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Functional diversity patterns of reef fish, corals and algae in the Brazilian biogeographical province

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Abstract

Aim: Functional diversity encapsulates whole-community responses to environmental gradients mediated by species traits. Under trait convergence, similar responses may cause distantly related taxa to exhibit spatially correlated functional diversity. We investigated whether similar responses of reef fish, coral and algal functional richness and disparity to the environment produce spatially correlated functional diversity patterns.

Location: Brazilian marine biogeographical province.

Taxon: Reef fish, corals, algae.

Methods: We analysed data from 40 coastal and oceanic sites distributed across 27 degrees of latitude in the Brazilian province. Using traits, we measured functional richness (FRic) and disparity (Rao's *Q*) and calculated Pearson's correlation (ρ_{obs}) between pairs of metrics and taxa. We used Bayesian multivariate linear models to model taxa functional richness and disparity relative to sea surface temperature (SST), turbidity, salinity, species richness and region, and to estimate the residual correlation (ρ_{res}) between metrics after accounting for these variables.

Results: The best fitted model contained SST, species richness and region, and explained about 56% of the variation in FRic and Rao's *Q* across taxa. Yet, FRic and Rao's *Q* of fish, algae and corals responded differently to environmental variables. Functional diversity metrics were less correlated between algae and corals than compared to fish. Observed correlations of FRic and Rao's *Q* were low to intermediate across taxa (average $\rho_{obs} = 0.14$), and residual correlations were even lower (average $\rho_{res} = 0.02$).

Main conclusions: SST, species richness and region had a widespread role in determining spatially congruent functional diversity offish, algae and corals across Brazilian reefs, despite their fundamentally different evolutionary histories. Low residual spatial correlations suggest that other mechanisms might also contribute to functional diversity patterns of reef taxa independently. Given the role of SST, species richness and region, the functional structure of these reefs might be compromised by climate change, pollution and overfishing.

KEYWORDS

community assembly, cross-taxon diversity, functional metrics, niche differentiation, trait space

1 | INTRODUCTION

Spatially correlated (or congruent) patterns refer to concordant diversity values from distinct organisms across space (Gaston, 2000). A congruent pattern emerges when multiple taxa respond in the same direction and magnitude to large-scale environmental gradients, such as temperature and salinity, or even biogeographical history (Bellwood & Hughes, 2001; Gaston, 2000; Mittelbach et al., 2007). Congruence might also emerge from the association among taxa (Gaston, 2000) when, for example, ecological engineers such as scleractinian corals provide habitat for associated organisms (Darling et al., 2017). Likewise, disturbance regimes and habitat conditions might cause congruent diversity patterns when coexisting species share adaptations to the local environment (Mouillot et al., 2013). Large-scale gradients can trickle down and interact with sub-regional and local processes to determine which species can persist and interact, a process of community assembly largely mediated by organismal traits (Weiher & Keddy, 1995).

Disentangling the mechanisms behind trait-based congruence might help understand whether communities of different taxa are structured under common assembly rules (Violle et al., 2014). Many morphological, physiological and behavioural traits respond to large- and local-scale environmental conditions (called 'response traits', Díaz & Cabido, 2001). As such, biological traits enable the detection and inference of spatial congruence that emerges as community trait-based responses to the environment (Allen et al., 2002; Brown et al., 2004). This is of primary importance in studies investigating congruent diversity gradients for phylogenetically distant taxa (e.g. Renema et al., 2008). Functional richness and divergence are two complementary dimensions of functional diversity to be assessed in a spatial congruence context (Mason et al., 2008; Mouchet et al., 2010; Villéger et al., 2008). Functional richness (FRic) measures the total volume occupied by species in the trait space (Villéger et al., 2008). FRic tends to increase with species richness (until saturating in species-rich communities) (Guillemot et al., 2011; Halpern & Floeter, 2008) and might be higher in heterogeneous and stable environments (Mouillot et al., 2013). Congruent FRic could reveal whether the environment leads to an equally wide range of ecological strategies across taxa. Functional divergence (or 'disparity', term used henceforth), often measured by the Rao's Quadratic Entropy (Rao's Q), represents the sum of the squared distances between each pair of species in an assemblage weighted by their abundance (Botta-Dukát, 2005; Rao, 1982). Rao's Q actually summarizes abundance, functional richness and disparity in a single metric so that a community with a wide range of traits and even abundance distribution will depict high Rao's Q value (Mouchet et al., 2010). Congruent Rao's Q provides insights into whether abundance alters the patterns of functional diversity across taxa.

There are numerous cases of spatially congruent patterns of taxonomic diversity, especially considering latitude, altitude and temperature gradients (Jankowski et al., 2013; Thomson et al., 2014; Tisseuil et al., 2013; Tittensor et al., 2010). Such spatial congruence has been identified for bird species richness and woody plant guilds as a common response to overall vegetation complexity (Kissling et al., 2008). In Neotropical savannas, ants and trees have congruent species richness in space probably caused by their similar responses to temperature and productivity gradients (Vasconcelos et al., 2019). Freshwater taxa also depict congruent species richness and, to a lesser extent, congruent endemism (fish, amphibians and birds) in space caused by their similar response to contemporary and historical environments (Tisseuil et al., 2013). In marine ecosystems, congruence has been observed for coral and reef fish species richness, particularly in the Indo-Pacific Ocean (Bellwood & Hughes, 2001; Hughes et al., 2002). Despite the multitude of examples of spatial congruence for species richness and endemism, there are relatively few studies proposing (Heino et al., 2013) or in fact assessing (e.g. Kissling et al., 2008; Mori et al., 2015; Murray et al., 2017; Xu et al., 2019) congruence on community functional diversity.

In reef ecosystems, fishes, corals and algae constitute key functional components, but their response to environmental conditions is rarely assessed (Bellwood & Hughes, 2001; Cord et al., 2022; Thomson et al., 2014; Tittensor et al., 2010). In the Brazilian marine biogeographical province (Briggs, 1974; Floeter et al., 2008; Pinheiro et al., 2018), these taxonomic groups coexist locally in marginal reefs with turbid and nutrient-rich waters (Aued et al., 2018; Loiola et al., 2019; Mies et al., 2020). The continental shelf has a varied width and hosts coral and rocky reefs disposed along 27 degrees of latitude, thus being exposed to varied temperature, productivity and salinity settings, producing a north/northeast and south/southeast regionalization of the coast (Cord et al., 2022; Pinheiro et al., 2018; Figure 1). There are four isolated oceanic islands that harbour low species richness and high endemism levels, with low similarity in species composition to that of coastal reefs (Cord et al., 2022; Pinheiro et al., 2018). Despite the large latitudinal range of the Brazilian coast, reef fish and benthos species richness do not conform to the classic latitudinal gradient (Mittelbach et al., 2007), but peak at intermediate latitudes (Aued et al., 2018; Cord et al., 2022; Morais et al., 2017; Pinheiro et al., 2018). A recent assessment of nine marine taxa (among them reef fish, corals and macroalgae) along the Brazilian province showed spatially consistent taxonomic composition across these taxa, largely determined by broad-scale variation in sea surface temperature (SST), current velocity and water turbidity gradients (Cord et al., 2022). Nevertheless, spatial congruence in functional diversity patterns and its underlying



FIGURE 1 Spatial distribution of sampled reef assemblages along the Brazilian province. The map depicts the spatial distribution of the 40 studied sites across three regions. The y-axes depict latitude so that the data plots can horizontally match the locations on the map. The numbers indicate the sites selected for Figure 2. Some points seem visually darker than others on the map because sites overlap at this spatial resolution. Data plots display spatial variation in species richness, sea surface temperature, turbidity and salinity for fish (blue), corals (orange) and algae (green). Environmental data derived from BioOracle (Tyberghein et al., 2012). Map in Equirectangular projection. Individual plots were produced in the R programming environment and the panel organization edited in Inkscape v.1.0.

causes (as environmental variables) have never been assessed at the Brazilian province scale. Furthermore, assessing congruence on reef fish, coral and algal functional diversity will complement the body of literature on reef species richness patterns at broad scales (Bellwood & Hughes, 2001; Cord et al., 2022; Thomson et al., 2014; Tittensor et al., 2010; Yeager et al., 2017), and could guide future progress in mapping reef ecosystem functions and services across taxa.

We assessed whether functional richness and disparity of reef fish, corals and algae exhibit (I) similar responses (magnitude and direction) to environmental variables, and (II) positive spatial correlation (i.e. spatial congruence) at the Brazilian province scale. Our first hypothesis was that, despite their limited phylogenetic relatedness, reef fish, corals and algae should exhibit similar responses to SST and region. SST directly influences the metabolic processes, activity and growth of different marine taxa (Allen et al., 2002; Barneche et al., 2019; Brown et al., 2004), while the coastal (northern and southern regions) and oceanic island regions impose different conditions for organism dispersal, colonization and establishment, and exhibit environmental differences (Cord et al., 2022; Pinheiro et al., 2018). Alternatively, other environmental variables could influence functional diversity, such as turbidity-due to its influence on light irradiance and microhabitat conditions-(Cord et al., 2022; Santana et al., 2023), and species richness—a recognized proxy of biotic constraints on local functional diversity (Halpern & Floeter, 2008; Mason et al., 2008). We built different Bayesian models to verify the relative support of these concurrent hypotheses. Similar magnitude and direction of response to the environment would lead to positively correlated diversity across taxa (Tisseuil et al., 2013). Thus, our second hypothesis was that if this holds true,

then cross-taxon residual correlation of functional richness and disparity would be reduced after accounting for the influence of SST and region, revealing that these variables determine the spatial variation in functional diversity metrics of reef organisms along the Brazilian marine province.

2 | MATERIALS AND METHODS

2.1 | Data

Brazilian reefs are distributed across four oceanic islands and a variable shelf area along the vast ~8.000km of Brazilian coast (Leão et al., 2016). The Brazilian biogeographical province is located in the Southwestern Atlantic Ocean and is separated from the Caribbean and Western Africa provinces by biogeographical barriers including the Amazon-Orinoco and the Plata River's plume, ocean currents and the mid-Atlantic ridge (Briggs, 1974; Floeter et al., 2008; Pinheiro et al., 2018). The province harbours benthic assemblages predominantly composed of macroalgae, crustose coralline algae and scleractinian corals (Aued et al., 2018). Also, its reefs are predominantly marginal because turbidity and nutrient conditions are considered suboptimal for most coral species to thrive (Aued et al., 2018; Loiola et al., 2019; Mies et al., 2020).

We compiled two extensive datasets of reef fish and benthic assemblages of algae and corals which were originally collected along the Brazilian biogeographical province (Aued et al., 2018; Morais et al., 2017; respectively). Both datasets comprise large-scale spatial snapshots of fish and benthic assemblages in coastal and oceanicisland reefs, from which 40 sites matched and were used here to



FIGURE 2 Functional trait spaces, functional richness (FRic) and functional disparity (Rao's *Q*) values for fish (blue), coral (orange) and algal assemblages (green) for selected sites (site numbers from the map in Figure 1). Sites were chosen to contemplate variation in functional diversity of all groups across the sites and were roughly equidistant latitudinally (0°, 4°S, 10°S, 17°S, 22°S, 24°S, 27°S). Dark-coloured polygons represent regional trait spaces, while light-coloured polygons are local trait spaces built with the local subset of species from the regional trait space. In assemblages with low species richness (≤ 2 species), it was not possible to measure FRic (e.g. corals on site 1 and 36). The variation of trait data explained by the two first PCoA axes, for each group, are presented on site '1'. Circle sizes in trait spaces denote the relative abundance of organisms in each site. Individual plots were produced in the R programming environment and the panel organization edited in Inkscape v.1.0.

analyse spatial congruence on functional diversity metrics (Figure 1). Within these sites, a varied number of underwater visual censuses $(40 \text{ m}^2 \text{ belt transects}; n = 1692, \text{ average} \pm \text{SD of } 42.30 \pm 42.64 \text{ transects}$ sects per site, ranging from six to 242 transects) and plots (2 m² plots: n = 354, average of 8.63 ± 4.57 plots per site, ranging from three to 21 plots) have been sampled at two depth strata (1–7 and 8–15 m) to ensure local representativeness of reef fish and benthic organisms. In each underwater visual census, one diver counted, identified and tallied the size of every sighted fish (see Morais et al., 2017 for further details). In each plot, the cover (%) of benthic organisms was quantified using the photoQuad software (see Aued et al., 2018 for further details). Benthic coverage comprised the average percentage across subsamples (photo quadrats) within plots (Aued et al., 2018). Benthic taxa not identified with precision (32% of 103 taxa) were grouped into broader taxonomic groups (e.g. crustose coralline algae, turf algae) or placed at higher taxonomic levels (e.g. Halimeda, Ulvophyceae). This also occurred for corals for which photo identification is challenging (e.g. Millepora nitida, Millepora braziliensis, Siderastrea stellata, Siderastrea siderea, Agaricia agaricitis, Agaricia fragilis, Agaricia humilis). We are aware that this could underestimate functional diversity, especially for algae, as identification based on microscopic methods is far more accurate (Aued et al., 2018). Also, sampling did not cover shallow areas (~1 m depth) with seaweed beds (Eggertsen et al., 2017). While acknowledging these limitations, describing algae through their functional traits, rather than allocating them into functional groups, seems to be the best strategy for studying algal functional diversity (Ryznar et al., 2021).

2.2 | Environmental variables

To characterize the environmental gradients along the Brazilian marine province, we extracted annual averages of SST (°C), turbidity (Diffuse Attenuation Coefficient, $\mathrm{K}_{\mathrm{d490}}$) and salinity (Practical Salinity Scale, PSS) from BioOracle (Tyberghein et al., 2012) using the geographical coordinates of each site (using the 'sdmpredictors' R package; Bosch, 2018). We also considered using primary productivity (gm⁻³ day⁻¹, also from BioOracle) and coastal distance (measured using the function 'dist2line' available in the 'geosphere' package; Hijmans, 2019), but they were significantly correlated (at $\alpha \leq 0.05$) with other variables (Figure S1.1) and were excluded from further analyses. Region was considered as a threelevel factor: Northern region (comprising the North and Northeast regions), the Southern (comprising the South and Southeast regions) and oceanic islands (Cord et al., 2022; Pinheiro et al., 2018). The last predictor in our models was local species richness of each group, consisting of the number of species observed in each assemblage. Since predictors are in different units (e.g. °C, counts), all quantitative variables were scaled by their average and standard deviation to improve parameter estimation and comparability between model coefficients.

We chose these predictors because SST influences the overall energy availability in the environment as well as organism physiology (Brown et al., 2004). Salinity represents land influence on reefs (e.g. freshwater discharge, anthropogenic activities) and tends to be high at sites far from the coast, representing an important challenge for organism osmoregulation (Aued et al., 2018; Loiola et al., 2019). Turbidity is influenced by freshwater discharges along estuaries (Aued et al., 2018; Loiola et al., 2019) and it cannot only hinder the capacity of primary producers (e.g. macroalgae) to photosynthesize, but also increases the frequency of mixotrophic strategies (Aued et al., 2018; Loiola et al., 2019). Plankton growth is strongly limited by light irradiance in marginal reefs, with implications for planktivorous fish occurrence (Barneche et al., 2014; Francini-Filho & Moura, 2008). Region indicates the set of biogeographical regions occupied by reef fish, algae and corals (Cord et al., 2022; Pinheiro et al., 2018), and therefore characterizes how the history of colonization and establishment of those groups influences functional diversity. Finally, species richness is often used as a proxy of biotic constraints to saturated communities where the addition of novel species does not necessarily cause increases in trait space volume (Guillemot et al., 2011; Halpern & Floeter, 2008).

2.3 | Traits of reef fish, corals and algae

We estimated two functional metrics, functional richness (FRic) and disparity (Rao's Q), which link species traits to their response to environmental factors (Mouchet et al., 2010; Mouillot et al., 2013). Fish traits were as follows: total length (cm), average preferred temperature (T°C), average preferred depth of occurrence (meters), home range size (three levels: sedentary (home range size $< 10 \text{ m}^2$), mobile (home range size $> 100 \text{ m}^2$, capacity to move between reef areas), very mobile (frequently move between reefs, or travel large distances on the same reef each day)), school size (five levels: solitary, pair, small group (3-20 individuals), medium group (21-50 individuals), large group (> 50 individuals)), and body shape (six categories: box shaped, compressed, depressed, eel like, elongated, fusiform). These data were gathered from Quimbayo et al. (2021). Coral functional traits were sexual system (either gonochoric or hermaphrodite), growth rate (either slow or fast), growth form (three categories: branching, massive, plate), reproduction mode (either brooding or spawning) and lower depth of occurrence (meters). These data were compiled by J. Bleuel (personal communication). Finally, algal traits were as follows: size (four categories: small (< 10 cm), medium (\geq 10 and < 50), large (\geq 50 and \leq 400), very large (> 400 cm)), growth form (five categories: branching, encrusting, filamentous, encrusting/filamentous, massive) and carbonate accretion capacity (either yes or no). These data were compiled by A.W. Aued (personal communication), largely based on Costello et al. (2015). We used the average of quantitative traits and the mode of categorical and ordered traits (i.e. gathered the most frequent category and rank) to assign trait values to taxa identified at the genus level. Traits used here are potentially associated with organismal colonization and establishment strategies under varied environmental settings, and have been successfully used in assessments of fish and benthic functional diversity elsewhere (e.g. Bender et al., 2013; Bremner et al., 2006; Darling et al., 2017; McWilliam et al., 2018; Mouillot et al., 2014).

2.4 | Functional diversity analyses

We used FRic and Rao's Quadratic Entropy, calculated using the 'FD' package (Laliberté et al., 2014), to describe the whole assemblage response to environmental gradients as mediated by species traits. FRic represents the range of trait values among species, as represented by the convex-hull volume linking extreme trait values, whereas Rao's Quadratic Entropy represents species, traits and abundance distributions within the convex hull. We used the standardized version of FRic (i.e. convex hull volume standardized between 0 and 1) in our analyses, and used the Rao's Q metric weighted by species relative abundance in each site. We used the 'max' criterion (maximum number of axes that allows the number of species to be larger than the number of traits) to select the number of axes from the Principal Coordinate Analysis to keep for calculating the convex hull volume. As functional diversity metrics can only be calculated for assemblages with at least two species, we set FRic and Rao's Q to zero for assemblages without species (as was the case of coral assemblages in Santa Catarina, where corals are rare and are under sampled with the photoguadrat method).

2.5 | Statistical analysis

We combined fish, coral and algal FRic and Rao's Q into a multivariate response variable, and modelled it in function of environmental variables using Generalized Linear Models in a Bayesian inference framework as implemented in the R package 'brms' (Bürkner, 2017, 2018). Bayesian inference is a statistical method that applies the Bayes Theorem to update prior information about parameter values with observed data to then estimate the posterior probability of parameters. The prior information, generally represented by statistical distributions, are updated by their integration with data and likelihood estimation across independent Monte Carlo Markov Chains (MCMC). Variation in parameter estimates across posterior distribution draws represents an appropriate measure of parameter uncertainty (Kruschke & Liddell, 2018). In this sense, the Credible Intervals (CI), built using the quantiles of the posterior distribution draws of each parameter, depict the interval where most posterior distribution draws are and, therefore, delimit the area in which we have large certainty of finding the true parameter value (Kruschke & Liddell, 2018).

Bayesian multivariate linear models can model the effect of environmental variables on each metric and taxon, and estimate the correlation between metrics across taxa after accounting for the environmental effect (i.e. a residual effect; see equations below). Thus, we know which variable(s) better explain variation in each functional diversity metric, as well as whether any correlation between metrics is produced by model variables. As residual correlations can only be estimated in a multivariate normal distribution (Bürkner, 2017, 2018), we transformed FRic and Rao's Q using ln (x+1) to achieve a normal distribution, and modelled them as a linear function of model

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variables. The ln (x+1) was used to avoid infinite response variables produced by zero FRic and Rao's *Q*.

In this multivariate model, the observed values (natural log scale) of FRic and Rao's *Q* (the 'y' presented below) for each taxon and site (denoted, respectively, by the subscripts *k* and *i*) are taken from a multivariate normal distribution (*MVNormal*) with average μ , covariance matrix *S*, and residual correlation matrix *R*, which are specific to each metric and taxon (as described below).



 $\mu_{FRic,k^{i}} = \beta_{0FRic,k} + \beta_{FRic} X + \varepsilon_{FRic,k^{i}}$ $\mu_{O,k^{i}} = \beta_{0Q,k} + \beta_{Q} X + \varepsilon_{Q,k^{i}}$

$$\beta = \begin{bmatrix} \beta_{1,\text{fish}} & \beta_{1,\text{corals}} & \beta_{1,\text{algae}} \\ \vdots & \vdots & \vdots \\ \beta_{n,\text{fish}} & \beta_{n,\text{corals}} & \beta_{n,\text{algae}} \\ X = \begin{bmatrix} x_{1,i=1} & \cdots & x_{n,i=1} \\ \vdots & \ddots & \vdots \\ x_{1,i=l} & \cdots & x_{n,i=l} \end{bmatrix}$$

 β_0 is the regression intercept, and β represents a vector of regression coefficients estimated for *n* environmental variables in the matrix X, whose values vary between i = 1 and l = 40 sites. The priors for all β_0 and β were assumed to have a normal distribution (β_{0} , $\beta \sim N$ ($\mu = 0$, $\sigma = 4$). The σ parameter of the normal distribution (the width of the normal curve) and the error term ε were all assumed to have a Student's *t*-distribution (σ , $\varepsilon \sim t$ (3, 0, 2.5)). Finally, the residual correlation $\rho_{\rm res}$ is estimated as part of S in the multivariate model, and associated distributional sampling error of ρ_{res} is measured across the MCMC posterior distribution draws. The observed correlations $\rho_{\rm obs}$ are based on the input data, and the predicted correlation $(\hat{\rho})$ is estimated conditional on the structure of the best-ranked model (i.e. making predictions based on the variables in the selected model, and including distributional sampling error using the function 'posterior_predict' from the 'brms' package). Our Bayesian models were run using three independent MCMC (using the Hamilton Monte Carlo sampling algorithm), with 20,000 iterations and a warm up period of 18,000 iterations each chain. We retained 2000 post-warm up draws of each chain, resulting in 6000 posterior distribution draws of each

model parameter which were used to make statistical inference and test our hypotheses.

To investigate whether reef fish, coral and algal functional richness and disparity respond in the same direction and magnitude to environmental variables (hypothesis I), we interpreted variation in the regression coefficient β across metrics and taxa using interval plots ('bayesplot' R package, Gabry et al., 2019) showing the median of β and the associated 95% and 80% CIs. The posterior exceedance probability (p) of each regression coefficient β refers to the proportion of posterior probability draws higher or lower than zero (the zone of no variable effect). For region levels (Southern ('S') and oceanic islands ('islands')), we calculated p by checking whether the regression coefficients were higher or lower than the intercept (reference: the Northern region ('N')). Thus, a $p \sim 0.5$ indicates an equal probability of the regression coefficient to be either higher or lower than the zero for quantitative variables, and either higher or lower than the intercept for factors. Predictions were made by applying the equation of the selected model to the interval of values within the range of each variable being predicted, while fixing all other variables to zero.

While our first hypothesis involved the test of congruent response to SST and region across taxa, there are other variables that could affect functional diversity. Thus, we built and compared four alternative models regarding the environmental influence on FRic and Rao's Q (Table 1). In brief, the first model only accounted for the influence of SST and region, and the other models were more complex as we included more variables in the following order: species richness, turbidity and salinity. It is worth mentioning that we defined different model formulas for different taxa so that the species richness of one taxon was only included in the models of that taxon (see Appendix S2). We chose the best model using Leave-One-Out cross-validation Information Criterion (LOOIC) avoiding disagreement in chain mixing (by setting 'adapt_delta' = 0.99 and 'max_ treedepth' = 15), allowing a moment matching ('moment match = $\frac{1}{2}$ T') and model refitting ('reloo = T') along with Leave-One-Out crossvalidation produced in the case of problematic observations (Vehtari et al., 2017, 2020). The Leave-One-Out cross-validation consists of refitting the model several times after removing problematic observations that might affect model performance, one observation each time. The algorithm then shows the average LOOIC and the error after the refitting procedure. As the Akaike Information Criterion (AIC), lower values of LOOIC indicate more adequate models given the data. We calculated the difference between models (similar to Δ AIC) by estimating the expected log pointwise predictive density (ELPD) and the associated standard errors, which shows LOOIC overlap across models. Under models that are equally plausible (i.e. those with similar LOOIC, small ELPD and superimposed errors), we applied the parsimony principle and selected the simplest model. Finally, the Bayesian R-squared statistic (Gelman et al., 2018) was estimated for the selected model, showing the overall variation explained by model variables.

To investigate whether cross-taxon correlation of functional diversity would be reduced after accounting for variable influence TABLE 1 Model selection ranking of a Bayesian multivariate linear model assuming a multivariate normal distribution, based on LOOIC (Leave-One-Out-cross validation Information Criterion).

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	LOOIC		Number of parameters		ELPD			
Model	Estimate	SE	Estimate	SE	Difference	SE		
MV (FRic, Rao's Q) ~ SR + SST + Turbidity + Salinity + Region								
	-1036.77	28.63	53.04	7.24	0.00	0.00		
MV (FRic, Rao's Q)~SR+SST+Region								
	-1036.61	30.16	44.20	6.53	-0.78	3.54		
MV (FRic, Rao's Q)~SR+SST+Turbidity+Region								
	-1035.22	30.03	49.28	6.50	-0.08	5.25		
MV (FRic, Rao's Q)~SST+Region								
	-896.99	23.80	38.18	4.50	-69.89	8.51		

Note: The estimated number of parameters is also shown, depicting model complexity and specificity. This number is the sum of all model parameters (in our case intercepts, regression coefficients and correlations between all metrics). Models were compared using ELPD (expected log pointwise predictive density) estimates and associated errors across the 6000 posterior distribution draws. 'MV' depicts the multivariate normal distribution assumed in each model. The Standard Errors (SE) were calculated across the 6000 posterior MCMC draws.

Abbreviations: FRic, Functional richness; Rao' Q, Rao's Quadratic Entropy; SR, species richness; SST, sea surface temperature.

(hypothesis II), we plotted and compared the observed correlation (ρ_{obs}), the residual correlation (ρ_{res}) and the predicted correlation ($\hat{\rho}$). The median and associated 95% CI of residual and predicted correlations were calculated from 6000 posterior MCMC draws. All analyses were run in the R programming environment v.4.2.2 (R Core Team, 2022).

3 | RESULTS

We analysed species composition and trait data from a total of 198 fish species, 35 algae taxa (12 at species level, 13 at genus level and the remaining 10 at higher taxonomic levels) and 20 coral taxa (14 at species level, six at genus level) along the 40 studied sites (Figure 1). Coral richness was higher in tropical reefs, whereas fish and algae richness were higher in subtropical or transitional areas (i.e. where both tropical and subtropical species are found) (Figure 1). SST was higher in tropical reefs, whereas salinity and turbidity were higher at intermediate latitudes (Figure 1).

Functional richness and disparity (FRic and Rao's *Q*, respectively) varied considerably in space and across taxa (Figure 2). Fish functional richness and disparity were higher in the south, while coral functional richness and disparity peaked in the north and at intermediate latitudes (Figure 2). Algae, in their turn, had high functional richness and disparity in the north and southern limits of the Brazilian province (Figure 2). Three models were equally plausible according to LOOIC and ELPD estimates, and the most parsimonious and selected model included SST, region and species richness as variables (Table 1). Model parameters converged across the MCMC runs, showing Rhat statistic values ≤ 1.05 (i.e. high consistency across the posterior MCMC draws) and acceptable effective sample size across the three independent MCMC (Figures S1.2 and S1.3). Together, these factors explained from 24% to 90% of the variation on FRic and Rao's Q across groups (average of 56%) (Table 2). TABLE 2 Bayesian R-squared statistics ('Estimate') showing the overall variance explained by SST, turbidity and species richness on each functional diversity metric.

		Standard	Credible intervals	
	Estimate	deviation	2.5%	97.5%
Fish FRic	0.61	0.07	0.4	0.7
Fish Rao's Q	0.4	0.09	0.19	0.54
Algal FRic	0.9	0.01	0.86	0.91
Algal Rao's Q	0.24	0.1	0.06	0.41
Coral FRic	0.75	0.04	0.63	0.8
Coral Rao's Q	0.49	0.08	0.29	0.61

Note: 'Standard deviation' and 'Credible intervals' (lower 2.5% and upper 97.5% CI) are measurement of error and uncertainty of Bayesian R-squared statistics, calculated across the 6000 posterior distribution draws. The 'Estimate' consists of the median of these 6000 posterior distribution draws.

Abbreviations: FRic, functional richness; Rao' Q, Rao's Quadratic Entropy.

Species richness had a positive influence on the functional richness (posterior exceedance probability p = 1 for all taxa) and functional disparity of all taxa (p = 0.86, 0.98, and 1 for fish, algae and corals, respectively) (Figure 3). The effect of species richness was stronger than the effect of other variables, as shown by higher regression coefficients and non-overlap of Cls, with a more substantial effect on corals than fish and algae (Figures 3 and 4). SST had a positive influence on algal functional richness (p = 0.97) and coral functional disparity (p = 0.88). In contrast, it had a negative influence on fish functional richness (p = 0.89) and disparity (p = 0.93), coral functional richness (p = 0.77) and on algal functional disparity (p = 0.61) (Figures 3 and 4).



FIGURE 3 The estimated effect of sea surface temperature (SST), species richness and region on functional richness (FRic) and disparity (Rao's Q) of fish, coral and algl assemblages in the Brazilian province. The central dot represents the median regression coefficient, calculated across 6000 posterior distribution draws. The grey vertical line at zero depicts the theoretical zone of no effect of a variable. The thin and thick lines represent, respectively, the 95%, and 80% Credible Intervals around the posterior distribution estimates. 'N': Northern region; 'S': Southern region; 'Islands': Oceanic Islands. Estimates of 'N' were represented in the model intercept. The figure was produced in the R programming environment and edited in Inkscape v.1.0.

For regions, fish functional richness was higher in oceanic islands ('islands') than in the Northern region ('N', p = 0.99), and lower in the Southern ('S') than in the Northern region (p = 0.70). Islands also exhibited higher fish functional disparity than the N (p = 1), while the N and S regions had similar fish functional disparity (p = 0.50) (Figure 4). Algal functional richness was higher in the S than in the N (p = 0.98), being lower in the islands than in the N (p = 0.8). Algal functional disparity followed the opposite pattern of FRic, being lower in S relative to the N (p = 0.86) and to islands (p = 0.59) (Figure 4). Finally, coral functional richness was slightly higher in the N relative to the S (p = 0.57), whereas it was similar between the islands and the N (p = 0.99 and p = 0.64, respectively) (Figure 4).

Functional richness and functional disparity of reef fish, coral and algal assemblages exhibited weak to intermediate correlation in space (average of observed $\rho_{obs} = 0.14$, range of -0.29 and 0.64; blue points, Figure 5). Predicted correlations were generally lower than the observed correlations (average $\hat{\rho} = 0.08$, range of -0.25and 0.64), and often converged in direction (purple vs. blue points, Figure 5). The highest observed correlation was found between functional richness and functional disparity of coral assemblages ($\rho_{obs} = 0.64$). Between taxa, the highest positive correlations were found for fish and algal FRic ($\rho_{obs} = 0.36$) and fish functional richness and coral functional disparity ($\rho_{obs} = 0.30$; Figure 5). Negative correlations—both observed, predicted and residual—were only found between fish and coral functional disparity, and between fish functional disparity and coral functional richness (Figure 5). Residual correlations were low overall (average $\rho_{res} = 0.02$, range of -0.27 and 0.45; green points, Figure 5).

4 | DISCUSSION

We examined the role of SST, turbidity, salinity, species richness and region in explaining spatially congruent functional diversity across reef taxa in the Brazilian marine biogeographical province. All variables but salinity and turbidity composed the most parsimonious model. Functional richness, which depicts the range of traits in a local community (Villéger et al., 2008), increased with species richness for all taxa, but the rate of increase was higher for corals than algae and fish. In turn, functional disparity was not as strongly influenced by these variables as functional richness. While algae and corals, as sessile organisms, are expected to respond similarly to abiotic conditions and exhibit correlated functional diversity, our findings did not support such expectation. Notably, correlation of functional diversity metrics was stronger between corals and fish, and algae and fish, than between corals and algae. This could be explained by the diversity of habitats provided by corals and algae for fish assemblages (Darling et al., 2017; Fulton et al., 2019; Luza et al., 2022), and



FIGURE 4 Predicted values of functional richness (FRic) and disparity (Rao's Q) for fish, coral and algal assemblages, as functions of sea surface temperature (top), region (middle) and species richness (bottom), which correspond to the variables in the selected Bayesian multivariate linear model. The solid thick lines (top and bottom rows) and points (region) represent the predicted medians which were calculated across 6000 posterior distribution draws. The light and dark grey bands represent, respectively, 95% and 80% Bayesian credible intervals around the median relationship. On the y-axes, we show the predicted FRic and Rao's Q on the response scale (In(x + 1)). To improve visualization, y-axes have been allowed to vary across plots (see regression coefficients in Figure 3). Individual plots were produced in the R programming environment and the panel organization edited in Inkscape v.1.0.

competition for space between algae and corals (Grillo et al., 2018; Lonzetti et al., 2022). Finally, pairwise residuals' correlations of functional richness and disparity between taxa were overall weak, suggesting that independent mechanisms for each taxonomic group might also be operating in structuring functional diversity along the Brazilian province. Because the variation explained by SST, region and species richness was substantial, our results suggest that the functional structure of these reefs might be vulnerable to the loss of species and its impacts on functional redundancy caused by climate change, pollution and overfishing.

Our results support the role of SST, region and species richness in determining spatially congruent cross-taxon functional diversity in Brazilian reefs. Among these, species richness had the strongest and most widespread effect on fish, coral and algal functional richness, an outcome of increases in trait space volume with species richness. The shape of species-functional richness relationship has been extensively studied across several taxa to infer mechanisms underlying niche differentiation, community assembly and composition, revealing the limits (or lack thereof) of coexistence (Aros-Mualin et al., 2021; Guillemot et al., 2011; Halpern & Floeter, 2008; Mason et al., 2008; Stegen & Swenson, 2009). However, to our knowledge, there are no such assessments across co-occurring marine groups

such as reef fish, corals and algae. While a positive species richnessfunctional richness relationship is an expected outcome given their mutual dependence (Villéger et al., 2008), it is worth observing how assemblages of taxa with distinct evolutionary history, but occasionally with similar species richness values, might exhibit different functional richness. Indeed, the rate of change in functional richness with respect to species richness was faster for corals than algae and fish, with four possible explanations for this pattern: (i) A shallow regression slope might arise from low taxonomic resolution and limited trait differences within a taxon or group (Stegen & Swenson, 2009), as could be the case of algae. However, algal functional richness had an intermediate regression coefficient when compared to coral and fish functional richness (the taxa with higher taxonomic resolution), suggesting that other factors might be at play, namely (ii) biotic interactions, (iii) ecological and phylogenetic diversity within groups, and (iv) strong environmental gradients producing peaks in species richness.

Biotic interactions (ii) might be more intense among benthic organisms than fish so that corals and algae must compete for reef space leading to niche differentiation (Grillo et al., 2018; Lonzetti et al., 2022). Fish, in their turn, coexist in small reef areas where there are many functionally similar species (Barneche et al., 2019; Halpern & Floeter, 2008; Mouillot et al., 2014). There is a higher



FIGURE 5 Correlation between pairs of taxa (fish, corals and algae) and functional metrics (functional richness, FRic, and disparity, Rao's Q). Correlations between metrics within taxa are presented in the top, and correlations across taxa are presented in the bottom. Correlation values (*X*-axis) represent the following estimates: 'Observed': Pearson's correlation between raw functional metric values; 'Predicted': median and 95% Credible Intervals of Pearson's correlation between functional metrics predicted by the Bayesian multivariate linear model with sea surface temperature, region and species richness as variables in the model; 'Residual': median and 95% Credible Intervals of residual correlation after considering the effect of these variables. The vertical solid line represents the point of no correlation between metrics (Pearson's correlation $\rho = 0$), and the horizontal dashed lines represent how distant each correlation is from zero. The figure was produced in the R programming environment and edited in Inkscape v.1.0.

ecological and phylogenetic diversity within corals and algae than within fish (iii). For instance, corals include massive, plate and branching growth forms, from Hydrocorallia and Hexacorallia subclasses, and algae include green algae with soft tissues and rock-hard calcareous red algae, all of them from ecologically and phylogenetic disparate groups (Aued et al., 2018) whose coexistence generates high functional diversity. Finally, (iv) there is a considerable improvement of conditions for coral development when moving northwards (Aued et al., 2018; Leão et al., 2016) and from north to south for algae (Kerswell, 2006), thus generating peaks in species richness. Most Brazilian reefs are marginal for coral development, being predominantly covered by algae (Aued et al., 2018). Coral species richness and functional richness found in the Brazilian reefs are substantially lower than those of Caribbean and Indo-Pacific tropical reefs (McWilliam et al., 2018). As waters get clearer, warmer and comparatively oligotrophic towards the north, coral species richness increases and, along with it, functional richness. Algal assemblages show the opposite pattern (Aued et al., 2018). Collectively, these factors produce a sharp latitudinal gradient of coral and algal species richness and functional diversity along the Brazilian marine province.

The correlation between functional richness and disparity was stronger for fish and benthic groups (coral and algae) than for corals and algae. Such cross-taxon correlation might emerge from the functional dependence among fish and benthic organisms. Fish frequently rely on habitats provided by corals and algae for foraging, sheltering and reproducing (Darling et al., 2017; Eggertsen et al., 2017; Fulton et al., 2019; Luza et al., 2022). Here, more functionally diverse coral and algal assemblages coincide with fish assemblages with high functional diversity. Interestingly, the strongest positive cross-taxon correlation identified-between fish functional disparity and algal functional richness-shows that more even distribution of fish abundances across traits occur in more functionally diverse algal assemblages, and vice-versa. Nonetheless, this mutual relationship was not evidenced between fish and corals-as shown by the positive correlation between fish FRic and coral Rao's Q, and the negative correlation between fish Rao's Q and coral FRic. These divergent correlations indicate that more functionally rich fish assemblages are found in reefs with more even coral assemblages, while the converse is not true. It is unclear whether these correlations imply bottom-up or top-down causal effects, that of benthic organisms on fish and, in turn, that of fish on the benthos, given the varied degree of association between these groups in Brazil (Luza et al., 2022). Such patterns are more likely to be driven by a similar response of the assemblages to sea surface temperature, or other variables such as width of the continental shelf (Cord et al., 2022). Corals and algae diverged in their local functional diversity, possibly as a by-product of competition for space (Francini-Filho et al., 2013; Grillo et al., 2018; Lonzetti et al., 2022).

Our results have important implications for conservation planning of Brazilian reefs. Spatial correlation of functional richness and functional disparity between fish, corals and algae were largely determined by SST, region and species richness. In fact, we found weaker correlations after dismantling the spatial structure determined by these factors and analysing the residual correlation. Temperature represents environmental energy, and directly influences the metabolic processes, activity and growth of marine organisms, being a leading determinant of the distribution of species and traits in ecological communities (Barneche et al., 2019; Brown et al., 2004; Tittensor et al., 2010). Temperature may underlie the assembly of congruent freshwater taxa richness at global scale (Tisseuil et al., 2013), congruent marine taxa richness at regional and local scales (Cord et al., 2022; Thomson et al., 2014), and congruent taxonomic and functional beta diversity along elevational gradients (Mori et al., 2015). Recent projections on the response of Brazilian reef fish and corals to rising SST show that these groups will expand southwards and modify biotic interactions (Bleuel et al., 2021; Inagaki et al., 2020; Lonzetti et al., 2022). For instance, the intensity of fish trophic interactions on the benthos (bites per time and area) was projected to increase in extratropical areas but decrease in tropical areas of the Western Atlantic (Inagaki et al., 2020), which could result in greater competition for space among benthic organisms under warmer climates (Lonzetti et al., 2022). Less herbivory and invertivory in tropical reefs could favour future algal establishment (Inagaki et al., 2020) causing 'phase shifts' from coral to algaedominated states (Hughes et al., 2007). Under experimental ocean warming conditions (3°C increase relative to current temperatures), scleractinian corals were more easily outcompeted by zoanthids (Lonzetti et al., 2022). The factor 'region' rescues the evolutionary history of each particular region, marked by different speciation, extinction and colonization processes (Cord et al., 2022; Pinheiro et al., 2018). Also, it captures the history of organisms' establishment in areas with varied isolation, turbidity and salinity (missing in the best selected model but present in the whole set of tested models) (Bender et al., 2013; Cord et al., 2022; Leão et al., 2016; Pinheiro et al., 2018). Along the Brazilian province, coastal and oceanic island reefs are home to endemic species and functionally distinct assemblages (Bender et al., 2013; Floeter et al., 2008; Pinheiro et al., 2018). While the depauperate oceanic islands harbour a large proportion of endemics, coastal assemblages are more speciose and functionally diverse (Bender et al., 2013; Pinheiro et al., 2018). Assemblage structure can be influenced by both climate change (Bleuel et al., 2021), land sedimentation (Loiola et al., 2019) and fishing impacts that selectively remove individuals and functional groups (Graham et al., 2017), posing a threat to multiple species and altering local abundance patterns and therefore functional diversity (Magris et al., 2021; Vila-Nova et al., 2014).

Reef fish, corals and algae were spatially associated in the Brazilian province, with overall low to intermediate correlation values. These low correlation values possibly rescue a broad regionalscale response to environmental variables, as temperature and region (Burrascano et al., 2018; Thomson et al., 2014; Yeager et al., 2017). Journal of Biogeography

Functional diversity was mostly structured by species richness, sea surface temperature and the regions within this biogeographical province, which calls for attention of the escalating disturbances to global reef ecosystems (Hughes et al., 2007; Magris et al., 2021). Cumulative anthropogenic impacts can undermine and destabilize such spatial correlations between marine organisms (Fogliarini et al., 2022; Inagaki et al., 2020; Magris et al., 2021), and emergent reef ecosystem processes and services. Also, altered organisms' distribution patterns jeopardize our ability to plan, monitor and conserve reef biodiversity. As functional diversity often correlates with ecosystem functioning (Díaz & Cabido, 2001), our results subsidize future progress in mapping emergent ecosystem properties from multiple coexisting reef taxa.

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CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Fish and benthic data were sampled by the SISBIOTA-Mar and PELD-ILOC initiatives and compiled by the Reef Synthesis Working Group 12

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(ReefSYN). Scripts and data useful for reproducing our findings can be found on GitHub (https://github.com/Sinbiose-Reefs/reefdiv_drive rs.git) and Zenodo (https://doi.org/10.5281/zenodo.7665191). Data of Quimbayo et al. (2021) are available at: https://doi.org/10.1002/ ecy.3298. Data of Aued et al. (2018) are available at: https://datad ryad.org/stash/dataset/doi:10.5061/dryad.f5s90.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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