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Influence of reef cover classes on functional diversity of reef fish in the Banyak Islands Marine Nature Park, Aceh Province, Indonesia

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Abstract. *Nasution MA, Najmi N, Hermi R, Lubis F, Lisdayanti E, Saputra F. 2025. Influence of reef cover classes on functional diversity of reef fish in the Banyak Islands Marine Nature Park, Aceh Province, Indonesia. Biodiversitas 26: 4346-4362.* Coral reefs are critical marine ecosystems that are increasingly threatened by human and environmental pressures, prompting research into how habitats shape biodiversity. This study explored how seven reef cover classes: reef slopes, sheltered reef slopes, reef crests, reef flats, plateaus, backreef slopes, and lagoons, influence reef fish functional diversity in the Banyak Islands Marine Nature Park, Aceh Province, Indonesia. Using underwater visual censuses across 20 sites with 60 belt transects (250 m² each), we surveyed 131 reef fish species at 3-12 m depths. We measured four functional diversities of reef fish: Functional Richness (FRic), Functional Divergence (FDiv), Functional Evenness (FEve), and Rao's Quadratic entropy (RaoQ). Bayesian multivariate models revealed that reef slopes, sheltered reef slopes, and reef crests significantly influenced functional diversity, explaining 2-55% of variance, average 28.5%. Reef slopes showed the strongest effects, positively influencing FEve (posterior probability: 0.95) and RaoQ (posterior probability: 0.99), indicating balanced trait distribution and enhanced functional diversity in structurally complex habitats. However, reef slopes negatively affected FDiv (posterior probability: 0.89). Reef slopes notably boost RaoQ and FEve, reflecting balanced trait distribution and diverse ecological roles. The effects on functional richness and divergence were less pronounced, indicating limited trait range expansion. This study reveals that certain reef formations play a crucial role in maintaining healthy aquatic ecosystems, which is vital for conservation efforts in less-than-ideal reef environments.

Keywords: Banyak Islands, functional diversity, reef cover class, reef fish, reef slopes

INTRODUCTION

Coral reefs are vital ecosystems renowned for their extraordinary biodiversity and ecological significance. They host an estimated one-quarter of all marine species while occupying less than zero-point one percent of the ocean floor (Gupta et al. 2022; Isdianto et al. 2024; Handoko et al. 2025). These habitats support millions of people globally through fisheries, tourism, and coastal protection (Lachs and Oñate-Casado 2019; Williams et al. 2022; Storlazzi et al. 2025). However, coral reefs face escalating threats from overfishing, pollution, coastal development, and climate-driven impacts precipitating extensive coral bleaching, habitat degradation, and marked biodiversity declines (Achmad et al. 2022; Painter et al. 2023; Sobha et al. 2023). With coral reef ecosystems increasingly at risk, there is an urgent need to understand the factors that sustain their ecological integrity. Research on reef ecosystems offers critical insights into conservation, particularly in regions where marine biodiversity remains understudied and is highly threatened (Good and Bahr 2021; Obura et al. 2021).

Reef fish play a crucial role in coral reef ecosystem functionality through herbivory, predation, and nutrient cycling control algal growth, facilitating coral recovery, and maintain energy flow (Herbig et al. 2022; Rolim et al. 2022; Galbraith et al. 2023; Butler et al. 2024). While species richness has traditionally dominated biodiversity research, functional diversity provides superior insights into ecosystem dynamics by encompassing the variety of ecological functions and characteristics, including feeding behavior, mobility patterns, and trophic position, provides more comprehensive insights into the mechanisms by which fish communities contribute to ecosystem stability (Danet et al. 2021; Jaroensutasinee et al. 2021; Gomes et al. 2023). For instance, a reef with varied functional traits may be more resilient to disturbances because different species can fulfill overlapping roles. Exploring how habitat features shape this diversity is key to predicting how reef ecosystems respond to environmental pressures and to designing effective management strategies (McKinley et al. 2022). Recent advances in reef mapping have enabled precise categorization of reef cover classes—including reef slopes, crests, flats, and lagoons—each supporting distinct environmental conditions and fish assemblages (Kennedy et al. 2021). These classifications predict fish community structure and functional diversity patterns, making them essential for marine spatial planning and conservation (Brandl et al. 2019; Luza et al. 2023).

The Banyak Islands Marine Nature Park, situated along Sumatra's coastline in Indonesia, is a biodiverse yet threatened marine protected area. Covering more than 2,500 km² of Indian Ocean waters, this protected region encompasses coral formations, seagrass beds, and mangrove forests, forming a complex network of ecosystems that sustain diverse marine communities (Erniati et al. 2023). It serves as a sanctuary for numerous reef fish species, many of which are adapted to the park's unique marginal reef conditions characterized by fluctuating turbidity and nutrient levels (Putra et al. 2021). These challenges underscore the importance of studying how the park's diverse reef structures influence fish communities, thereby providing a foundation for targeted conservation efforts in this ecologically significant region.

This study focused on the Banyak Islands Marine Nature Park to investigate how varying reef cover classifications influence functional diversity within reef fish assemblages. Our objectives were to examine the connections between reef structures, specifically the reef slope, sheltered reef slope, and reef crest, and essential functional diversity measures, encompassing Functional Evenness (FEve), Functional Richness (FRic), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ) (Pérez-Matus et al. 2022). Using underwater visual censuses across 20 sites and Bayesian multivariate models, we sought to understand how these habitat types shape the ecological roles and trait distributions of fish assemblages (Doll and Jacquemin 2019). By addressing these aims, this study intends to enhance the knowledge of habitat-fish interactions in marginal reef systems and offer practical insights for conserving the park's marine biodiversity amidst ongoing environmental challenges.

MATERIALS AND METHODS

Study area

The Banyak Islands Marine Nature Park, located in the Indian Ocean within the Banyak Islands archipelago in Indonesia, represents a critical marine conservation zone distinguished by its diversity of reef fish species. The park is situated between 2°00'-2°22'N and 97°06'-97°28'E (Erniati et al. 2023) (Figure 1), encompassing of approximately 2,555.85 km², of which 2,281.83 km² (89.3% of the total area) is marine waters and 274.03 km² (10.7% of the total area) comprises terrestrial land (OSM 2024). This area encompasses ecosystems including coral reef formations (Rahmad 2023), seagrass beds (Erniati et al. 2023; Nasution et al. 2024), and mangroves (Nasution et al. 2025), maintaining regional ecological equilibrium (Simanjuntak et al. 2019; Hidayat et al. 2023). These habitats supporting various fish species assemblages, with many taxa adapted to marginal reef environments characterized by fluctuating turbidity and nutrient levels (Putra et al. 2021; Aji et al. 2024). Fish communities are subject to environmental variables, with species composition varying across distinct reef zones (Dhahiyat et al. 2017). Coral reefs are essential for sustaining fish populations, enhancing regional biodiversity (Disa et al. 2024) and provides habitats for both juvenile and adult fish (Fahlevy et al. 2019; Gaines et al. 2020; Pranata et al. 2022).

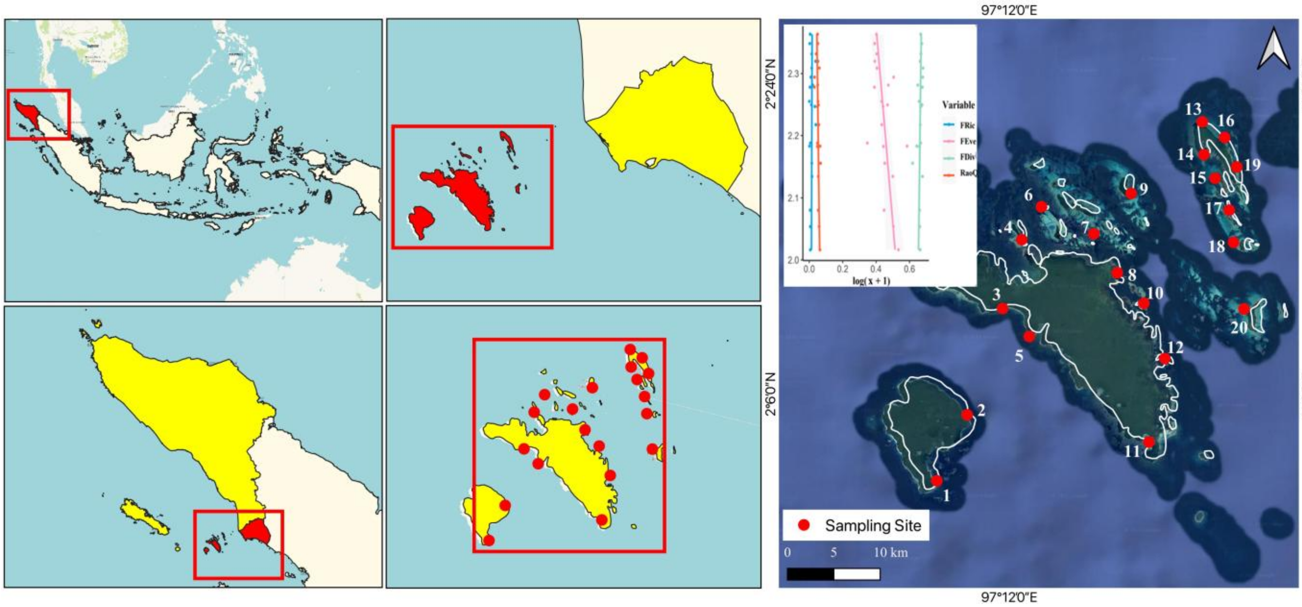

Figure 1. Detailed geographic mapping of 20 sampling sites for reef fish diversity across the Banyak Islands Marine Nature Park, Indonesia, featuring a color-coded map with latitude-aligned y-axes to match spatial data plots, where blue lines represent Functional Richness (FRic), pink lines indicate Functional Evenness (FEve), green lines show Functional Divergence (FDiv), and red lines depict Rao's Quadratic entropy (RaoQ) variations across the region

Reef fish survey

We assembled reef fish datasets collected from small islands of the Banyak Islands. These datasets included small-scale spatial snapshots of reef fish communities on both coastal and oceanic island reefs. Twenty sites were selected to represent a gradient of reef geomorphological classes. The selected sites are (sequentially site 1 to 20): Teluk Brasi, Bangkaru Barat, Ujung Sarang, Pulau Lamun, Tanjung Limau, Pulau Tailana, Pulau Orongan, Pulau Tambego, Pulau Sikandang, Pulau Pabandah, Ujung Lolok, Pulau Samut, Pulau Ujung Batu, Ujung Batu Selatan, Pulau Balai Barat, Ujung Batu Timur, Pulau Panjang, Pulau Rangit Besar, Pulau Balai Timur, and Pulau Palambak (Figure 1). At these sites, underwater visual censuses (250 m^2 belt transects; total n: 60, averaging three transects per site) were conducted at two depth ranges (3-6 m and 7-12 m). During each census, reef fish species were identified using the Indonesian Reef Fish Identification Guide by Kuiter (1992) and Allen (2020).

Reef cover class

We used coral reef geomorphic zone classification using remote sensing data by Kennedy et al. (2021) as a predictor and extracted data on the area (km^2) of nine reef cover classes from allencoralatlas.org within a 500 m radius of the center of the reef fish observation point coordinates. To extract these data, we created 20 circular Areas of Interest (AOIs) using GeoJSON files for each observation location, with a radius of 500 m from the observation midpoint, using R (R Core Team 2022) and the sf package. We uploaded these 20 AOIs to ‘My Area’ and downloaded the area’s assets. These zones include the reef slope, a steeply sloping submerged area extending seaward, which supports diverse fish communities that vary with depth. The sheltered reef slope, protected from strong winds and currents, supports calmer-environment fish species (Sherman et al. 2010); reef crest is the shallowest zone that absorbs the most wave energy and hosts a high biomass of herbivorous fishes (Oakley-Cogan et al. 2020); The reef flat, which is divided into Outer Reef Flat, Inner Reef Flat, and Terrestrial Reef Flat, each characterized by varying levels of wave energy exposure and sediment composition, serves as habitat for various fish species (Oakley-Cogan et al. 2020). The Plateau represents a deeper zone with hard substrates, supporting both reef-associated and pelagic species (Blanchon et al. 2022), whereas the back reef slope is a sediment-rich, sheltered zone behind the reef flat, crucial for juvenile fish development (Toller et al. 2010). The Lagoon is divided into shallow and deep lagoons, with varying depths and sediment compositions, providing habitats for seagrass-dwelling and juvenile fish (Vroom et al. 2005). All predictors were standardized to improve the accuracy of the variable calculations and facilitate the comparability of the model coefficients.

Fish functional traits selection

Fish functional traits were compiled from FishLife (Thorson et al. 2017), Reef Life Survey (Atlas of Living Australia 2017), Borealis (Gleiber et al. 2022), and FishBase (Froese and Pauly 2025). Four functional diversity indices: Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao’s Quadratic entropy (RaoQ) (Botta-Dukát 2005; Villéger et al. 2008; Laliberté and Legendre 2010; Mouchet et al. 2010; Mouillot et al. 2013; Carturan et al. 2022) were calculated. Six ecologically relevant traits were selected based on their importance in reef fish ecology and data availability across species (Table 1).

Table 1. Functional traits used to calculate functional diversity indices

Trait	Categories	Ecological significance	Data source
Diet	Corallivore, Grazer, Grazer-detritivore, Invertivore, Mixed-diet-forager, Omnivore, Piscivore, Planktivore, Scraper (categorical)	Controls energy flow, algal dynamics, coral health maintenance and growth regulation	FishLife (Thorson et al. 2017), Borealis (Gleiber et al. 2022), and FishBase (Froese and Pauly 2025)
Mobility	Sedentary, Within reef, Between reefs (categorical)	Affects nutrient cycling, habitat connectivity, and spatial resource utilization patterns	FishLife (Thorson et al. 2017), Borealis (Gleiber et al. 2022), and FishBase (Froese and Pauly 2025)
Schooling	Solitary, Pairs, Groups (3-10), Small groups (10-20), Medium groups (20-50), Large groups (>50) (categorical)	Influences predation risk reduction, reproductive success, and social structure dynamics	FishBase (Froese and Pauly 2025) and Reef Life Survey (Atlas of Living Australia 2017)
Water Colum Position	Benthic, Benthopelagic, Pelagic (categorical)	Determines vertical habitat use, feeding strategies, and energy transfer across ecosystem layers	FishLife (Thorson et al. 2017), Borealis (Gleiber et al. 2022), and FishBase (Froese and Pauly 2025)
Trophic Level	2.0-4.5 (continuous)	Indicates position in food web, ecosystem role, and potential for cascading effects	FishLife (Thorson et al. 2017) and FishBase (Froese and Pauly 2025)
Biomass Estimation	Length-weight relationships (continuous)	Crucial for assessing ecosystem health, energy transfer, and fisheries management applications	FishBase (Froese and Pauly 2025)

The selected traits encompass key ecological dimensions that determine species' functional roles in reef ecosystems. Dietary traits are classified into nine categories, ranging from corallivore to scraper, highlighting the diversity in feeding habits and their impact on ecosystem functions, including coral health maintenance and algal growth regulation, herbivorous species in controlling algae (Green and Bellwood 2009; Ruttenberg et al. 2019). Mobility traits reflect different spatial usage patterns and habitat preferences that influence nutrient cycling and habitat connectivity (Olds et al. 2012; Nash and Graham 2016). School size affects social behavior, predation risk, and reproductive strategies. Schooling influences predation risk reduction, such as dilution effect and increased vigilance in schooling fish, and affects reproductive success and social structures (Hoare et al. 2004; Croft et al. 2006; Ward et al. 2011).

Water column position highlights vertical habitat preferences that dictate feeding behaviors and organism interactions, affecting nutrient cycling and energy transfer across ecosystem layers (Brooks et al. 2007; Heenan et al. 2016). Trophic levels reveal species roles in food web dynamics and ecosystem resilience, where changes in apex predator populations can cause significant shifts throughout ecosystems (Ritchie et al. 2012; Britten et al. 2014). Biomass estimation, crucial for assessing ecosystem health and fisheries management, utilizes length-weight relationships with species-specific allometric constants from FishBase for accurate population energy and nutrient assessments (Froese 2006; Cheung et al. 2013; Froese and Pauly 2025).

Functional space

Following Maire et al. (2015), we constructed and selected appropriate functional space through the 'mFD' package (Magneville et al. 2022) combined with the quality.fspaces function in R. This approach involves generating functional dendrograms Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering and constructing multidimensional functional spaces spanning one to ten dimensions through Principal Coordinate Analysis (PCoA) (Figure 2). Dendrogram construction and PCoA both used a Gower distance matrix (Gower 1971), which effectively handles mixed non-continuous trait data types (Magneville et al. 2022).

We assessed functional space quality using two quality metrics: Mean Absolute Deviation (MAD) and Root Mean Square Deviation (RMSD) (Figure 2). MAD represents the average absolute deviation of functional traits from their mean value, providing a measure of trait distribution spread, while RMSD is the root mean squared deviations, highlighting outliers or extreme values (Magneville et al. 2022). Reduced MAD and RMSD values minimize bias, linking trait-based distances with those within the reduced functional space. This approach ensured that the functional space accurately represented functional relationships among study species. By targeting minimal values, functional space captures the essential dimensions for accurate functional diversity representation without inflating distances among taxa with comparable traits (Maire et al. 2015; Magneville et al. 2022).

Among functional spaces evaluated, the 5-dimensional (5D) space exhibited the lowest deviation across all indices (MAD: 0.046), indicating the best representation of trait-based distances with minimal deviation between trait-based and space-based distances. Lower quality metrics correspond to closer matches between trait-based and space-based distances, indicating higher quality functional space (Maire et al. 2015).

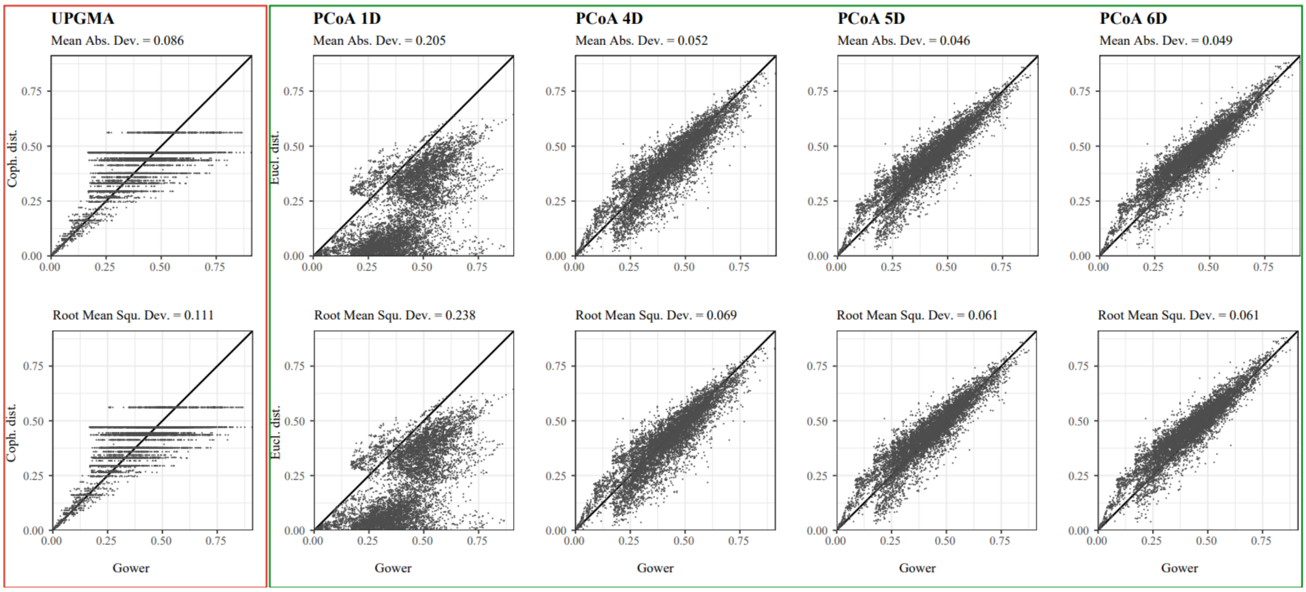

Figure 2. Functional space quality assessment: Red box Unweighted Pair Group Method with Arithmetic Mean (UPGMA) and green box Principal Coordinates Analysis (PCoA) with top row Mean Absolute Deviation (MAD) and bottom row Root Mean Square Deviation (RMSD)

Functional diversity analyses indices

We used four functional diversity indices—Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ)—to assess the response of fish assemblages to variations in reef cover class area. These indices were calculated using the 'mFD' and 'FD' packages (Laliberté et al. 2014; Magneville et al. 2022) in R. This approach was based on the framework established by Kennedy et al. (2020), who considered how different species traits mediate the response of assemblages to habitat characteristics.

FRic quantifies the fraction of functional space occupied by taxa within communities, representing the volume within the convex hull boundaries that encompass all present taxa. Elevated FRic values signify more diverse functional trait ranges within communities, suggesting more adaptable assemblages capable of fulfilling various ecological roles (Maire et al. 2015). For FRic computation, taxa numbers must exceed functional axes numbers plus one, ensuring that the convex hull volume remains well-defined and ecologically meaningful (Mouillot et al. 2013). FEve measures biomass distribution across the functional space. This metric employs the Minimum Spanning Tree (MST) method to link all community taxa, emphasizing the branch length evenness within MST structures. Elevated FEve values signify that taxa are uniformly distributed across functional spaces, indicating efficient resource utilization and reduced competition among taxa occupying similar ecological niches (Schlüter et al. 2017). Conversely, a low FEve suggests that certain functional traits dominate, potentially leading to resource overlap and competition (Pakeman and Fielding 2020). Functional Divergence (FDiv) captures how species deviate from the center of the functional trait space. FDiv measures the divergence of species traits relative to mean trait values, focusing on extreme trait values within the community. Higher FDiv suggests greater differentiation among species in available resources use, with species occupying more specialized niches. This metric is valuable for assessing how environmental pressures, such as changes in habitat structure, influence assemblages by selecting species with divergent functional traits (Zhao et al. 2022; Costa et al. 2023). RaoQ accounts for both functional differences among species and their relative abundances in assemblages. It provides functional diversity sensitive to species turnover and shifts in community composition across sites (Rosado et al. 2018). RaoQ was calculated by weighting each species' functional traits by their relative abundance, enhancing understanding of how biodiversity contributes to ecosystem functioning (Laliberté and Legendre 2010).

To determine axes to retain from the Principal Coordinate Analysis (PCoA) for calculating convex hull volume, we applied the 'max' criterion. This method retains the greatest number of axes, ensuring that species exceed traits considered. This method enhances robustness of functional diversity measures by capturing the maximum variation in species traits, while preventing overfitting (Blonder et al. 2018). By maintaining balance between trait complexity and species representation, the 'max' criterion ensures that functional diversity indices accurately reflect ecological dynamics of the reef systems studied (Magneville et al. 2022).

Statistical analysis

To explore reef cover class area effects on reef fish functional diversity, we used comprehensive Bayesian multivariate statistical analysis. This approach to simultaneously model multiple functional diversity metrics, Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ) while accounting for inherent correlations between metrics and incorporating uncertainty in parameter estimates. Bayesian modeling is advantageous in ecological studies where data can be sparse and prior knowledge can be incorporated to improve parameter estimation and model inference.

We applied Bayesian multivariate models using the brms package to analyze functional diversity metrics FRic, FEve, FDiv, and RaoQ as multivariate response variables. Analysis was conducted using 'Brms' package in R (Bürkner 2018). Bayesian inference employs Bayes' theorem to update prior knowledge using empirical data, enabling estimation of posterior probabilities of parameters. Priors, typically depicted by statistical distributions, are updated by incorporating observed data through Markov Chain Monte Carlo (MCMC) (Sahoo and Patra 2020). This approach provides estimation of parameter variation across posterior distributions, captured by credible intervals as uncertainty (Pirikahu et al. 2021). These credible intervals, drawn from quantiles of posterior distributions, provide ranges within which we can confidently expect true parameter values to fall, thereby ensuring a reliable interpretation of the results (Gunawan et al. 2020).

Bayesian multivariate linear modeling was employed to examine relationships between reef cover class area and different metrics, while simultaneously calculating correlations among metrics while controlling for reef cover effects. This approach identifies variables that most effectively explain variations in functional diversity measures and determines whether metric correlations resulted from included model parameters. Because residual correlation estimation requires multivariate normal distribution (Noh et al. 2020), we implemented log(x + 1) transformations for diversity measures containing zero values (FRic, FEve, FDiv, and RaoQ) to avoid computational issues.

Within this multivariate framework, observed values (on a natural logarithmic scale) of FRic, FEve, FDiv, and RaoQ for reef fish taxa and site (i) were adhere to a Multivariate Normal Distribution (MND). This distribution is characterized by the mean (μ), residual correlation matrix (R), and covariance matrix (S). These parameters are specific to each metric and taxon as follows:

$$\begin{bmatrix} y^{i}_{FRic} \\ y^{i}_{FEve} \\ y^{i}_{FDiv} \\ y^{i}_{Rao'sQ} \end{bmatrix} \sim \text{MND}\left(\begin{bmatrix} \mu^{i}_{FRic} \\ \mu^{i}_{FEve} \\ \mu^{i}_{FDiv} \\ \mu^{i}_{Rao'sQ} \end{bmatrix}, S\right)$$

$$S = \begin{bmatrix} \sigma_{FRic} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \sigma_{Rao's\,Q} \end{bmatrix} R \begin{bmatrix} \sigma_{FRic} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \sigma_{Rao's\,Q} \end{bmatrix}$$

$$\mu^i_{FRic} = \beta_{0FRic} + \beta_{FRic}X + \epsilon^i_{FRic}$$

$$\mu^i_{FEve} = \beta_{0FEve} + \beta_{FEve}X + \epsilon^i_{FEve}$$

$$\mu^i_{FDiv} = \beta_{0FDiv} + \beta_{FDiv}X + \epsilon^i_{FDiv}$$

$$\mu^i_{Rao's\,Q} = \beta_{0Rao's\,Q} + \beta_{FRao's\,Q}X + \epsilon^i_{Rao's\,Q}$$

$$\beta = \begin{bmatrix} \beta_{FRic} \\ \beta_{FEve} \\ \beta_{FDiv} \\ \beta_{FRao's\,Q} \end{bmatrix}$$

$$X = \begin{bmatrix} x_{1,i=1} & \cdots & x_{n,i=1} \\ \vdots & \ddots & \vdots \\ x_{1,i=I} & \cdots & x_{n,i=I} \end{bmatrix}$$

In this model, β_0 denotes the intercept, and β is a vector of regression coefficients estimated for n reef cover class areas within matrix X, with values ranging from i: 1 to I: 20 sites. Priors for both β_0 and β were specified to follow a normal distribution (β_0,//β ~ N..(μ: 0, σ: 4)). The parameter σ, which characterizing the dispersion of the normal distributions, along with the error term ε, was modeled using Student's t-distribution (σ, ε ~ t(3, 0, 2.5)). This type of prior distribution allows flexible handling of multivariate datasets (Noh et al. 2020; Guhaniyogi et al. 2022; Jiao et al. 2023). Residual correlation (ρres) was estimated as a part of the covariance matrix S in the multivariate model, with its sampling error measured from the posterior distribution draws generated through the MCMC. The modified approach we adopted was similar to Luza et al. (2023), who derived observed correlations (ρobs) from the input data, whereas the predicted correlations were calculated based on the best-fitting model structure. This process accounted for the distributional sampling error by utilizing the 'posterior_predict' function in the brms package. We used three Markov Chain Monte Carlo (MCMC) simulations to run our Bayesian models, each employing Hamiltonian Monte Carlo algorithm. Each chain performed 20,000 iterations, with the first 18,000 iterations used for warm-up. We tested our hypotheses and made inferences using 6,000 posterior draws for each model parameter, retaining 2,000 draws after warm-up for each chain (Dorndorf et al. 2021; Ni et al. 2022; Dubuc et al. 2023).

To test our hypothesis regarding whether reef fish functional diversity indices (FRic, FEve, FDiv, and RaoQ) exhibited comparable directional patterns and magnitudes of response to reef cover class predictors, we examined how the regression coefficients (β) varied among the different functional diversity measures. We employed interval plotting techniques using the 'bayesplot' R package (Gabry et al. 2019) to display β medians alongside their corresponding 95% and 80% Credible Intervals (CIs). For each regression parameter β, the posterior exceedance probability (p) quantifies the fraction of posterior samples exceeding zero (or falling below zero), indicating whether meaningful effects exist on response variables.

We conducted model selection utilizing both Widely Applicable Information Criterion (WAIC) and Leave-One-Out Cross-validation Information Criterion (LOOIC), with chain convergence optimized by configuring 'adapt_delta' at 0.99 and 'max_treedepth' at 15. To address computational issues, we implemented moment matching ('moment_match: T') alongside model refitting procedures ('reloo: T') (Liang and Luo 2020; Kelter 2021). Leave-one-out cross-validation systematically excludes each problematic data point, refitting the analysis and computing the mean LOOIC values and associated errors through successive iterations (Lartillot 2022). Lower LOOIC and WAIC scores signify superior model performance (Vehtari et al. 2021). Additionally, we evaluated models using expected Log Pointwise Predictive Density (ELPD) metric and corresponding standard errors, examining how the LOOIC and WAIC distributions intersect among competing models. In cases where models demonstrated comparable LOOIC, WAIC, and ELPD statistics with overlapping error ranges, we applied parsimony principles to choose the straight-forwards model. We computed Bayesian R-squared metrics to quantify the total variance captured by chosen model predictors (Vranckx et al. 2021; Bazarova and Raseta 2023).

RESULTS AND DISCUSSION

Correlations between functional traits

The relationships between individual functional traits and the principal coordinate axes revealed significant associations that help explain the underlying structure of the functional space. Kruskal-Wallis tests for categorical traits and linear models for continuous traits demonstrated varying degrees of association with PC3 (57.49% of variance) and PC5 (76.66% of variance).

The relationships between individual functional traits and the principal coordinate axes revealed significant associations with the functional space structure. Diet showed the strongest association with PC5 (η^2: 0.707, p<0.001) and a moderate association with PC3 (η^2: 0.144, p=0.001). Schooling behavior exhibited substantial associations with both PC3 (η^2: 0.326, p<0.001) and PC5 (η^2: 0.317, p<0.001). Mobility patterns showed a moderate association with PC3 (η^2: 0.129, p<0.001), while water column position demonstrated a weaker but significant association with PC3 (η^2: 0.100, p<0.001). Among continuous traits, trophic level showed a strong association with PC5 (r^2: 0.356, p<0.001), whereas mean biomass exhibited a weak association with PC5 (r^2: 0.030, p=0.050).

Functional space quality

Functional Space (FS) was constructed using six categorical traits (Table 1), with the optimal FS determined to have five dimensions (MAD: 0.046, RMSD: 0.061). The five-dimensional space had lower MAD and RMSD values than the four-, six-, and one-dimensional spaces (Figure 2), and exhibited nearly five times the accuracy of the one-dimensional space (MAD: 0.205, RMSD: 0.238). It also surpassed the most effective functional dendrogram created using UPGMA clustering (MAD: 0.086, RMSD: 0.111). While ten dimensions have been shown to effectively capture within-collection FD variations, the increased computational cost, a five-dimensional space was selected based on its lower computational cost and acceptable accuracy metrics.

Reef structure and habitat complexity across study sites

Reef class area (km^2) measurements were analyzed across the study sites, incorporating geographical location and ecological indices. The reef structures examined included reef slopes, sheltered reef slopes, reef crests, reef flats, plateaus, backreef slopes, and lagoons. The distribution of the reef structures varied across sites. The reef slopes had an average area of 0.044±0.043 (mean±standard deviation), with the most pronounced at Site 12 (0.1457) and absent at Sites 7, 8, 14, and 16. Sheltered reef slopes were rare, occurring at only seven sites with an average area of 0.013±0.025. Reef crests were present at seven sites, averaging 0.003±0.006, with the largest at Site 11 (0.0226). Reef flats were the most widespread, with an average area of 0.140±0.120, and the largest at Site 11 (0.4212). Plateaus were minimal, averaging 0.005±0.010, but peaked at Site 13 (0.047). Backreef slopes were generally sparse, with an average area of 0.005±0.012 and the highest value at Site 4 (0.0481). Lagoons were present across multiple sites, averaging 0.080±0.090, with site 14 containing the largest lagoon area (0.2877). The reef structure types and their area measurements varied across sites, potentially influencing the species composition and functional diversity.

Functional diversity across sites

Functional diversity metrics were analyzed for 131 reef fish species across 20 study sites (Figure 1), encompassing 58 genera and 26 families. Site 19 and Site 20 both support 35 species each. Site 19 has a total abundance of 1.032 individuals, with *Pomacentrus moluccensis* having the highest abundance at 229 individuals. Meanwhile, Site 20 also has 35 species and a total abundance of 909 individuals, with *Chromis viridis* being the most abundant species, with 396 individuals. On the other hand, Site 3 has the lowest number of species, with only 19 species and a total abundance of 449 individuals, where *Dascyllus carneus* has the highest abundance at 57 individuals. The genus Chaetodon is the most species-rich genus, comprising 16 species, while the family Pomacentridae holds the highest number of species, with 31 species. Across all sites, *C. viridis* stands out as the most abundant species, with a total of 3.036 individuals observed.

Four key indices were used to assess the functional diversity of reef fish assemblages: Functional Evenness (FEve), Functional Richness (FRic), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ) (Figure 3). FEve, which measures the evenness of functional trait distribution, averaged 0.5670±0.0913 (mean±standard deviation) and ranged from 0.4157 at Site 10 to 0.7952 at Site 3, where the functional trait distribution was most balanced. The FRic, which quantifies the range of functional traits, averaged 0.0156±0.0152 and varied from 0.00053 at Site 7 to 0.0567 at Site 20, indicating the greatest trait range at Site 20. FDiv, which captures the extent of niche differentiation, averaged 0.9416±0.0276 and ranged from 0.8555 at Site 5 to 0.9754 at Site 15, with Site 15 exhibiting the highest degree of functional divergence. RaoQ, a composite measure of functional diversity incorporating species abundance and trait dissimilarity, averaged 0.0535±0.0099 and was the highest at Site 5 (0.0699) and lowest at Site 17 (0.0314), suggesting that Site 5 contained the most functionally diverse fish assemblages. Overall, Site 5 demonstrated the highest functional diversity based on the RaoQ, with moderate variability in functional evenness, richness, and divergence.

Model evaluation and functional diversity predictions

To assess the determinants of functional diversity, seven models were evaluated using LOOIC and WAIC criteria. Among these, three models were considered equally plausible, based on their LOOIC and ELPD estimates. The most parsimonious model included reef slope, sheltered reef slope, and reef crest as key predictors of functional diversity (Table 2). The model parameters demonstrated convergence across MCMC runs, with all hat values ≤1. The effective sample sizes were adequate, with Bulk ESS ratios ranging from 0.25 to 0.31 and Tail ESS ratios from 0.22 to 0.24. The chosen model explained 2-55% of the variance in functional diversity metrics (FRic, FEve, FDiv, and RaoQ) across different reef cover classes, with an average explained variance of 28.5% (Table 3).

Effects of reef structures on functional diversity metrics

The effects of reef slope, sheltered reef slope, and reef crest on functional diversity metrics varied (Figures 4 and 5). Functional Richness (FRic) exhibited weak associations with all reef structures, with negligible effects observed for the reef slope and sheltered reef slope (median: 0.00, CI: -0.01 to 0.01), whereas the reef crest had a slightly higher probability of a positive effect (p: 0.74).

Rao's Quadratic entropy (RaoQ) was positively influenced by the reef slope (p: 0.99), whereas weaker effects were detected for the sheltered reef slope (p: 0.85) and reef crest (p: 0.68). Functional Divergence (FDiv) showed a negative trend in the reef slope (p: 0.11). By contrast, FDiv exhibited mixed effects on the sheltered reef slope (p: 0.47) and reef crest (p: 0.42), indicating uncertainty in the direction of influence. Functional Evenness (FEve) showed the strongest positive effect on the reef slope (p: 0.95), indicating a more balanced trait distribution in this habitat, whereas sheltered reef slope (p: 0.32) and reef crest (p: 0.47) had weaker and less consistent effects (Figure 5).

Figure 3. Comparative visualization of regional and local functional diversity of reef fish in the Banyak Islands Marine Nature Park, Indonesia, is illustrated by dark green polygons representing regional trait space and light-yellow polygons indicating local trait space derived from species subsets, with circle sizes in varying shades of cream reflecting the relative abundance of organisms at each site, and the two primary PCoA axes showing trait variation

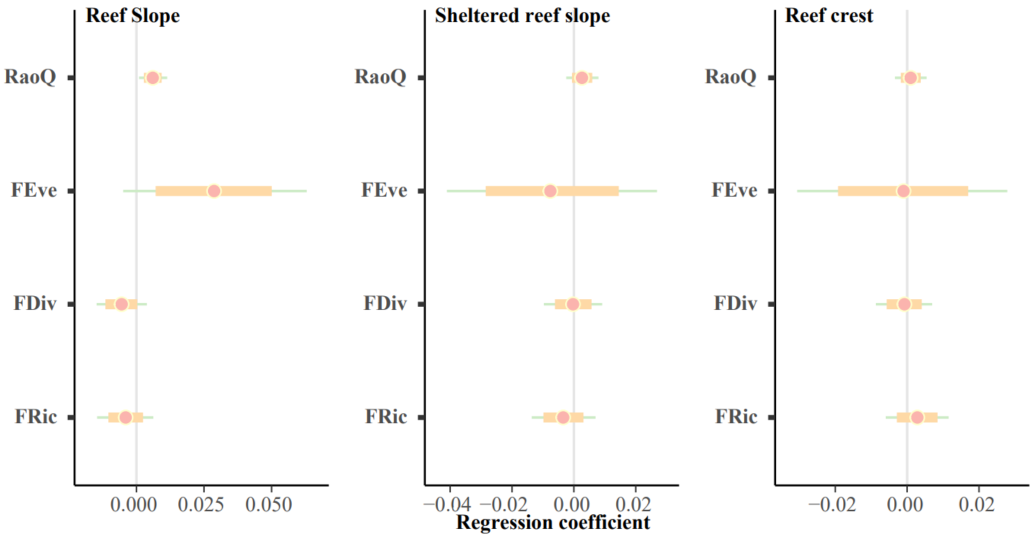

Figure 4. The quantitative impact of reef slope, sheltered reef slope, and reef crest on Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ) of reef fish populations in the banyak islands, presented with central pink dots for median regression coefficient from 6000 posterior draws. grey vertical line positioned at zero represents the theoretical point where a variable has no impact or influence, and thin green line for 95% credible intervals and a thick orange line for 80% credible intervals to indicate uncertainty levels

Table 2. Model selection of a Bayesian multivariate linear model assuming a multivariate normal distribution, based on the Leave-One-Out Cross-validation Information Criterion (LOOIC) and Widely Available Information Criterion (WAIC). display the total parameter count for each model, which indicates how complex and detailed the model, includes all the model's components, specifically the intercepts, regression coefficients, and correlations among all measured variables. Evaluate and compare the different models, used Expected Log Pointwise Predictive Density (ELPD) as assessment metric

Model	LOOIC		ELPD_LOOIC	WAIC		ELPD_WAIC
	Estimate	SE		Estimate	SE	
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope + Sheltered reef slope + Reef crest + Reef flat + Plateu + Backreef slope + Lagon	-395.41	18.88	226.53	-465.19	22.97	232.59
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope + Sheltered reef slope + Reef crest + Reef flat + Plateu + Backreef slope	-407.19	20.30	221.92	-456.78	21.11	228.38
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope + Sheltered reef slope + Reef crest + Reef flat + Plateu	-417.94	21.89	218.03	-450.90	19.58	225.45
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope + Sheltered reef slope + Reef crest + Reef flat	-427.04	23.99	213.52	-445.43	17.87	222.71
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope + Sheltered reef slope + Reef crest	-436.06	25.67	208.97	-438.43	16.21	219.21
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope + Sheltered reef slope	-443.84	26.62	203.59	-429.25	14.17	214.63
Mv (Fric, FEve, FDiv, RaoQ) ~ Reef slope	-453.06	28.73	197.70	-423.86	12.52	211.93

Note: Multivariate normal distribution (Mv), Standard Errors (SE), Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ)

Table 3. Bayesian R- squared statistics ('Estimate') showing the overall variance explained by reef slope, sheltered reef slope, and reef crest on each functional diversity metric. 'Standard deviation' and 'Credible intervals' (ranging from the lower 2.5% to upper 97.5%) quantify the uncertainty and variability in our Bayesian R-squared values, derived from 6000 posterior distribution

Functional diversity	Estimate	Standar deviation	Credible interval	
			2.5 %	97.5%
Fric	0.19	0.12	0.02	0.41
FEve	0.37	0.14	0.08	0.55
FDiv	0.23	0.13	0.03	0.44
RaoQ	0.35	0.13	0.07	0.54

Note: Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ)

Correlations among functional diversity metrics

Correlations among functional diversity metrics were assessed using observed (ρobs), predicted (ρpred), and residual (ρres) correlations (Figure 6). The observed correlations indicated that FEve and RaoQ exhibited the strongest positive correlations (ρobs: 0.39). The strongest negative correlation was observed between FDiv and RaoQ (ρobs: -0.55), suggesting a potential trade-off between niche differentiation and overall Rao's Quadratic entropy. Predicted correlations were generally lower than observed correlations (mean ρpred: -0.078, range: -0.42 to 0.31), although the direction of correlations aligned with observed trends, such as FEve-RaoQ (ρpred: 0.31) and FDiv-RaoQ (ρpred: -0.42). Residual correlations were uniformly low (mean ρres: -0.051, range: -0.33 to 0.16), and most of the variance in functional diversity metrics was driven by external environmental factors rather than by intrinsic biological relationships. Notably, FDiv-RaoQ retained a residual correlation of -0.33, whereas FEve-RaoQ maintained a positive residual correlation of 0.16.

Discussion

In this study, we investigated the intricate relationship between various reef cover classes and their impact on the functional diversity of reef fish communities within the Banyak Islands Marine Nature Park, a critical area designated for conservation. Our findings revealed that the structural characteristics of the reef, specifically the reef slope, sheltered reef slope, and reef crest, play a pivotal role in shaping key functional diversity metrics, including Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ). Among these, reef slope emerged as the most influential factor, demonstrating a significant ability to affect these diversity metrics (Figure 4). Notably, the reef slope was positively correlated with Functional Evenness (FEve), with a posterior probability of a positive effect (Prob_Pos) of 0.952, and RaoQ (Table 4), which had an even higher probability (Prob_Pos: 0.987). These results suggest that steeper reef environments tend to support fish communities that are not only more evenly distributed, but also exhibit greater functional diversity. This pattern reflects the fundamental relationship between habitat structural complexity and niche partitioning in coral reef ecosystems. Reef slopes provide significantly greater three-dimensional habitat complexity than reef flats and crests, creating diverse microhabitat conditions that support complementary functional traits and ecological roles (Veron et al. 2009; Darling et al. 2017). These findings on physical complexity and community structure underscore the importance of our study's focus on reef cover classes, aligning with the objectives to explore how these factors contribute to functional diversity, as highlighted by Anderson et al. (2023), thereby promoting a balanced (Nay et al. 2020) and resilient community structure (Caetano et al. 2021). Although the positive impacts on FEve and RaoQ highlighted the beneficial aspects of reef slopes, deeper examination revealed a more complex influence on Functional Richness (FRic) and Functional Divergence (FDiv).

The weak correlation with FRic (Prob_Positif: 0.211) suggests that, while the reef slope influences the distribution of functional traits within the community, it does not necessarily lead to an increase in the number of functional roles represented. Furthermore, the observed downward trend in FDiv was marked by a posterior probability of a negative effect (Prob_Negative: 0.890) as the steepness of the reef slope increased, indicating that the relationship between habitat complexity and functional diversity was far from straightforward (Cunha et al. 2019). Although our findings partially support the hypothesis that reef cover classes significantly influence functional diversity, they also illuminate nuanced trait-based responses within marginal reef ecosystems, as evidenced by previous studies (Maire et al. 2015; Brandl et al. 2019). This complexity underscores the need for detailed examination of each reef cover class to inform effective conservation strategies in the future.

The strong positive effect of the reef slope on FEve and RaoQ aligns with the expectation that structurally complex habitats support diverse ecological roles (Graham and Nash 2013; Darling et al. 2017). This pattern is consistent with findings from other reefs within the Coral Triangle, where habitat complexity has been shown to be a primary driver of functional diversity. For instance, studies in Raja Ampat, located in the heart of the Coral Triangle and sharing similar marginal reef characteristics, have demonstrated that reef slopes support 25-30% higher functional diversity compared to reef flats (Pakiding et al. 2019; Dubuc et al. 2023). Reef slopes, characterized by steep gradients and varied microhabitats, likely provide a range of niches for species with distinct traits, such as herbivorous scrapers and benthopelagic predators (Cooper et al. 2019; Dubuc et al. 2023). The high FEve in these areas suggests efficient resource partitioning, which reduces competition among species with similar traits (Villéger et al. 2008; Stuart-Smith et al. 2013). This resource partitioning is particularly crucial in marginal reef systems like those in the Banyak Islands, where environmental stressors may limit available resources (McKinley et al. 2022). Similarly, the elevated RaoQ on reef slopes reflects greater Rao's Quadratic entropy driven by species with divergent traits (e.g., varied diets and mobility) and balanced abundance distributions (Botta-Dukát 2005; Upton et al. 2018). However, the negligible effect on FRic was unexpected because structurally complex habitats typically expand trait space by supporting more species (Mouillot et al. 2013; Zhao et al. 2022). This may be due to the relatively moderate taxonomic diversity, with an average of 28.0 species across 20 sites (ranging from 19 to 40 species), which is notably lower than other Coral Triangle locations such as Raja Ampat (mean: 165 species per site) or the Bird's Head Peninsula (mean: 153 species per site) (Allen and Erdmann 2012; Marwayana et al. 2022), or the marginal nature of these reefs, where high turbidity and nutrient levels constrain the range of functional traits (Pérez-Matus et al. 2022; Costa et al. 2023; Bleuel et al. 2024). Having established the significant influence of reef slopes on FEve and RaoQ, we now focus on the complexities surrounding FRic and FDiv.

The negative trend in FDiv with increasing reef slope steepness suggests that steeper slopes may limit niche differentiation, potentially because of environmental filtering that favors species with convergent traits (e.g., sedentary, benthic species) (MacNeil et al. 2015; Maire et al. 2015). This contrasts markedly with patterns observed in other Indonesian Marine Protected Areas (MPAs) within the Coral Triangle, where complex habitats typically enhance functional divergence. For example, in Karimunjawa National Park, Java Sea, reef slopes showed positive effects on FDiv (β: 0.42, $p<0.01$), attributed to clearer waters and higher coral cover (Yuliana et al. 2016). Similarly, in the Lesser Sunda Ecoregion, reef slopes support 40% higher functional divergence compared to other reef zones (TNC Indonesia 2011).

Table 4. Estimated effects of reef cover class variables on reef fish functional diversity metrics, including median values, credible intervals, and probability estimates, calculated across 6000 posterior distribution draws

Factor	**Median**	**CI_2.5%**	**CI_97.5%**	**Prob_Positif**	**Prob_Negative**
FRic reef slope	0.00	-0.0	0.0	0.2	0.79
RaoQ reef slope	0.0	0.00	0.0	0.99	0.0
FDiv reef slope	-0.0	-0.0	0.00	0.	0.89
FEve reef slope	0.03	-0.0	0.06	0.95	0.05
FRic sheltered reef slope	0.00	-0.0	0.0	0.24	0.76
RaoQ sheltered reef slope	0.00	0.00	0.0	0.85	0.5
FDiv sheltered reef slope	0.00	-0.0	0.0	0.47	0.53
FEve sheltered reef slope	-0.0	-0.04	0.03	0.32	0.68
FRic reef crest	0.00	-0.0	0.0	0.74	0.26
RaoQ reef crest	0.00	0.00	0.0	0.68	0.32
FDiv reef crest	0.00	-0.0	0.0	0.42	0.58
FEve reef crest	0.00	-0.03	0.03	0.47	0.53

Note: Credible Interval (CI), Probability estimates (Probs), Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ)

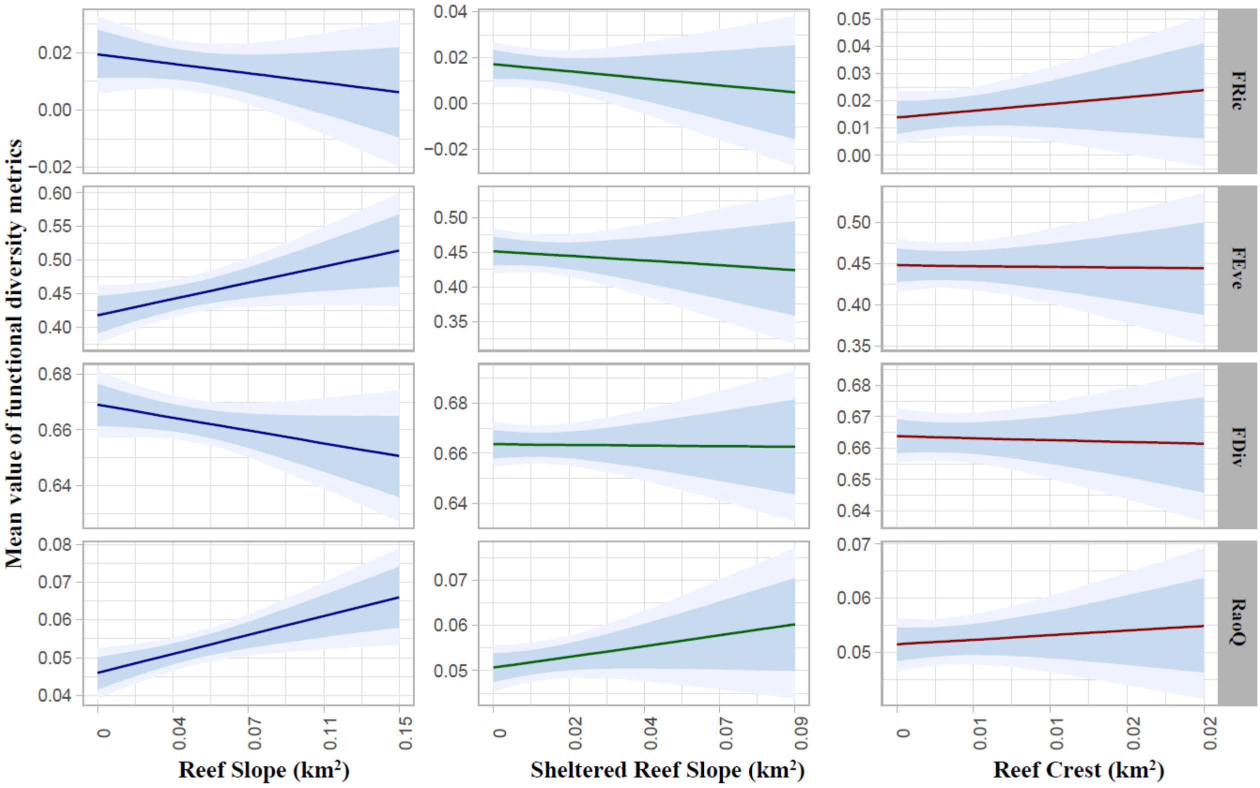

Figure 5. Predicted trends in functional diversity metrics of reef fish across the Banyak Islands Marine Nature Park, Aceh Province, Indonesia, modeled using reef slopes, sheltered reef slopes, and reef crest variables, displayed with thick blue, green, and red lines for median predictions from 6000 posterior draws, accompanied by light blue shaded bands for 95% credible intervals, and dark blue shaded bands for 80% Bayesian credible intervals to reflect predictive uncertainty

The weaker effects of the sheltered reef slope (e.g., Prob_Pos for RaoQ: 0.852 and Prob_Neg for FEve: 0.676) and reef crest (e.g., Prob_Pos for FRic: 0.744 and Prob_Neg for FDiv: 0.581) likely reflect their lower structural complexity and limited distribution across sites (Figure 1). Sheltered slopes, present at only three sites, may support fewer specialized species owing to reduced wave energy and sediment accumulation (Sherman et al. 2010). Similarly, reef crests, despite hosting high herbivore biomass (Helder et al. 2022), showed inconsistent effects, possibly because of wave energy selection for specific functional groups (e.g., mobile and schooling species) (Bellwood et al. 2004; Green and Bellwood 2009; Brandl et al. 2019).

Correlations among the functional diversity metrics provided further insights into community assembly and ecosystem resilience mechanisms (Figure 6). The strong positive correlation between FEve and RaoQ (observed correlation, ρobs: 0.388) indicates that assemblages with evenly distributed traits also exhibited high Rao's Quadratic entropy, reflecting balanced ecological roles across sites (Laliberté and Legendre 2010; Stuart-Smith et al. 2013) and enhanced functional redundancy, a key component of reef resilience (Biggs et al. 2012; McLeod et al. 2019). Conversely, the strong negative correlation between FDiv and RaoQ (ρobs: -0.549) suggests a trade-off, where assemblages with high Rao's Quadratic entropy have fewer divergent traits, possibly because of environmental constraints limiting extreme trait values (Mouchet et al. 2010; Costa et al. 2023). This trade-off has important implications for reef resilience, as it suggests that while the Banyak Islands reefs maintain functional redundancy through even trait distribution (high FEve), they may be vulnerable to novel disturbances that require functionally divergent species for adaptation (Mori et al. 2013). Predicted correlations (mean ρpred: -0.003) were lower than those observed, and residual correlations were minimal (mean ρres: -0.051), suggesting that reef cover classes explained much of the variation in functional diversity. Low residual correlations imply that unmeasured factors, such as biotic interactions (e.g., predation and competition) or environmental variables (e.g., turbidity and current velocity), also independently shape functional diversity independently (Dubuc et al. 2023; Luza et al. 2023).

Ecological significance and reef resilience

Our findings have important implications for understanding reef resilience in marginal reef systems. The observed patterns of functional diversity align with key principles of resilience theory, particularly the insurance hypothesis, which posits that functional redundancy provides ecosystems with the capacity to maintain function following disturbances (Yachi and Loreau 1999; Nyström 2006). The high FEve on reef slopes indicates functional redundancy within the fish assemblage, where multiple species can perform similar ecological roles. This redundancy is crucial for maintaining ecosystem processes such as herbivory, which controls algal growth and facilitates coral recruitment, both essential for reef recovery following disturbances (Bellwood et al. 2004; McLeod et al. 2019).

However, the low FRic and negative trend in FDiv suggest limited response diversity, the variety of responses to environmental change among species contributing to the same ecosystem function (Elmqvist et al. 2003; Mori et al. 2013). This limitation may compromise the long-term resilience of Banyak Islands reefs, particularly under novel or extreme disturbances. As noted by Anthony et al. (2015), reefs with high functional redundancy but low response diversity may maintain ecosystem functions under moderate disturbances but could experience functional collapse under severe or novel stressors.

Comparison with coral triangle and other MPAs

When compared to other MPAs within the Coral Triangle, the Banyak Islands exhibit unique patterns that reflect their marginal reef status. Studies from the Bird's Head Seascape in Raja Ampat, which hosts 95% of the Coral Triangle's coral species, show significantly higher functional richness (mean FRic: 0.087) compared to our findings (mean FRic: 0.0156) (Pakiding et al. 2019). Similarly, MPAs in the Philippines' Verde Island Passage, recognized as the center of the Coral Triangle's biodiversity, demonstrate higher functional divergence on reef slopes (FDiv: 0.96) compared to our study (FDiv: 0.94) (Licuanan et al. 2017). These differences likely reflect the marginal nature of Banyak Islands reefs, which experience higher turbidity, nutrient levels, and human pressures compared to more pristine areas of the Coral Triangle. However, our findings suggest that even marginal reefs can maintain important functional diversity patterns, particularly in terms of functional evenness and redundancy, which are crucial for ecosystem stability.

The moderate explanatory power of our model (average R^2: 0.285, range 0.19-0.37) reflects the complex drivers of functional diversity in marginal reefs, with reef slopes strongly influencing trait distribution (FEve, R^2: 0.37; RaoQ, R^2: 0.35) but less so trait range (FRic, R^2: 0.19) and divergence (FDiv, R^2: 0.23) (Table 3). Variable species richness (19-40 species across sites) and unmeasured factors are likely to contribute to these patterns (MacNeil et al. 2015; Luza et al. 2023). Our findings provide direct guidance for coral reef management in the Banyak Islands Marine Nature Park. Reef slopes, which significantly enhance functional evenness and diversity, should be prioritized as core protection zones in marine spatial planning to preserve essential ecological functions. The weaker effects of sheltered slopes and reef crests suggest these areas could serve as sustainable-use zones with regulated fishing to maintain key functional groups, particularly herbivores critical for algal control. Restoration efforts should focus on maintaining or enhancing structural complexity on reef slopes to support balanced fish assemblages. These science-based zoning recommendations can inform adaptive management strategies that balance conservation goals with local community needs in this important marine protected area. We propose focusing on the functional diversity of reef fish in marginal reefs. The possible explanations for these findings are as follows: (i) habitat heterogeneity on reef slopes promotes even trait distributions but not trait range; (ii) marginal reef conditions, such as potentially high turbidity and nutrient levels, may filter species and reduce FRic; (iii) biotic interactions, including competition and predation, shape Rao's Quadratic entropy (Wilson et al. 2006; Green and Bellwood 2009). Below, we explore these explanations and highlight their ecological basis and conservation implications for the Banyak Islands Marine Nature Park.

Habitat heterogeneity on reef slopes fosters even trait distributions, enhancing FEve and RaoQ, but limits FRic owing to the constrained trait range. The diverse microhabitats of reef slopes support complementary traits, such as herbivorous scrapers and benthopelagic predators, promoting resource partitioning and balanced ecological roles, as shown by the FEve-RaoQ correlation (ρobs: 0.388) (Graham et al. 2015; Darling et al. 2017). However, moderate taxonomic diversity (19-40 species) restricts trait space, potentially excluding groups such as deep-water specialists, which limits FRic (Cooper et al. 2019). This pattern is common in marginal reefs, where complex habitats enhance trait evenness but not diversity owing to species pool constraints (Pérez-Matus et al. 2022). Preserving reef slope complexity is critical for maintaining these balanced assemblages, as habitat loss can reduce niche availability and functional evenness (Cinner et al. 2016).

Marginal reef conditions, such as the potentially high turbidity and nutrient levels typical of the Banyak Islands, may act as environmental filters, limiting FRic by favoring specific traits. Although not measured in this study, turbid waters and nutrient enrichment, which are common in marginal reefs, are likely to be selected for benthic or sediment-tolerant species, while excluding those requiring clear water, such as planktivorous or visually oriented predators (McKinley et al. 2022; Pombo-Ayora et al. 2024). This hypothesized filtering could explain the low R^2 for FRic (0.19) as trait diversity is constrained, a pattern observed in other reef systems with similar conditions (MacNeil et al. 2015; Costa et al. 2023). Conservation strategies should address potential water quality issues, such as reducing sediment runoff through coastal buffer zones, to support a broader range of functional traits and enhance ecosystem resilience (Yonvitner et al. 2022).

Biotic interactions, including competition among herbivores and predation pressure, shaped Rao's Quadratic entropy, contributing to the low R^2 for FDiv (0.23) (Table 3). Intense competition for algal resources on steep slopes may favor convergent traits, such as territorial grazers, reducing FDiv (Prob_Neg: 0.890) (Table 4), whereas predators select for mobile or schooling species, further limiting divergent traits (Green and Bellwood 2009; Helder et al. 2022). This is reflected in the negative FDiv-RaoQ correlation (ρobs: -0.549) (Figure 6), indicating a trade-off between quadratic entropy and divergence (Mouchet et al.

2010). Similar dynamics occur in complex reef habitats where biotic interactions drive trait convergence (Luza et al. 2023). Protecting herbivores and prey species is essential for maintaining quadratic entropy and ecosystem functions, such as algal control, which can be achieved through marine-protected areas with fishing regulations (Fahlevy et al. 2019; Putra et al. 2021).

Conservation and management implications of Banyak Islands Marine Nature Park

Our findings have direct implications for the zoning and management of the Banyak Islands Marine Nature Park. The critical role of reef slopes in maintaining functional diversity suggests these areas should be prioritized for protection within the park's zoning system. Following the Indonesian MPA zoning framework, which includes core zones (no-take areas), sustainable fisheries zones, and utilization zones (Peraturan Pemerintah No. 60 2007), we recommend: Core Zone Designation: Reef slopes with high FEve and RaoQ values should be designated as core zones to protect the functional redundancy essential for ecosystem resilience. Based on our results, sites 5, 11, and 20, which showed the highest functional diversity metrics, should be prioritized for strict protection. Sustainable Fisheries Zones: Sheltered reef slopes and reef crests, which showed moderate effects on functional diversity (Figure 4), could be designated as sustainable fisheries zones with regulated gear types and catch limits to maintain functional groups, particularly herbivores. Adaptive Management Zones: Given the moderate explanatory power of our model and the complex drivers of functional diversity, we recommend establishing adaptive management zones where different management strategies can be tested and monitored. This approach aligns with Indonesia's commitment to improving MPA management effectiveness, as only 45% of Indonesian MPAs currently demonstrate effective management (Amkieltiela et al. 2022). Connectivity Considerations: The park's zoning should consider connectivity between reef slopes and other habitats to maintain larval supply and adult fish movement, crucial for sustaining functional diversity across the MPA network (Ahmadia et al. 2015). These recommendations align with the broader Coral Triangle Initiative goals and Indonesia's target of effectively managing 30 million hectares of MPAs by 2030, emphasizing the need for science-based zoning that considers functional diversity patterns (CTI-CFF 2013).

The vulnerability of functional diversity to habitat degradation is particularly concerning given that Reef slopes, which are critical for diverse fish assemblages, are threatened by coastal development, sedimentation, and climate-driven changes in wave energy (Wilson et al. 2006; Kennedy et al. 2020). The loss of these habitats could reduce functional evenness and quadratic entropy, impairing ecosystem functions, such as nutrient cycling and algal control (Graham et al. 2015; Brandl et al. 2019). The negative FDiv trend on steep slopes suggests that niche differentiation may already be limited, increasing susceptibility to disturbances, such as overfishing, which selectively removes functionally distinct species (MacNeil et al. 2015; Fahlevy et al. 2019). Our findings support spatially explicit conservation strategies that prioritize reef slopes for protection within the Banyak Islands Marine Nature Park (Cinner et al. 2016; Yonvitner et al. 2022). Integrating functional diversity into management plans can enhance ecosystem resilience, particularly in marginal reefs facing multiple stressors (Putra et al. 2021).

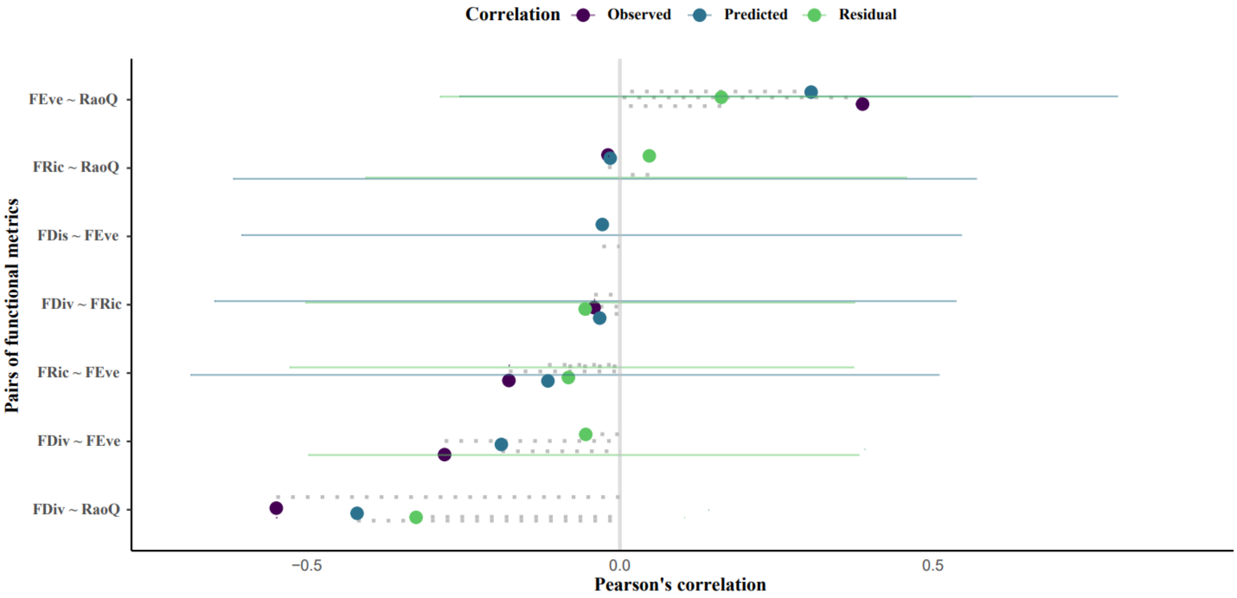

Figure 6. Detailed analysis of correlations among functional diversity metrics (Functional Richness (Fric), Functional Evenness (Feve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ)) of reef fish in the Banyak Islands Marine Nature Park, Indonesia, is illustrated with blue bars for observed Pearson correlations, purple bars with black outlines for predicted medians and 95% credible intervals, and green bars with dashed outlines for residual correlations

The limitations of our study include the focus on the three reef cover classes, which may not capture the full range of habitat complexities (e.g., lagoons and plateaus). The sampling depth (3-12 m) may have excluded species with deeper or shallower preferences, potentially underestimating FRic, especially given the observed variability in species richness (19-40 species) (Cooper et al. 2019). Additionally, unmeasured variables such as water quality and fishing pressure may influence functional diversity (Bleuel et al. 2024). Future research should incorporate these factors and extend the sampling to other reef zones to better understand their role in shaping fish assemblages. Exploring phylogenetic diversity could also clarify whether evolutionary constraints limit trait range in marginal reefs (Luza et al. 2023).

In conclusion, this study highlights the intricate relationships between reef cover classes and the functional diversity metrics of reef fish communities within the Banyak Islands Marine Nature Park. These findings emphasize the significant role of the structural characteristics of the reef, particularly the reef slope, sheltered reef slope, and reef crest, in shaping functional diversity, as evidenced by metrics such as Functional Richness (FRic), Functional Evenness (Feve), Functional Divergence (FDiv), and Rao's Quadratic entropy (RaoQ). Our results indicate that while reef slopes promote even trait distribution and enhance functional diversity, they do not necessarily increase the range of functional traits represented within the community. The observed negative trend in FDiv suggests that habitat complexity may limit niche differentiation, potentially because of environmental filtering that favors convergent traits. Understanding these patterns is crucial for developing effective conservation strategies that maintain both functional redundancy and response diversity, key components of reef resilience in the face of global environmental change. Our study provides essential baseline data for adaptive management of this important marine protected area within the Banyak Islands Marine Nature Park, contributing to Indonesia's broader marine conservation goals and the preservation of global marine biodiversity.

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