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No Sign of Homogenisation in Reef Fish Communities Across an Ecological Transition Zone Exposed to Warming

Fernanda C. Silva[1,2] | Juan P. Quimbayo[3] | Tim Spanheeden Dencker[1] | Laurene Pecuchet[4] | Sergio R. Floeter[2] | Martin Lindegren[1]

[1]Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, Kongens Lyngby, Denmark | [2]Marine Macroecology and Biogeography Lab, Universidade Federal de Santa Catarina, Florianopolis, Brazil | [3]BioScales Lab, Department of Biology, University of Miami, Miami, Florida, USA | [4]The Arctic University of Norway, Tromsø, Norway

Correspondence: Fernanda C. Silva (silva.fernandacarol@gmail.com)

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ABSTRACT

Aim: Marine organisms are responding to warming by altering their distribution ranges, causing biogeographic range shifts and in some cases, favouring the community homogenisation. Transition zones can act as natural laboratories to explore the consequences of homogenisation. However, these habitats are relatively poorly studied in coastal areas. In this study, we aimed to investigate biotic homogenisation and changes in reef fish community composition from both a taxonomic and trait-based perspective.

Location: Seven islands in the South-western Atlantic transition zone.

Methods: We used a long-term survey data set of reef fish species abundances and traits of communities to calculate beta-diversity indices. By analysing the data, we derived temporal trends of beta-diversity values by separately comparing the North and South regions of the transition zone and performed pairwise comparisons to explore their dynamics when considered together.

Results: Contrary to previous expectations, we found no sign of homogenisation. The colder islands (Southern) experienced a decrease in taxonomic and trait richness metrics, whereas for the warmer islands (Northern), the taxonomic and trait richness fluctuated without any significant temporal trends.

Main Conclusions: While taxonomic composition may change over time, the trait composition is generally more conserved, highlighting the trait redundancy in South-western Atlantic communities and supporting the idea that these communities can maintain a range of ecological processes despite changes in taxonomic composition. Finally, the study revealed that despite non-homogenisation, the species that contribute most to variation, especially in the South, have common trait combinations indicating an increase in the trait redundancy of fish communities over time. We underline that local-scale conservation efforts may be particularly effective in preserving and protecting species and ecological functions in areas experiencing unique and fast changes in biodiversity.

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1 | Introduction

Marine organisms worldwide have shown pronounced alterations in their distribution ranges in response to warming (Lenoir et al. 2020; Pinsky, Selden, and Kitchel 2020). Species may respond to warming by moving either poleward, deeper or decreasing in abundance (Perry 2005; McLean et al. 2021). One well-known consequence of such climate-driven range shifts includes tropicalisation, caused by warm-affinity species expanding their distribution and increasing in proportion in more temperate locations (Vergés et al. 2016). In concert with tropicalisation, climate-driven range shifts are expected to lead to an overall homogenisation of communities (Pradervand et al. 2014; Stewart et al. 2018). The homogenisation process is primarily a result of the gradual replacement of native communities by range-expanding species, which increases the similarity of biotas (McKinney and Lockwood 1999). In this process, fast-growing and generalist species increase both in terms of distribution and abundance, largely thanks to their broad niche tolerances and ability to colonise new habitats (Clavel, Julliard, and Devictor 2011). In contrast, more specialised species, which typically have particular feeding and habitat affinities, slower growth and lower fecundity, may be less capable to adapt or shift their distribution and thus render them more susceptible to climate-induced variations (Graham et al. 2011). Taken together, the decrease and replacement of specialists by more abundant and widespread generalist species may contribute to greater similarity in species and trait composition, thus leading to homogenisation and a resulting decline in diversity (Clavel, Julliard, and Devictor 2011; Pool and Olden 2012; Zwiener et al. 2018). Furthermore, the underlying processes contributing to species range shifts and homogenisation can have important implications also in terms of the structure and functioning of ecosystems (Beger et al. 2014; Vergés et al. 2019; Maureaud et al. 2020). For instance, in Australian reefs, warming led to an increase in tropical herbivorous fish species and the decline of temperate planktivorous species, which in turn modified the community structure and energy flux (Smith et al. 2021). Therefore, the consideration of both species and traits in diversity studies is key to better understand the underlying processes contributing to community changes (including homogenisation) and their variability in space and time (Bellwood et al. 2002; Swenson, Anglada-Cordero, and Barone 2011; Soininen et al. 2016; Richardson et al. 2018).

Empirical studies have shown that regional diversity may be partitioned into multiple components (Cavender-Bares et al. 2009). One of these components encompasses beta-diversity, which describe the turnover in species composition across space and time (Loreau 2000; Maxwell et al. 2022). Studies using beta-diversity have shown signs of homogenisations in both marine and terrestrial taxa, for example, birds, fish, marine meiofauna, mammals and plants (Brustolin et al. 2019; Davey et al. 2012; Hidasi-Neto et al. 2019; Pool and Olden 2012; Zwiener et al. 2018). However, the degree to which homogenisation affects both the taxonomic and trait structure of communities is poorly known, especially when accounting for species abundances (Pool and Olden 2012).

Transition zones where environmental conditions change markedly, even over limited geographical distances may act as natural laboratories allowing us to explore the effects of homogenisation. This is because sharp environmental gradients favour communities characterised by species adapted to different conditions (Ferro and Morrone 2014). Studying transition zones may provide key test cases to investigate the impacts of global warming on regional scale community responses, as species in these areas are close to their physiological tolerance limits (Sommer et al. 2017). The combination of high biodiversity, natural variability and proximity to environmental thresholds makes transition zones particularly susceptible to biotic reorganisation. Consequently, they are more likely to experience shifts in species distributions, composition and dominance due to environmental changes. As a result of climatic changes, these areas are expected to show an increase in taxonomic and trait homogenisation over time due to the most responsive organisms (likely common and dominant warm-affinity species) expanding their range (Favoretto, Sánchez, and Aburto-Oropeza 2022) and increasing the frequency of general traits in the community. Despite their potential to provide new insights regarding community changes and responses to warming, transition zones are relatively poorly studied, at least in marine ecosystems (Vergés et al. 2016; Iknayan and Beissinger 2020).

In this study, we investigate signs of homogenisation and potential changes in community composition from both a taxonomic and trait perspective, using a unique, long-term survey data set of reef fish species abundances and traits sampled across the South-western Atlantic transition zone as an illustrative case study. More specifically, we aim to identify the patterns and compare long-term changes in richness and turnover among reef fish communities in islands from two regions exposed to warming, but characterised by generally warmer or colder water masses, as well as differences in the level of exploitation. To achieve this overall aim, we pursued the following research questions: (i) How does the overall species and trait diversity change over time in each region? (ii) To what extent have potential changes in richness been accompanied by underlying alterations in composition and abundances? (iii) Have changes in community composition and abundances led to increased taxonomic or trait homogenisation between regions over time?

2 | Methods

2.1 | Study Area

The study area encompasses reef fish assemblages sampled in seven continental islands located in the subtropical-warm temperate transition zone of the South-western Atlantic (Figure 1). Due to the sampling limitations (Figure S1), the islands were grouped into the Northern warm region (Galé—50 ha, Arvoredo—342 ha and Deserta—16 ha) and the Southern temperate region (Aranhas—27 ha, Xavier—10 ha, Campeche—49 ha and Moleques do Sul islands—14 ha). The distance between islands ranges from 4 to 31 km and the overall study extent is 74 km. The Northern islands show generally higher mean temperatures, whereas the southernmost islands experience cooler conditions. Both areas are exposed to similar regional variation in temperature dynamics, which plays an important role in shaping ecological communities due to fast temperature change (Beger et al. 2014). A warming trend is evident in terms of the mean observed sea surface temperatures (SST;

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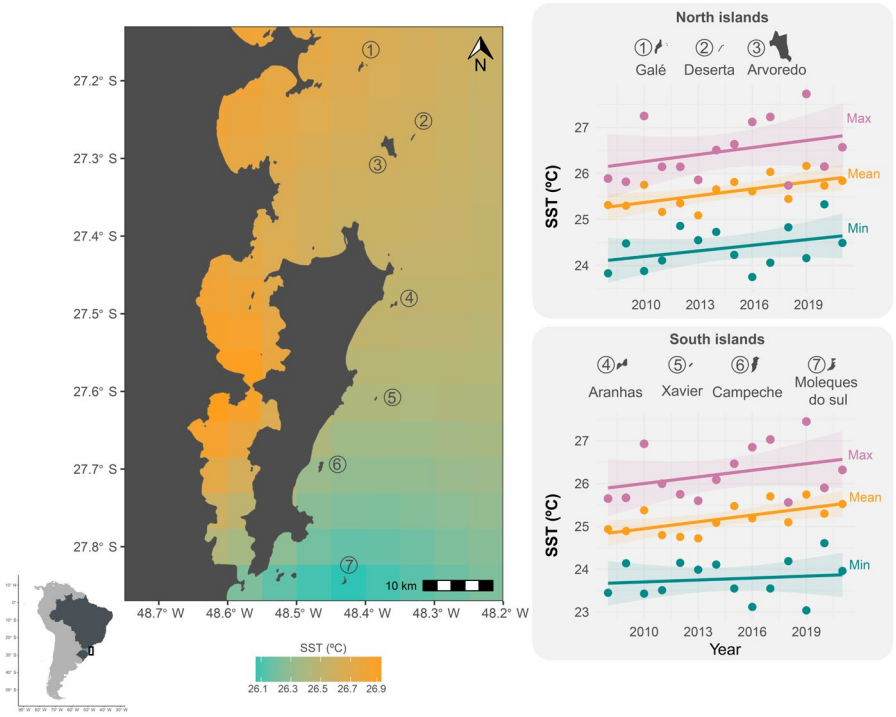

FIGURE 1 | Map of the study area, including the Northern (1–3) and Southern (4–7) islands across the transition zone. The colour range represents the mean sea surface temperature (SST, °C) gradient during the austral summer. The right panel shows time series and trends in the mean, minimum and maximum SST for both regions.

North mean SST: $p = 0.01$, $r^2 = 0.41$; South mean SST: $p = 0.01$, $r^2 = 0.42$) against time. Furthermore, the Northern islands are located inside the Arvoredo Marine Protected Area (MPA), while the Southern islands are located outside the MPA and are therefore exposed to higher human pressures, including both artisanal and recreational fishing. The rocky reefs in all localities are covered mainly 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 1306 underwater visual censuses (UVCs) carried out during summers from 2008 to 2022 (Figure S1). The sampling protocol consists of identifying and counting all actinopterygian (ray-finned) fish species observed within a belt transect of 40 m^2 (20 × 2 m). At each transect, the diver visually identified, counted and estimated the total length (to the nearest centimetre bin) of all species in the water column while unwinding a measuring tape. When retracting the tape on the way back, the diver follows the same protocol for smaller and cryptic species, usually associated with the bottom (Morais, Ferreira, and Floeter 2017). The UVCs were carried out at shallow depths ranging between 1.5 and 16 m depth (95% CI, Figure S2). All UVCs data available in Quimbayo et al. (2023).

2.3 | Standardisation of Sampling Effort

Sampling effort was not uniform across years and islands (Figure S1) and this heterogeneity can lead to biased estimates of diversity and composition (Chao and Jost 2012). To account for such differences in sampling effort, we constructed species accumulation curves (SACs, Figure S3) for each island and year to assess the level of taxonomic completeness of sampling using the 'vegan' package in R (Oksanen et al. 2016). For each estimated SAC, we then fitted Michaelis–Menten functions (Maureaud et al. 2020) and estimated the asymptotic species richness based on all available samples for each year-island combination (Table S1). Subsequently, we estimated the number of samples needed to achieve 75% completeness of the estimated asymptotic species richness (i.e., here ranging from 9 to 67 samples). Only one island-year combination had insufficient sampling to reach the required number of samples for the desired level of completeness and was therefore removed from the analysis (Table S1).

2.4 | Life History Traits

In order to reflect the general ecology of all species recorded in the UVCs ($N = 142$), a set of 11 biological traits broadly characterising their morphological, physiological or behavioural adaptations related to feeding, growth and survival were considered (Table 1). The classification and selection of traits builds on previous trait-based descriptions of marine organisms (Litchman and Klausmeier 2008; Litchman, Ohman, and Kiørboe 2013), adopted in recent studies on marine fish community structure and changes (Dencker et al. 2017; Pecuchet et al. 2017; Beukhof, Dencker, et al. 2019; Silva et al. 2023). All trait information was compiled through a review of published checklists, online repositories, local reports, books and monographs compiled by Quimbayo et al. (2021). To avoid multi-collinearity among traits,

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TABLE 1 | Life-history traits and their definitions, as provided by Quimbayo et al. (2021). Categorical and numerical traits characterising the main ecological aspects of species were compiled to conduct the analysis.

Trait	Definition and categories	Category	Levels	Class
Activity	Period of the day that species feed and breed	Categoric	Day, night or both	Feeding/Resource acquisition
Level water	Position in water column	Categoric	Bottom (staying at the bottom all the time), low (live slightly above the bottom, occasionally rest on the bottom) or high (several metres above the bottom)	
Mouth position	Anatomic jaw position	Categoric	Superior (lower jaw protruding upwards), terminal (upper and lower jaws equal in length), subterminal (upper jaw protruding downwards), inferior (mouth in ventral position), tubular (enlargement of mouth cavity) or elongated (long snout due to the increase in the bones premaxillary, maxillary and dental)	
PLD	Pelagic larval duration measured in days	Discrete	—	Growth/ Reproduction
Maximum body size	Length of the largest individual of the species observed in the census	Numeric	—	
Spawning	The way that species deposit eggs in water	Categoric	Attach to objects, demersal (deposit directly on the substrate), live (birth without external larval stage), oral (parental care when female or male keep the eggs in their mouth) or pelagic	
Trophic level	Position in the food web based on diet composition and mean trophic level of food items	Numeric	—	
Body shape	Morphological specialisation for swimming	Categoric	Box shaped (globular as in Diodontidae), compressed (flattened laterally), depressed (flattened dorsoventrally), eel-like (elongated, snake-like shape and locomotion), elongated (long in relation to length) or fusiform (spindle shape, most hydrodynamic form)	
Caudal fin aspect ratio	An indicative value of species activity calculated from the squared height of caudal fin (h) divided by its surface (s) area (h^2/s)	Numeric	—	Survival/Predator avoidance
Group size	Gregariousness behaviour	Categoric	Solitary, pairing, small groups (3–20 individuals), medium groups (20–50 individuals) or large groups (> 50 individuals)	
Mobility	Area of activity	Categoric	Sedentary, territorial, mobile or very mobile	

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we performed a Pearson correlation test for numerical traits, a PCoA using Euclidean distances among species based on categorical traits and a final sensitivity test calculating trait richness when removing traits one by one (Figures S4–S6).

2.5 | Species and Trait Signs of Homogenisation

Since temporal changes in diversity and composition within an area may result in a decreasing or increasing degree of similarity between areas over time, we first investigated changes in species richness and composition in the Northern and Southern region separately. We randomly re-sampled the number of UVCs needed to reach 75% of the asymptotic species richness for each year-island combination. For each of the 99 permutations (with replacement), we calculated taxonomic and trait diversity metrics, both weighted and non-weighted by species abundances. The α-diversity metrics included species richness (SRic), trait-based richness, as well as species and trait-based evenness estimated through the vegan and FD packages (Oksanen et al. 2016; Laliberté, Legendre, and Shipley 2015). These indices were selected to facilitate the detection of the appearance or disappearance of species and/or traits in the transition zone. We assessed whether the observed patterns deviated significantly from those expected by chance. We built null distributions for trait diversity by randomising the species pool 99 times, with each random selection based on 99 bootstraps of transects. The permutations were conducted using independent swaps of species identities while maintaining assemblage richness and species occurrence frequencies constant. The randomised occurrence matrices were used to calculate trait diversity based on convex hulls (i.e., trait richness). For each permutation, we fitted a linear model with year as a predictor to assess the slope of the temporal trends in each region. Subsequently, we compared the distribution of slopes based on the null model relative to the observed slopes. We also calculated the temporal variation of the standardised effect size (SES) of trait richness following the equation: $\text{Trait richness}_{\text{observed}} - \text{Trait richness}_{\text{mean.null}}/\text{SD}_{\text{null}}$ (Dubuc et al. 2023), where $\text{Trait richness}_{\text{observed}}$ is the mean value obtained from the SACs, $\text{Trait richness}_{\text{mean.null}}$ is the mean of null trait richness distribution, and SD_{null} is the standard deviation of the null trait richness distribution. Positive values indicate that trait richness is greater than expected by chance, whereas negative values indicate the opposite. To account for temporal shifts in the taxonomic composition within each region, we calculated β-diversity using Jaccard dissimilarity index for presence/absence data and Bray–Curtis dissimilarity index for abundance data using the beta.pair function from the betapart package (Baselga, David, and Orme 2012). A mean value of β-diversity for each year combination derived from the dissimilarity matrix in each region was calculated and used for visualisation. In terms of traits, we calculated β-diversity for presence/absence data by using Gower's distance, capable of accounting for both continuous and categorical variables (Gower 1971). Subsequently, a PCoA was built using the three first axes of the resulting distance matrix (Laliberté and Legendre 2010), as they cumulatively explained more than 50% of the variation in traits.

The trait β-diversity weighted by abundances was calculated using kernel density *n*-dimensional hypervolumes as implemented in the 'BAT' package (Cardoso, Rigal, and Carvalho 2015). Community trait hypervolume was constructed for each year-island combination with the 'hypervolume' package (Blonder et al. 2022) incorporating categorical variables through Gower dissimilarity and keeping three orthogonal axes. We estimated trait β-diversity following (Mammola and Cardoso 2020), that is, by computing the overall differentiation among kernel hypervolumes.

To reflect temporal turnover throughout the time period, all the β-indices above were calculated for North and South separately by comparing the start year (first year of the time series) to all subsequent years with increasing temporal distance. As an addition to the calculations above, we used the similarity percentage analysis (SIMPER) to identify species contributing the most to the estimated dissimilarities in composition between the starting and end year for each region. To better explore the trait composition of the identified species and determine the extent to which species contributing to compositional changes are predominantly generalists or specialists, we calculated the trait distinctiveness with and without abundances, within each region. This analysis followed the methodologies of Murgier et al. (2021) and Violle et al. (2017), using the 'funrar' package to calculate the dissimilarity matrix (Grenié et al. 2017). Trait distances were calculated for the entire community between all pairs of species independently of the year of occurrence. This index represents the dissimilarity of any one species in terms of their traits relative to all the other species in the community (Violle et al. 2017). Finally, we investigated potential signs of homogenisation across the transition zone by calculating β-diversity values reflecting the pairwise dissimilarity in species and trait composition between the North and South regions. The dissimilarities were obtained for each year both weighted and unweighted by abundances. All indices were represented by the average values and 95% confidence intervals across the random permutations and the workflow is represented by a diagram in Figure 2.

3 | Results

The Northern and Southern islands showed pronounced temporal variations in species and trait richness (Figure 3). We did not observe clear long-term trends in the Northern region (species richness: $p = 0.49$, $r^2 = 0.03$; trait richness: $p = 0.78$, $r^2 < 0.01$). However, species and trait richness in the South showed a slight long-term decline (species richness: $p = 0.02$, $r^2 = 0.38$; trait richness: $p < 0.01$, $r^2 = 0.47$). When comparing the first and last years of the time series, the species richness in the Southern region showed a pronounced decline by 50.5%. Our results demonstrate that both species and trait richness are higher in the Northern (warmer) areas compared to the Southern (colder) areas. Although the trends are different when comparing regions individually, the inter-annual variation between them is correlated and follows the same pattern (Figure S7). In terms of species and trait evenness, we did not observe linear trends for any region (species evenness—North region: $p = 0.78$, $r^2 < 0.01$; South region: $p = 0.08$, $r^2 = 0.25$; trait evenness—North region: $p = 0.87$, $r^2 < 0.01$; South region: $p = 0.14$, $r^2 = 0.18$). The null distribution for trait richness showed no marked trends in the trait richness for the North and South regions. This was evidenced

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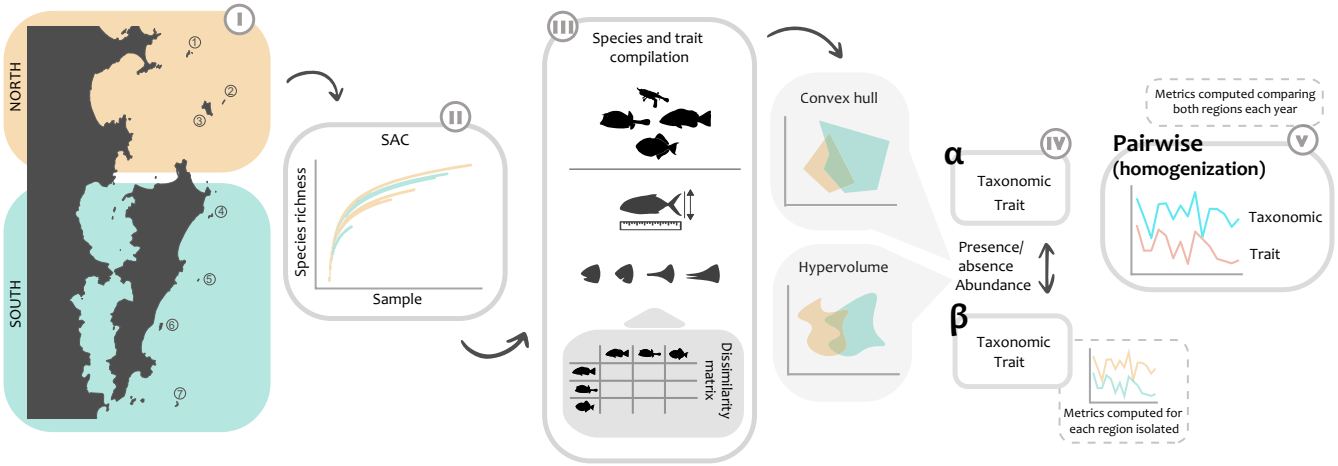

FIGURE 2 | Method diagram illustrating the three main steps to calculate temporal trends in fish communities in the North and South regions of the South-western Atlantic. The communities were grouped by region (I), and a species accumulation curve (SAC) was fitted for each year-region combination (II). Species and trait compilation were then used to build dissimilarity matrices (III). Trait diversity was estimated through a dissimilarity matrix, calculating the multidimensional space (convex hull for α-diversity) and a hypervolume for β-diversity. Temporal taxonomic and trait α- and β-diversity for each region separated were computed using presence/absence and abundance data (IV). Homogenisation was evaluated comparing pairwise distance between North and South regions in each year (V).

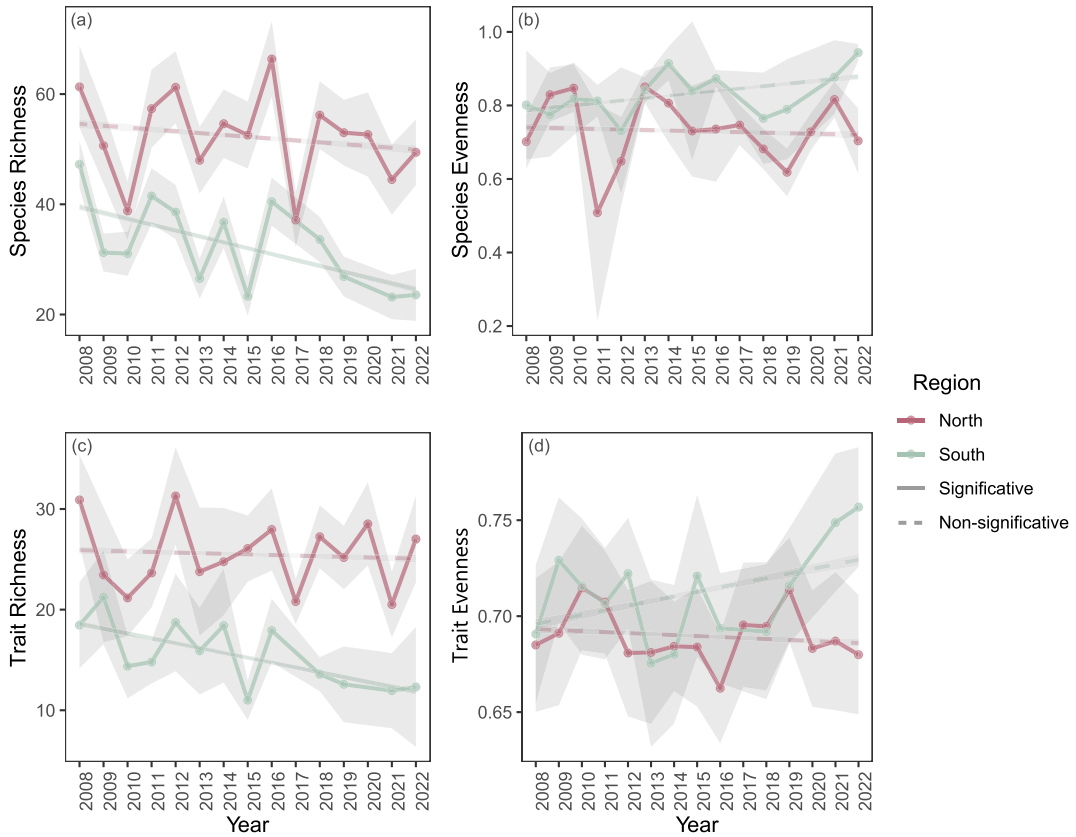

FIGURE 3 | Temporal taxonomic (a) and trait (c) richness trends and taxonomic (b) and trait (d) evenness in Northern (purple) and Southern (green) region. Lines and shaded areas represent the mean and 95% CI for each metric, while the solid colour lines show significant linear trends (derived from linear regressions with year as a predictor). Dashed colour lines represent non-significant trends.

by most SES values being above zero, highlighting that the trait richness in the North is more diverse than expected by the null model accounting for species richness. Overall, there is no significant temporal variation in SES for any region (Figures S8 and S9). Therefore, the trends obtained from SAC permutations are conserved, since after randomising the species pool (and consequently, traits), the results are similar with the slopes being centred around zero for both the null and observed model.

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Taxonomic temporal β-diversity had a higher turnover between years than trait turnover, especially for the Southern region (Figure 4). These differences were more pronounced for both metrics weighted by abundances compared to presence/absence. Although the Northern and Southern regions showed differences in local species and trait richness (Figure 4), the mean (or initial) level of turnover was similar (amounting to ~0.35). Furthermore, we demonstrate that while the Northern area shows a slight positive trend (especially for presence/absence data: $p < 0.01$, $r^2 = 0.88$), the Southern region demonstrates a pronounced increase in turnover over time, especially in terms of abundance-based taxonomic β-diversity ($p < 0.01$, $r^2 = 0.87$, Table S2).

When looking at the compositional differences between the first and the last year in more detail, our results from SIMPER demonstrate that 20 species contribute to at least 70% of the variation in abundance in the Northern region, while only eight species contribute to the variance in the South (Figure 5). We found that species contributing most to the β-diversity (dissimilarity) are predominately species with the lowest distinctiveness values (generalists), especially in the South (Figure 5, blue colours) and whose abundances are decreasing over time (Figures S10 and S11). The patterns obtained for distinctiveness weighted by abundances revealed the same patterns as for presence/absence data (Figure S12).

Finally, our pairwise comparison between the Northern and Southern region shows on average more similar trait composition (i.e., lower beta diversity) compared to taxonomic composition (Figure 6). This is especially evident if also accounting for abundances, where the average taxonomic and trait beta-diversity across all years amount to about 0.65 (SD = 0.13) and 0.30 (SD = 0.05), respectively. In terms of temporal changes, there is moderate inter-annual variability, yet no clear linear trend in the different metrics (taxonomic presence/absence: $p = 0.13$; $r^2 = 0.18$; trait abundance: $p = 0.62$; $r^2 = 0.02$), with the notable exception of trait turnover using presence/absence data ($p = 0.03$; $r^2 = 0.36$) and abundance-weighted taxonomic beta-diversity, that increased markedly throughout the time period ($p = 0.02$; $r^2 = 0.39$).

4 | Discussion

Global warming is generally expected to cause a loss of species in warmer, tropical areas, while colder, temperate areas will instead gain species from the more diverse pool of tropical taxa moving poleward (Sommer et al. 2017; Poloczanska et al. 2016). Our results contrast this general pattern, with the Southern (colder) region instead experiencing a marked decrease in taxonomic and trait richness, while in the Northern (warmer) region, richness remains largely stable. Moreover, we found no evidence of homogenisation between the two regions; rather, the communities are becoming distinct over time as seen for both turnover and pairwise comparison patterns. Although it is well known that the current biodiversity crisis and loss is global in scope (Bongaarts 2019), different

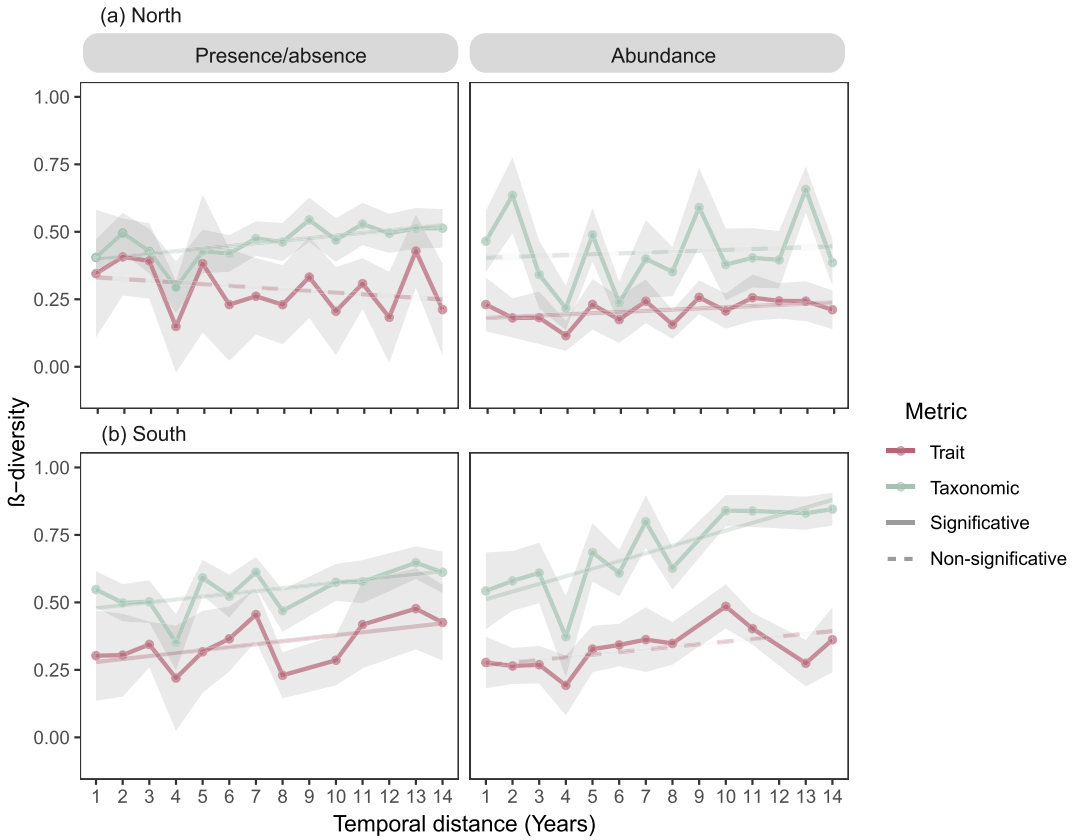

FIGURE 4 | Taxonomic and trait β-diversity turnover observed over time in North (a) and South (b) regions relative to the starting year. Lines and shaded areas represent the mean and 95% CIs for each metric when using presence/absence data or weighted by abundances. The solid colour lines show significant temporal trends (derived from linear regressions with year distance as a predictor) while dashed lines show non-significant trends.

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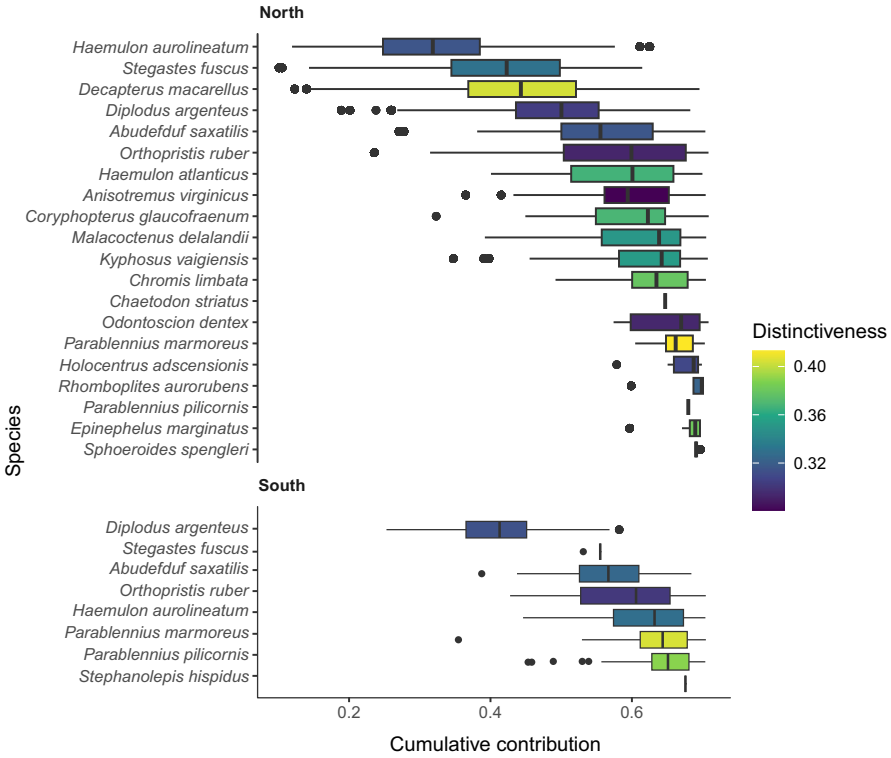

FIGURE 5 | Fish species contributing most to the cumulative dissimilarity (threshold value selected: 70%) between the first (2008) and last year (2022) in the Northern and Southern regions. The boxplots are based on values obtained from each of the 99 permutations. The colour gradient illustrates the respective value of species trait distinctiveness (i.e., representing the degree to which the species are generally considered as having a common set of traits [low distinctiveness] or a rare set of traits [high distinctiveness] in comparison to all species in each community).

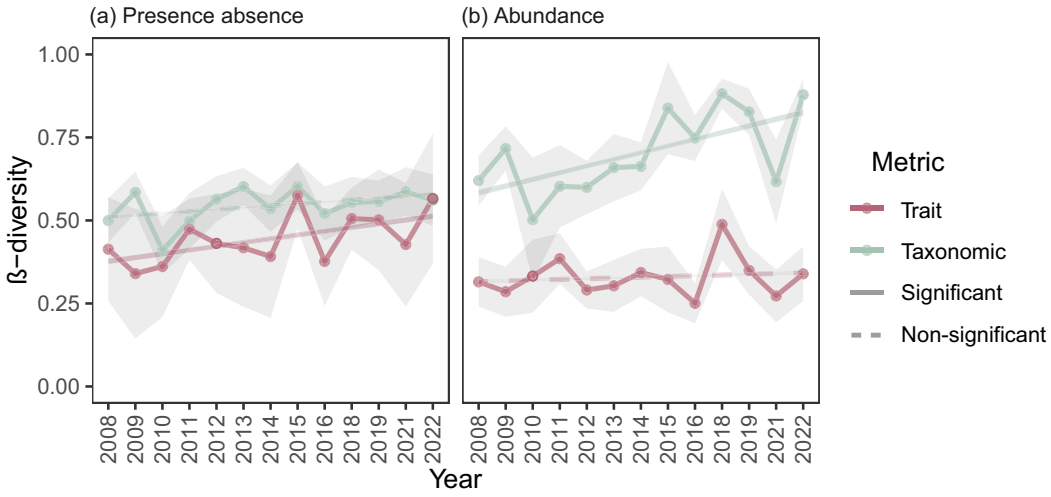

FIGURE 6 | Time series of annual pairwise taxonomic and trait β-diversity across the transition zone, reflecting the dissimilarity in species and trait composition between the Northern and Southern regions over time. Lines and shaded areas represent the mean and 95% CIs for each metric when using presence/absence data (a) or weighted by abundances (b), respectively. The solid lines show significant temporal trends (derived from linear regressions with year as a predictor) while dashed lines show non-significant trends.

and rapid changes are more likely to be observed at more local scales (Garcia et al. 2018). Our study conforms to such findings demonstrating pronounced local differences in diversity (turnover) trends across the South-western Atlantic transition zone, despite the general warming trend throughout the region.

Furthermore, we observed that while taxonomic composition may change over time, the trait composition is in general more conserved. This is particularly true in the South where the species composition in each consecutive year became more different compared to the starting year, whereas the turnover in trait composition was less pronounced. This may imply that the

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increasing taxonomic turnover in the South is primarily driven by the disappearance of species, rather than by species replacement. This is supported by the observation that species richness in this region is declining markedly. Higher turnover is often more evident in local species pools which are characterised by generally low richness, because overall composition is more sensitive to the disappearance of single species compared to speciose communities (Legendre 2014). Thus, the lower overall number of species, combined with declining richness trend, can explain the different compositional changes in the South compared to the more species-rich Northern region. Interestingly, the patterns are even more pronounced when accounting for abundances, indicating that not only changes in distribution and occurrences but also in terms of number of individuals is affecting community composition and turnover. The increased dissimilarity in taxonomic composition but unvarying dissimilarity in trait composition in the South can largely be explained by the low trait uniqueness of the species that contribute most to the cumulative change in composition from the first to the last year of the time series. These include some of the most frequently observed families in the South-western Atlantic, including Gobiidae, Haemulidae, Labridae, Serranidae, Lutjanidae and Pomacentridae (Floeter and Gasparini 2000; Bender et al. 2013). In terms of their traits, these species can broadly be described as common reef species (referred here as 'generalists') as they share combinations of traits with some or most of the regional species pool (i.e., mostly mobile invertebrate feeders, diurnal, territorial, benthopelagic associated, small group formers and pelagic spawners). Although these species share common traits, they are generally highly abundant (Pinheiro et al. 2018) and provide several common functions in the reefs (Siqueira et al. 2020), including secondary production and nutrient excretion (Brandl et al. 2019). Hence, as their abundances fluctuate and decline over time, it may lead to variations in terms of biomass accumulation and the availability of dissolved nutrients through excretion (Brandl et al. 2019).

Despite the general expectation of increased homogenisation caused by warming, our results show no directional change towards increased similarity in composition between the Northern and Southern region over time. This contrasts previous results found for different latitudes in other marine provinces (Magurran et al. 2015). Instead, the areas tend to become more different, especially when considering species composition weighted by abundances. Since the overall richness and composition in the North display no or only a marginal directional change throughout the period, the increased dissimilarity between areas is primarily caused by changes occurring in the South. Notably, it indicates that species previously shared between both areas (i.e., contributing to compositional similarity) are becoming less abundant and may even disappear locally in the South. However, as mentioned in the previous section, these declining species primarily constitute common and 'generalist' species sharing rather similar traits with the rest of the community (i.e., low distinctiveness). This in turn explains why the trait turnover between areas is rather consistent and unchanged throughout the time period.

Global warming has emerged as a main driver of species range shifts and community reorganisation worldwide (Pradervand et al. 2014; Magurran et al. 2015; Pinsky et al. 2013). Increasing temperatures has also been shown to impact the trait composition of marine fish communities, at both larger and regional scales (Frainer et al. 2017; Pecuchet et al. 2020; Beukhof, Frelat, et al. 2019; McLean et al. 2021), including the South-western Atlantic transition zone (Silva et al. 2023). Consequently, warming may potentially explain some of the observed changes in diversity and composition also in our study. Notably, the correlated inter-annual variability in species richness in both regions (Figure S7) suggests the presence of a similar underlying driver acting across regions. However, if responding similarly to warming, both regions would also show corresponding trends in diversity; yet only the Southern region shows marked trends in both α- and β-diversity. Hence, it is likely that the reef fish communities are responding differently, or to other aspects of temperature variations, beyond simply the increase in mean SST. For instance, there is evidence suggesting that the South-western Atlantic oceanic circulation is not only warming but also intensifying in the past decade (Franco et al. 2020; Sánchez et al. 2015) and that the thermal tolerance of fish in this region is being influenced by temperature (Silva et al. 2023). As observed in the study of Perez and Sant'Ana (2022), Brazil's current dynamics intensification is affecting species composition and biomass of warm- and cold-affinity species. In our study, we found a higher degree of temperature seasonality, especially in the South (Figure S13). It is plausible that the increasing difference between the minimum and maximum SST in the South may serve to constrain not only cold-adapted species limited by the warmer summers but also more warm-affinity species (from the North) limited by the consistently cooler winters. Whether such environmental filtering may explain the observed changes in richness and composition is unclear and merit further research to better understand the underlying mechanisms and responses of reef fish communities to climate change. Therefore, the trends observed in this manuscript offer valuable insights for future studies exploring the relationship between these trends and temperature, a factor well known to significantly impact the physiology, behaviour and population dynamics of species (Rijnsdorp et al. 2009).

It is also known that climate change potentially acts in synergy with other stressors, including human disturbance and overexploitation (Jackson 2008; Figueroa-Pico, Tortosa, and Carpio 2021). More specifically, fishing activity has been shown to modify community structure (Froese and Kesner-Reyes 2002; Young, Foale, and Bellwood 2014), thereby increasing the sensitivity of fish communities to climate variability (Jackson 2008). Interestingly, the region demonstrating temporal turnover in species composition corresponds to the Southernmost islands that are located outside an MPA and therefore exposed to fishing. Since the turnover is primarily evident if accounting for changes in abundances fishing may contribute to some of the observed changes in the overall β-diversity. However, among all the species targeted by the local fishery, only one (*Epinephelus marginatus*) is experiencing a decline in abundance (Figure S10). This indicates that the beta-diversity patterns observed in this study could potentially be influenced indirectly by fishing activities. Unfortunately, we lack accurate data on fishing activity in the area and its changes in space and time, making it challenging to establish and quantify effects of fishing on reef fish diversity and community composition. Hence, we emphasise the importance of having access to such information, as well as data on

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enforcement and performance of MPAs. Additionally, we acknowledge that the species are likely being impacted by several other factors, including the influence of temperature, ocean circulation and their specific thermal tolerances. Hence, further research is needed to understand the potential cumulative impacts of fishing and climate change acting on the diversity and composition of reef fish communities in the area and beyond.

Our findings highlight the importance of considering multiple metrics of taxonomic and trait α- and β-diversity, while accounting for both presence–absence and abundances, to better understand changes in diversity and its potential impacts on structure and functioning of systems. Although single metrics of α-diversity (typically species richness) can reveal spatial and temporal changes, it cannot alone capture important changes in the underlying composition and evenness of assemblages (Richardson et al. 2018). This limits our understanding of the potential implications for ecosystem functioning. Our study comparing multiple aspects of diversity of reef fish communities demonstrates that while pronounced differences exists in terms of species richness and composition, trait turnover is considerably weaker, or even unchanged within and between areas. This highlights a high degree of trait redundancy in these communities and supports the idea that the South-western Atlantic communities are able to maintain a range of ecological processes due to few functional entities (i.e., unique combinations of traits) performing similar functions (Mouillot et al. 2014). A higher trait redundancy may in turn increase the resilience of communities to change (Flensborg et al. 2023). However, rare and specialist species are likely to support vulnerable functions in reef ecosystems due to their unique functional roles (Mouillot et al. 2013; McLean et al. 2019). Hence, the replacement of specialists by generalist species resulting from homogenisation could result in ecological functions not perfectly performed as expected by more specialist species (Quimbayo et al. 2018). Therefore, studies exploring links between diversity, composition and ecosystem functions are key to a more holistic view of the effects of community changes on ecosystems (Duffy et al. 2016; Maureaud et al. 2020). In that regard, predictive models, for instance based on joint-species distribution models or trait-based food-web models (Maureaud et al. 2020; Ovaskainen et al. 2017; Jetz et al. 2019; van Denderen et al. 2021), could help to better characterise past, present and future changes in reef fish community composition and its potential impacts on ecosystem structure and functioning.

In summary, we observed a loss of taxonomic and trait richness in the Southern (colder) islands of the South-western Atlantic transition zone, while no directional trend was observed in the Northern (warmer) region. Furthermore, we found no compositional changes in terms of traits, but demonstrate pronounced turnover in taxonomic composition in the South, at least if accounting for species abundances. Taken together, our study shows no evidence of a directional change towards increased homogenisation across the transition zone, despite the general warming trend. On the contrary, our study shows increased differences in taxonomic composition, but high trait redundancy over time throughout the area. We emphasise the significance of the preservation of the trait structure of communities, alongside species composition, to predict potential responses to disturbances. (McLean et al. 2019). Other β-diversity components (e.g., nestedness and turnover) are worth exploring in follow-up research to better understand the taxonomic and trait variation among communities. Finally, future studies in transition zones could consider the specific responses of communities exposed to climate change and other drivers of biodiversity loss, such as habitat diversity, to compare with the findings obtained here.

Author Contributions

Fernanda C. Silva: writing – review and editing, writing – original draft, visualization, project administration, methodology, investigation, funding acquisition, formal analysis, data curation, conceptualization. **Juan P. Quimbayo:** writing – review and editing, writing – original draft, supervision, methodology, investigation, formal analysis, data curation, conceptualization. **Tim Spanheeden Dencker:** writing – review and editing, supervision, conceptualization. **Laurene Pecuchet:** writing – review and editing, supervision, conceptualization. **Sergio R. Floeter:** writing – review and editing, supervision, data curation. **Martin Lindegren:** writing – review and editing, writing – original draft, supervision, methodology, investigation, conceptualization.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data can be found at Zenodo repository: https://doi.org/10.5281/zenodo.8429218.

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