) (Fig. 3). Among the omnivores, *Abudefduf saxatilis* and *Diplodus argenteus* are the most abundant species in the communities, while the non-native *Chromis limbata* and juveniles of *Haemulon aurolineatum* were common among planktivores. Finally, herbivore/detritivores (e.g. *Stegastes, Sparisoma*), macroalgivores (e.g. *Kyphosus*), macrocarnivores (e.g. *Caranx, Epinephelus*), and sessile invertebrate feeders (e.g. *Sphoeroides*, *Chaetodon*) show on average relatively low richness and density throughout the area. Despite the overall north–south separation observed in the other

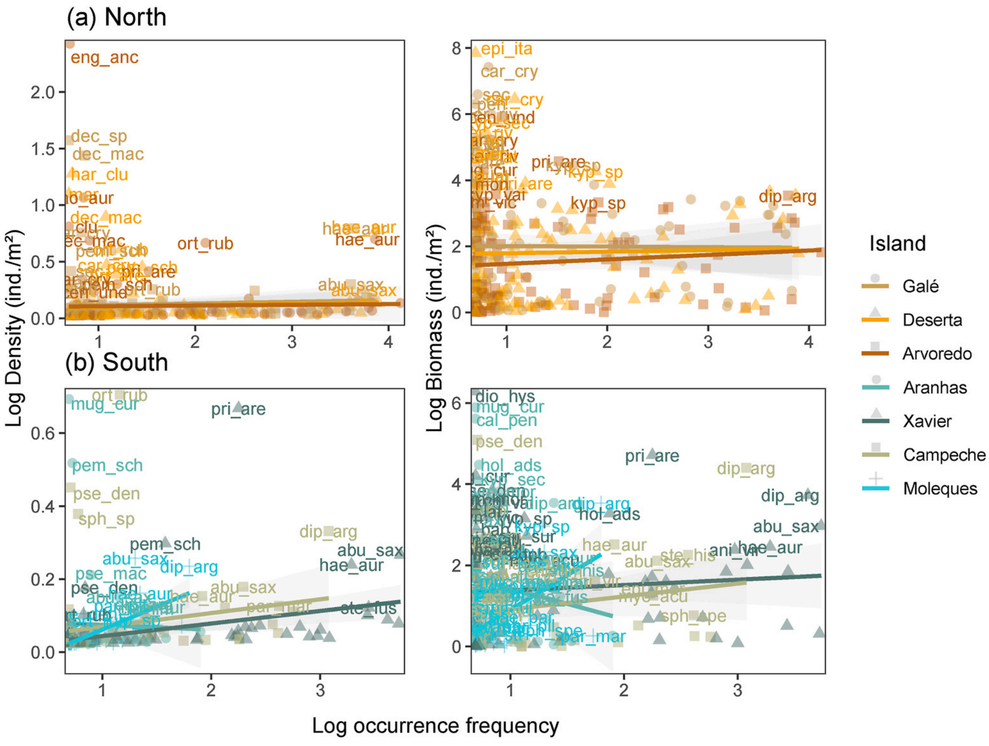

Fig. 2. Relationship between density/biomass and occurrence frequency of reef fish in the seven islands sampled. For convenience, separate plots were created for the North (a) and South region (b), which are represented by warm and cold color gradients and icons. The solid lines show the trends derived from linear regressions for each island. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

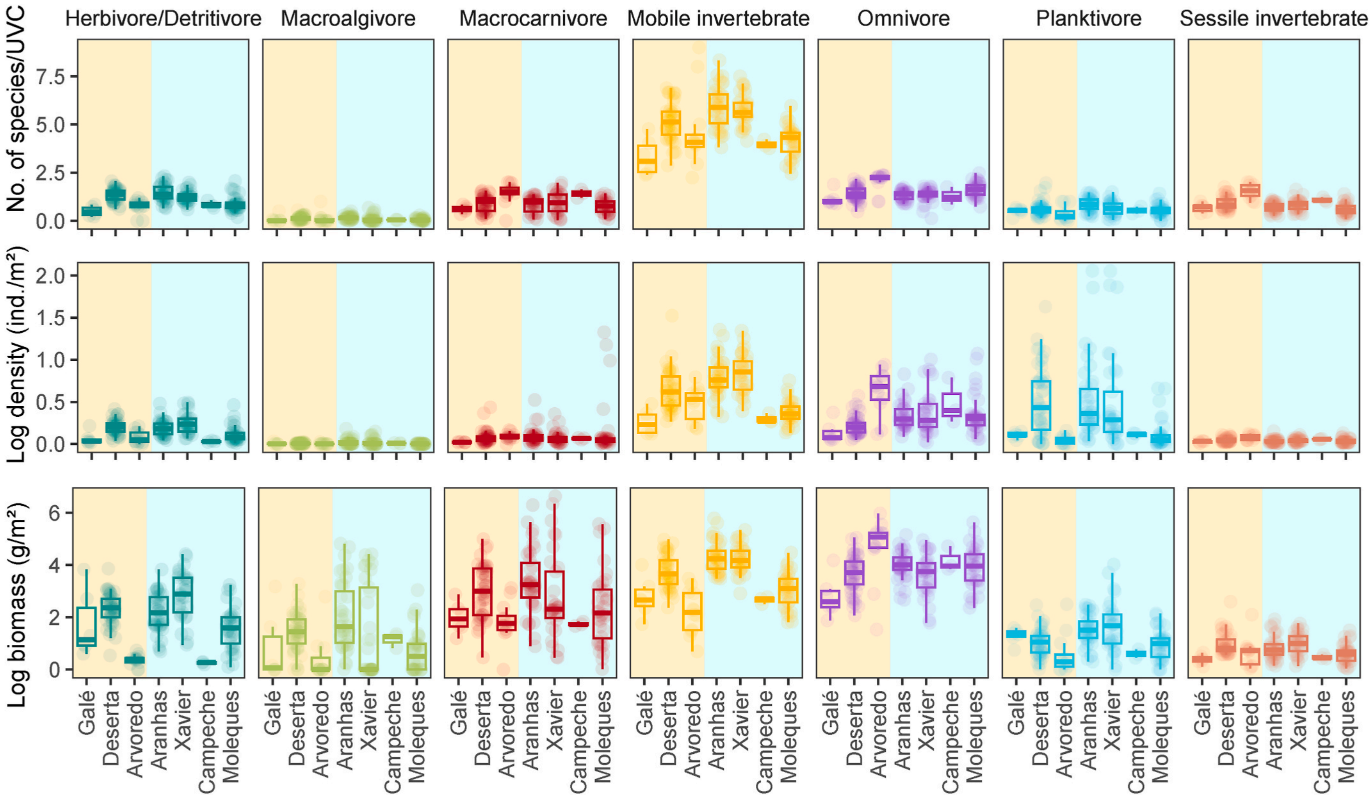

Fig. 3. Boxplots of number of species, density and biomass of trophic groups (columns) based on values obtained from the 999 permutations for each island. Yellow and blue backgrounds indicate the northern and southern islands, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

metrics, there were no clear differences between regions regarding trophic groups (Fig. 3).

Our models demonstrate that the number of species, density, and biomass varied across trophic groups, islands, and depths (Table 2). However, the specific effects and their direction differ among islands. For instance, the number of species of planktivores and mobile invertebrate feeders is higher in Deserta and Galé islands (NMDS stress = 0.076, Fig. 4a). The density of omnivores was higher on Campeche and Moleques compared to other trophic groups, while planktivores, herbivores/detritivores, and macroalgivores were more abundant on the northern islands (NMDS stress = 0.057, Fig. 4b). Furthermore, macrocarnivore biomass was high in Arvoredo, Deserta, and Galé, whereas omnivores dominated in Campeche and Moleques (NMDS stress = 0.095, Fig. 4c).

4. Discussion

Our study showed that reef fish communities exhibited marked differences along the studied transition zone, supporting our initial hypothesis that fish communities in the northern and southern islands have different thermal tolerance. Even on the local scale, we were able to identify islands with species exhibiting higher thermal tolerance, i.e. indicated by the broader thermal breadth of the colder southern islands. In contrast, the warmer northern islands are comprised of species with lower thermal tolerance. It is well known that temperature is a driver that influences biodiversity patterns, as well as physiology, growth, reproduction rate, and range distribution of species (Munday et al., 2008; Pinsky et al., 2013). Thus, the observed patterns likely result from species larvae or adults actively tracking suitable thermal conditions in space to ensure their survival (Burrows et al., 2019). Furthermore, the degree of seasonality potentially plays a crucial role in shaping communities, because species must have traits adapted to cyclic environmental conditions to endure the challenges of overwintering (Beukhof et al., 2019). It is well-known that thermal ranges of species can predict changes in the structure of communities during disturbances (Day et al., 2018; Stuart-Smith et al., 2015). Thus, our results suggest that communities in the southern islands may exhibit higher resilience in the face of warming events due to their high tolerance to temperature fluctuations.

In line with our second hypothesis, we also observed differences in species richness, density, and biomass between the northern and southern islands. On the northernmost islands, the increased diversity of species, coupled with their physiological preference for warmer temperatures, may result in greater population density. This, in turn, may trigger a cascading effect, potentially leading to elevated biomass levels in the north, while the southernmost islands may exhibit lower species

Table 2
Summary of ANOVA results testing the effects of island (location) and depth on species richness, density, and biomass of the trophic groups. Degrees of freedom (df), sums of squares (SS), F values, and associated p-values are reported. Significant effects ($p < 0.05$) are in bold.

	Richness				Density (ind./m^2)				Biomass (g/m^2)			
	df	SS	F	*p*	*df*	SS	F	*p*	*df*	SS	F	*p*
Island	6	6.4	7.03	**<0.01**	6	9.25	14.98	**<0.01**	6	158.3	12.61	**<0.01**
Troph. group	6	423.8	465.63	**<0.01**	6	32.02	51.87	**<0.01**	6	1329.9	105.95	**<0.01**
Depth	1	1.3	8.87	**<0.01**	1	0.05	0.47	0.49	1	8.5	4.06	**0.04**

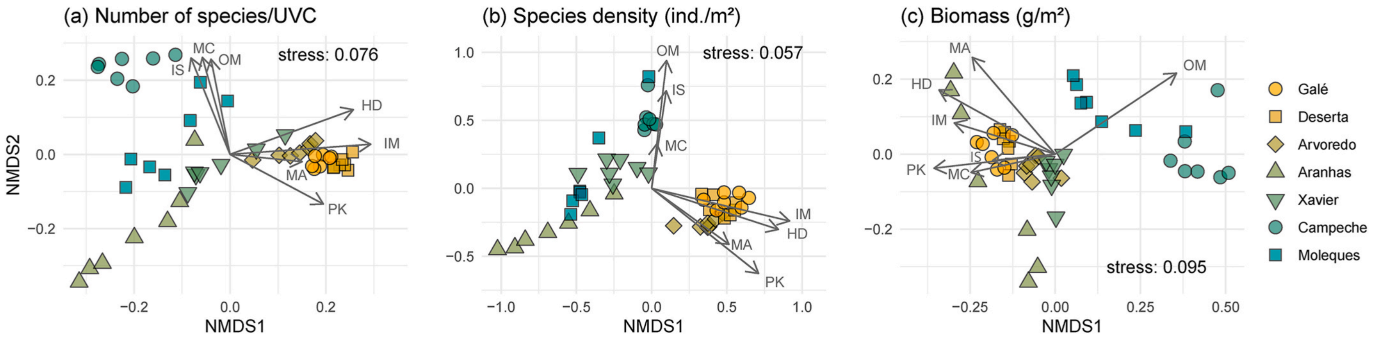

Fig. 4. Non-metric multidimensional scaling (NMDS) results showing the influence of number of species (richness) per UVC (a), density (b) and biomass per m^2 (c) of each trophic group and depth in the different islands sampled. An average value of each metric was calculated per island based on 999 random selections of 7 UVCs (the minimum number identified across all locations and years). This standardization underlies the use of 7 data points per island in the plots. Trophic groups: herbivores-detritivores (HD), macroalgae-feeder (MA), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK), macrocarnivores (MC) and omnivores (OM).

richness, abundance, and biomass. However, additional variables besides temperature (e.g., productivity, fishing, benthic composition, wave exposure) that are specific to each site may influence resource and niche suitability for species to inhabit (Hubert et al., 2011; Hutchinson, 1957; Ricklefs, 1987). Therefore, it is plausible that some of these other factors contribute to the nuances of the observed patterns, as different species may exhibit diverse responses to the surrounding abiotic and biotic conditions and present different densities and biomass. In particular, the level of protection could play a role in the patterns of density and biomass, since we observed high values of these metrics in Galé and Deserta, islands covered by a no-take MPA. It has been recognized that protection promotes higher rates of growth and survival in reef fish communities (Karlovic et al., 2021; Turnbull et al., 2018). Thus, the no-take MPA contributes to the maintenance of larger population sizes within its boundaries (Anderson et al., 2014). However, the temporal study of Boelter et al. (2024) suggests a populational decline of a key grouper species (*E. marginatus*) in recent years. In addition to temperature, depth significantly influenced richness, density, and biomass. However, this effect does not reflect compositional differences among islands and only explains variations in species' frequencies of occurrence. This result is expected, as the benthic community in the reef slope is relatively uniform across sites, with no marked differences (Aued et al., 2018). Consequently, it provides consistent habitats for fish communities, influencing their distribution rather than their composition.

In addition to differences in overall richness, abundance, and biomass our study revealed significant heterogeneity in the relationship between the frequency of occurrence of species and their respective density or biomass across the seven islands. Notably, we observed a distinct pattern in terms of dominance when analyzing islands separately. More specifically, few species were highly abundant, while many were rare, corroborating the typical hyperbolic species-abundance distribution, reported for several groups such as birds, trees, mammals, amphibians and insects (Baldridge et al., 2016; Connolly et al., 2017; Matthews et al., 2017). For instance, in the northern region, *H. aurolineatum* emerged as the dominant species, whereas in the southern region, *D. argenteus* and *A. saxatilis* were the most representative species. These findings align with the commonly investigated assemblage-level properties, specifically the species abundance distribution, reflecting a prevalence of low commonness and high rarity among species (Connolly et al., 2005, 2014; McGill et al., 2007). Specifically on reefs, some schooling species may occasionally appear in large numbers, temporarily increasing density in a given UVC, despite being non-frequent (Alvarez-Filip et al., 2006). Conversely, territorial species may be frequently observed but not highly abundant in terms of density, depending on their behavior, for instance, *S. fuscus*. We observed the presence of schooling behaviors among relatively low frequent species present in the water column, particularly *M. curema* and *D. macarellus*. Even in low frequencies, these species have the potential to achieve high density and biomass and influencing the dynamic of communities. We emphasize that the dominant species observed in the southern islands are likely better adapted to cold conditions, confirming our earlier hypothesis of an environmental response. Furthermore, our results indicate that the community structure exhibits variations when comparing islands separately, highlighting the importance of considering local scales in understanding the dynamics of ecosystems (Garcia et al., 2018).

Despite marked variations in the above-mentioned metrics, our study indicates that mobile invertebrate feeders exhibit higher richness, density and biomass values throughout all islands and regions, similarly as in most reefs on the Brazilian Province (Ferreira et al., 2004). However, we also demonstrate important differences in some trophic groups among the islands, with planktivores dominating in northern islands, while omnivores prevailing in the southern islands. This distribution pattern aligns with the oceanographic conditions of the region, characterized by clearer waters in the north that facilitate the development of zooplankton (Lopes et al., 2006) and consequently, large populations of *A. multilineata*, *C. limbata*, and juvenile haemulids (common and abundant species). Therefore, we highlight the crucial role of planktivores in reef food webs, which is consistent with similar findings in other rocky reefs (Maia et al., 2018; Truong et al., 2017). The observed density and biomass patterns of omnivores could likely be influenced by the habitat type and benthic composition of Campeche and Moleques do Sul islands, characterized by a substantial presence of turf algae, macroalgae, and sponges (Aued et al., 2018; Bouzon et al., 2012), as well as oceanographic conditions, such as the input of cold and freshwater from Prata River (de Mahiques et al., 2021). The lower richness and density and comparatively higher biomass of herbivores/detritivores, macroalgivores, and macrocarnivores reflect the low frequency of some species present in these groups (*M. curema*, *Kyphosus* sp., and *E. marginatus,* respectively). These findings are in agreement with other studies, showing that these trophic groups are less representative in coral reef assemblages when compared to planktivores and omnivores (Siqueira et al., 2021; Stergiou and Karpouzi, 2002). As expected, a higher biomass of herbivores was found in the northern islands, corroborating previous studies showing that the presence and feeding behavior of herbivores is enhanced by higher temperatures (Bosch et al., 2022; Longo et al., 2014; Vergés et al., 2018). When examining trophic groups, it is important to consider the ontogenetic diet shifts of certain species. One example is *H. aurolineatum*, which feeds on plankton during its juvenile stage but transitions into a mobile invertebrate feeder as an adult (Pereira et al., 2015). This species holds significant importance throughout the Brazilian reefs (Ferreira et al., 2004) thereby contributing to the patterns of two distinct trophic groups. Consequently, understanding the dietary preferences across different life stages of species becomes a valuable tool for characterizing community structure in terms of trophic groups.

Finally, our study contributes to the broader understanding of changes in community structure across marine transition zones exposed to different environmental conditions, even within relatively short distances. Because the dominant and rare species differs between islands, understanding whether and how communities differ or shift in space is critically important for predicting consequences of environmental changes for biodiversity and ecosystem functioning (Connolly et al., 2005). While acknowledging some limitations of our study, particularly the absence of data on habitat composition per transect and local oceanographic parameters to explore the underlying drivers of the observed patterns, we believe that our findings provide insights into future research on reef fish communities. Integrating additional perspectives and scales, such as investigating temporal dynamics and incorporating the use of more detailed functional traits, will help unravel the general patterns and processes occurring in transition zones.

CRediT authorship contribution statement

Fernanda C. Silva: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Juan P. Quimbayo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Martin Lindegren:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis. **Sergio R. Floeter:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107496.

Data availability

Data will be made available on request.

References

Alvarez-Filip, L., Reyes-Bonilla, H., Calderon-Aguilera, L.E., 2006. Community structure of fishes in Cabo Pulmo Reef, Gulf of California. Mar. Ecol. 27, 253–262. https://doi.org/10.1111/j.1439-0485.2006.00108.x.

Anderson, A.B., Bonaldo, R.M., Barneche, D.R., Hackradt, C.W., Félix-Hackradt, F., García-Charton, J.A., Floeter, S.R., 2014. Recovery of grouper assemblages indicates effectiveness of a marine protected area in Southern Brazil. Mar. Ecol. Prog. Ser. 514, 207–215. https://doi.org/10.3354/meps11032.

Anderson, A.B., Carvalho-Filho, A., Morais, R.A., Nunes, L.T., Quimbayo, J.P., Floeter, S. R., 2015. Brazilian tropical fishes in their southern limit of distribution: checklist of Santa Catarina's rocky reef ichthyofauna, remarks and new records. Check List. 11, 1–25. https://doi.org/10.15560/11.4.1688.

Anderson, A.B., Joyeux, J.C., Floeter, S.R., 2020. Spatiotemporal variations in density and biomass of rocky reef fish in a biogeographic climatic transition zone: trends over 9 years, inside and outside the only nearshore no-take marine-protected area on the southern Brazilian coast. J. Fish. Biol. 97, 845–859. https://doi.org/10.1111/jfb.14441.

Aued, A.W., Smith, F., Quimbayo, J.P., Cândido, D.V., Longo, G.O., Ferreira, C.E.L., Witman, J.D., Floeter, S.R., Segal, B., 2018. Large-scale patterns of benthic marine communities in the Brazilian province. PLoS One 13, e0198452. https://doi.org/10.1371/journal.pone.0198452.

Bacheler, N., Geraldi, N., Burton, M., Muñoz, R., Kellison, G., 2017. Comparing relative abundance, lengths, and habitat of temperate reef fishes using simultaneous underwater visual census, video, and trap sampling. Mar. Ecol. Prog. Ser. 574, 141–155. https://doi.org/10.3354/meps12172.

Baldridge, E., Harris, D.J., Xiao, X., White, E.P., 2016. An extensive comparison of species-abundance distribution models. PeerJ 4, e2823. https://doi.org/10.7717/peerj.2823.

Bates, D., Maechler, M., Bolker, B., Walwer, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bernhardt, J.R., Leslie, H.M., 2013. Resilience to climate change in coastal marine ecosystems. Ann. Rev. Mar. Sci 5, 371–392. https://doi.org/10.1146/annurev-marine-121211-172411.

Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A., Dencker, T.S., Sólmundsson, J., Punzón, A., Primicerio, R., Hidalgo, M., Möllmann, C., Lindegren, M., 2019. Marine fish traits follow fast-slow continuum across oceans. Sci. Rep. 9, 17878. https://doi.org/10.1038/s41598-019-53998-2.

Boelter, J.P., Silva, F.C., Quimbayo, J.P., Floeter, S.R., 2024. Broken expectations: population decline of a key grouper species within a 30-year-old no-take MPA in the Southwestern Atlantic. Ocean Coast Manag. 257, 107318. https://doi.org/10.1016/j.ocecoaman.2024.107318.

Bongaarts, J., 2019. IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. Popul. Dev. Rev. https://doi.org/10.1111/padr.12283.

Bosch, N.E., McLean, M., Zarco-Perello, S., Bennett, S., Stuart-Smith, R.D., Vergés, A., Pessarrodona, A., Tuya, F., Langlois, T., Spencer, C., Bell, S., Saunders, B.J., Harvey, E.S., Wernberg, T., 2022. Persistent thermally-driven shift in the functional trait structure of herbivorous fishes: evidence of top-down control on the rebound potential of temperate seaweed forests? Glob. Change Biol. https://doi.org/10.1111/gcb.16070.

Bouzon, J.L., Brandini, F.P., Rocha, R.M., 2012. Biodiversity of sessile fauna on rocky shores of coastal islands in Santa Catarina, Southern Brazil. Mar. Sci. 2, 39–47. https://doi.org/10.5923/j.ms.20120205.01.

Burrows, M.T., Bates, A.E., Costello, M.J., Edwards, M., Edgar, G.J., Fox, C.J., Halpern, B. S., Hiddink, J.G., Pinsky, M.L., Batt, R.D., García Molinos, J., Payne, B.L., Schoeman, D.S., Stuart-Smith, R.D., Poloczanska, E.S., 2019. Ocean community warming responses explained by thermal affinities and temperature gradients. Nat. Clim. Change 9, 959–963. https://doi.org/10.1038/s41558-019-0631-5.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches: Linking Classical and Contemporary Approaches. The University of Chicago Press, Chicago and London.

Connolly, S.R., Hughes, T.P., Bellwood, D.R., 2017. A unified model explains commonness and rarity on coral reefs. Ecol. Lett. https://doi.org/10.1111/ele.12751.

Connolly, S.R., Hughes, T.P., Bellwood, D.R., Karlson, R.H., 2005. Community structure of corals and reef fishes at multiple scales. Science 309, 1363–1365. https://doi.org/10.1126/science.1113281.

Connolly, S.R., MacNeil, M.A., Caley, M.J., Knowlton, N., Cripps, E., Hisano, M., Thibaut, L.M., Bhattacharya, B.D., Benedetti-Cecchi, L., Brainard, R.E., Brandt, A., Bulleri, F., Ellingsen, K.E., Kaiser, S., Kroncke, I., Linse, K., Maggi, E., O'Hara, T.D., Plaisance, L., Poore, G.C.B., Sarkar, S.K., Satpathy, K.K., Schuckel, U., Williams, A., Wilson, R.S., 2014. Commonness and rarity in the marine biosphere. Proc. Natl. Acad. Sci. 111, 8524–8529. https://doi.org/10.1073/pnas.1406664111.

Day, P.B., Stuart-Smith, R.D., Edgar, G.J., Bates, A.E., 2018. Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation. Divers. Distrib. 24, 1036–1046. https://doi.org/10.1111/ddi.12753.

de Mahiques, M.M., Violante, R., Franco-Fraguas, P., Burone, L., Rocha, C.B., Ortega, L., dos Santos, R.F., Kim, B.S.M., Figueira, R.C.L., Bícego, M.C., 2021. New insights of the influence of ocean circulation on the sedimentary distribution in the Southwestern Atlantic margin (23°S to 55° S) based on Nd and Pb isotopic fingerprinting. Ocean Sci. Discuss. 1213–1229.

Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L., Ferreira, B.P., Joyeux, J.C., 2004. Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. J. Biogeogr. 31, 1093–1106. https://doi.org/10.1111/j.1365-2699.2004.01044.x.

Floeter, S.R., Krohling, W., Gasparini, J.L., Ferreira, C.E.L., Zalmon, I.R., 2007. Reef fish community structure on coastal islands of the southeastern Brazil : the influence of exposure and benthic cover. Environ. Biol. Fish. 78, 147–160. https://doi.org/10.1007/s10641-006-9084-6.

Garcia, J., Pelletier, D., Carpentier, L., Roman, W., Bockel, T., 2018. Scale-dependency of the environmental influence on fish β-diversity: implications for ecoregionalization and conservation. J. Biogeogr. 45, 1818–1832. https://doi.org/10.1111/jbi.13381.

Horta E Costa, B., Assis, J., Franco, G., Erzini, K., Henriques, M., Gonçalves, E.J., Caselle, J.E., 2014. Tropicalization of fish assemblages in temperate biogeographic transition zones. Mar. Ecol. Prog. Ser. 504, 241–252. https://doi.org/10.3354/meps10749.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. University Press, Princeton.

Hubert, N., Paradis, E., Bruggemann, H.J., Planes, S., 2011. Community assembly and diversification in Indo-Pacific coral reef fishes. Ecol. Evol. 1, 229–277. https://doi.org/10.1002/ece3.19.

Hutchinson, G.E., 1957. Concluding remarks. In: Cold Spring Harb Symp Quant Biol, pp. 415–427.

Karlovic, T.C., Gomes, R.R., Paiva, P.C., Babcock, E.A., Dias, J.F., 2021. Functionality and effectiveness of marine protected areas in Southeastern Brazilian waters for demersal elasmobranchs. Front. Mar. Sci. 8, 1–18. https://doi.org/10.3389/fmars.2021.694846.

Lawton, J.H., 1999. Are there general laws in ecology? Introduction and definitions. Source Oikos 84, 177–192.

Levin, S.A., 2001. Encyclopedia of Biodiversity -, 3.

Longo, G.O., Ferreira, C.E.L., Floeter, S.R., 2014. Herbivory drives large-scale spatial variation in reef fish trophic interactions. Ecol. Evol. 4553–4566. https://doi.org/10.1002/ece3.1310.

Lopes, R.M., Katsuragawa, M., Dias, J.F., Montú, M.A., Muelbert, J.H., Gorri, C., Brandini, F.P., 2006. Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. Sci. Mar. 70, 189–202. https://doi.org/10.3989/scimar.2006.70n2189.

MacNeil, A.M., Graham, N.A.J., Polunin, N.V.C., Kulbicki, M., Galzin, R., Harmelin-Vivien, M.L., Rushton, S.P., 2009. Hierarchical drivers of reef-fish metacommunity structure. Ecology 90, 252–264.

Magurran, A.E., McGill, B.J., 2011. Biological Diversity Frontiers in Measurement and Assessment. Oxford University Press, New York, NY.

Maia, H.A., Morais, R.A., Quimbayo, J.P., Dias, M.S., Sampaio, C.L.S.S., Horta, P.A., Ferreira, C.E.L., Floeter, S.R., 2018. Spatial patterns and drivers of fish and benthic reef communities at São Tomé Island (Tropical Eastern Atlantic). Mar. Ecol. 39, e12520. https://doi.org/10.1111/maec.12520.

Matthews, T.J., Borges, P.A.V., de Azevedo, E.B., Whittaker, R.J., 2017. A biogeographical perspective on species abundance distributions: recent advances and opportunities for future research. J. Biogeogr. 44, 1705–1710. https://doi.org/10.1111/jbi.13008.

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E., 2015. Fifteen forms of biodiversity trend in the anthropocene. Trends Ecol. Evol. 30, 104–113. https://doi.org/10.1016/j.tree.2014.11.006.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.L.I., White, E.P., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecol. Lett. 10, 995–1015. https://doi.org/10.1111/j.1461-0248.2007.01094.x.

Morais, R.A., Ferreira, C.E.L., Floeter, S.R., 2017. Spatial patterns of fish standing biomass across Brazilian reefs, Southwestern Atlantic. J. Fish. Biol. 91, 1642–1667. https://doi.org/10.1111/jfb.13482.

Munday, P.L., Jones, G.P., Pratchett, M.S., Williams, A.J., 2008. Climate change and the future for coral reef fishes. Fish Fish. 9, 261–285. https://doi.org/10.1111/j.1467-2979.2008.00281.x.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, H.H., Wagner, H., 2016. Vegan: community ecology package. R Package Version 2, 3–4. https://CRAN.R-project.org/package=vegan.

Pereira, P.H.C., Barros, B., Zemoi, R., Ferreira, B.P., 2015. Ontogenetic diet changes and food partitioning of Haemulon spp. coral reef fishes, with a review of the genus diet. Rev. Fish Biol. Fish. 25, 245–260. https://doi.org/10.1007/s11160-014-9378-2.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411.

Pinsky, M.L., Selden, R.L., Kitchel, Z.J., 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. Ann. Rev. Mar. Sci 12, 153–179. https://doi.org/10.1146/annurev-marine-010419-010916.

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., Levin, S.A., 2013. Marine taxa track local climate velocities. Science 341, 1239–1242. https://doi.org/10.1126/science.1239352.

Quimbayo, J.P., Dias, M.S., Mendes, T.C., Lamb, R.W., Johnson, A.F., Aburto-Oropeza, O., Alvarado, J.J., Ayala-Bocos, A., Ferreira, C.E.L., Garcia, E., Luiz, O.J., Mascareñas-Osorio, I., Pinheiro, H.T., Rodriguez-Zaragoza, F., Salas, E., Zapata, F.A., Floeter, S.R., 2019. Determinants of reef fish assemblages in tropical oceanic islands. Ecography 42, 77–87. https://doi.org/10.1111/ecog.03506.

Quimbayo, J.P., Nunes, L.T., Silva, F.C., Anderson, A.B., Barneche, D.R., Canterle, A.M., Cord, I., Dalben, A., Ferrari, D.S., Fontoura, L., Fiuza, T.M.J., Liedke, A.M.R., Longo, G.O., Morais, R.A., Siqueira, A.C., Floeter, S.R., 2023. TimeFISH: long-term assessment of reef fish assemblages in a transition zone in the Southwestern Atlantic. Ecology e3966. https://doi.org/10.1002/ecy.3966.

Quimbayo, J.P., Silva, F.C., Mendes, T.C., Ferrari, D.S., Danielski, S.L., Bender, M.G., Parravicini, V., Kulbicki, M., Floeter, S.R., 2021. Life-history traits, geographical range, and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. Ecology. https://doi.org/10.1002/ecy.3298.

R Core Team, 2020. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science 235, 167–171.

Samoilys, M.A., Halford, A., Osuka, K., 2019. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. Ecol. Evol. 9, 4149–4167. https://doi.org/10.1002/ece3.5044.

Schuster, J.M., Stuart-Smith, R.D., Edgar, G.J., Bates, A.E., 2022. Tropicalization of temperate reef fish communities facilitated by urchin grazing and diversity of thermal affinities. Global Ecol. Biogeogr. 31, 995–1005. https://doi.org/10.1111/geb.13477.

Sexton, J.P., Mcintyre, P.J., Angert, A.L., Rice, K.J., 2009. Evolution and ecology of species range limits. Annu. Rev. Ecol. Evol. Syst. 40, 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317.

Silva, F.C., Floeter, S., Lindegren, M., Quimbayo, J., 2023. Warming-induced changes in reef fish community traits in the Southwestern Atlantic transition zone. Mar. Ecol. Prog. Ser. 710, 107–123. https://doi.org/10.3354/meps14288.

Silva, F.C., Quimbayo, J.P., Spanheeden Dencker, T., Pecuchet, L., Floeter, S.R., Lindegren, M., 2025. No sign of homogenisation in reef fish communities across an ecological transition zone exposed to warming. Divers. Distrib. 31, e13923. https://doi.org/10.1111/ddi.13923.

Simberloff, D., 2004. Community ecology: is it time to move on? Am. Nat. 163, 787–799. https://doi.org/10.1086/420777.

Siqueira, A.C., Morais, R.A., Bellwood, D.R., Cowman, P.F., 2021. Planktivores as trophic drivers of global coral reef fish diversity patterns. Proc. Natl. Acad. Sci. USA 118, e2019404118. https://doi.org/10.1073/pnas.2019404118.

Sommer, B., Beger, M., Harrison, P.L., Babcock, R.C., Pandolfi, J.M., 2017. Differential response to abiotic stress controls species distributions at biogeographic transition zones. Ecography 41, 478–490. https://doi.org/10.1111/ecog.02986.

Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish. Rev. Fish Biol. Fish. https://doi.org/10.1023/A:1020556722822.

Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J., Bates, A.E., 2015. Thermal biases and vulnerability to warming in the world's marine fauna. Nature 528, 88–92. https://doi.org/10.1038/nature16144.

Truong, L., Suthers, I.M., Cruz, D.O., Smith, J.A., 2017. Plankton supports the majority of fish biomass on temperate rocky reefs. Mar. Biol. 164. https://doi.org/10.1007/s00227-017-3101-5, 73–73.

Turnbull, J.W., Shah Esmaeili, Y., Clark, G.F., Figueira, W.F., Johnston, E.L., Ferrari, R., 2018. Key drivers of effectiveness in small marine protected areas. Biodivers. Conserv. https://doi.org/10.1007/s10531-018-1532-z.

Vergés, A., Doropoulos, C., Czarnik, R., McMahon, K., Llonch, N., Poore, A.G.B., 2018. Latitudinal variation in seagrass herbivory: global patterns and explanatory mechanisms. Global Ecol. Biogeogr. 27, 1068–1079. https://doi.org/10.1111/geb.12767.

Vergés, A., Mccosker, E., Pinto, M.M., Coleman, A., Wernberg, T., Ainsworth, T., Steinberg, P.D., 2019. Tropicalisation of temperate reefs : Implications for ecosystem functions and management actions. Funct. Ecol. 1000–1013. https://doi.org/10.1111/1365-2435.13310.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional. Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Williams, P.H., 1996. Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. Proc. R. Soc. B Biol. Sci. 263, 579–588. https://doi.org/10.1098/rspb.1996.0087.