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The Role of Functional Traits in Structuring Fish Assemblages Across the Four Macaronesia Archipelagos

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ABSTRACT

Aim: To investigate how functional traits shape the composition and functional structure of coastal fish assemblages across the four North-East Atlantic archipelagos, providing insights into the ecological drivers of species distributions and trait patterns in oceanic island systems.

Location: Four North-East Atlantic oceanic archipelagos within Macaronesia: the Azores, Madeira, Canary Islands and Cabo Verde.

Taxon: Coastal marine fishes occurring up to 200 m depth, comprising 682 species.

Methods: We compiled a validated checklist of coastal fish species (≤ 200 m depth) for each archipelago and integrated these data with a functional trait matrix comprising size category, trophic category, habitat affinity, milieu and climatic affinity. Generalised Linear Models (GLMs) were used to assess the influence of traits on species occurrences. Functional community structure was quantified using six functional diversity indices: functional richness (FRic), evenness (FEve), divergence (FDiv), dispersion (FDis), Rao's quadratic entropy (RaoQ) and FRic intersection (FRic Inter). Model performance was evaluated using AIC, BIC, pseudo R^2 and post hoc comparisons. Trait-based GLMs were complemented with assemblage-level RLQ ordination and fourth-corner tests to evaluate trait–environment coupling while accounting for species co-occurrence.

Results: Species richness followed a clear latitudinal gradient, peaking in the Canary Islands and declining towards higher latitudes. RLQ revealed strong global trait–environment co-structure (Axis 1 = 91.7% of projected inertia), whereas Fourth-Corner tests detected no individually significant trait–environment associations after Holm correction. RV tests indicated a significant link between trait structure and species composition (Q–L), but not between environmental context and species composition (R–L). Among traits, body size and habitat affinity were the strongest predictors of species occurrences, with larger-bodied and reef-associated species more frequent in the southern archipelagos. Functional richness was highest in the Azores, indicating functional distinctiveness despite comparatively low species richness. Incorporating functional diversity indices into GLMs did not improve explanatory power beyond species-level traits.

Main Conclusions: Body size and habitat affinity are key determinants of coastal fish assemblages across the Macaronesia archipelagos. Functional diversity peaks in the Azores, while Madeira exhibits intermediate trait compositions between temperate and tropical systems. These patterns provide insight into community assembly mechanisms and may inform predictions of species turnover under future climate change scenarios.

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1 | Introduction

The biogeographic unity of Macaronesia has long been debated. While some studies support its coherence for selected taxa, others argue that the region does not form a consistent biogeographic entity, particularly for marine organisms (Freitas et al. 2019a; Melo et al. 2023). Macaronesia biogeography is shaped by interacting geological, environmental and historical factors, including volcanic origin, island age, surface area and distance to the mainland (Tuya and Haroun 2009). Pleistocene sea-level fluctuations further altered island configuration and species distributions, leaving a legacy of both relictual lineages and recent colonisation events (Florencio et al. 2021; Rijsdijk et al. 2014).

Situated in the North-East Atlantic, the four Macaronesian archipelagos—the Azores, Madeira (including the Selvagens), the Canary Islands and Cabo Verde—span a pronounced latitudinal gradient from cool-temperate to tropical climates (Carracedo and Troll 2021). This gradient, combined with strong isolation, complex oceanography and varied geomorphology, makes Macaronesia an exceptional natural laboratory for studying marine biogeographic processes, species turnover and ecological filtering (Florencio et al. 2021; Bowen et al. 2013; Freitas et al. 2019a; Calado et al. 2020).

Coastal fish assemblages are central to ecosystem functioning, contributing to nutrient cycling, trophic regulation and habitat maintenance (Stuart-Smith et al. 2013). Their composition reflects both historical contingencies and environmental filtering (Guillemot et al. 2011). In insular systems, spatial isolation, habitat heterogeneity and dispersal limitations strongly influence taxonomic and functional diversity (Floeter et al. 2004; Bender et al. 2013; Schumm et al. 2019). While species richness typically decreases with increasing isolation, functional diversity may follow different or nonlinear patterns (Halpern and Floeter 2008; Schumm et al. 2019).

Functional traits of marine fish exhibit marked spatial variation across environmental gradients. Body size and trophic level generally increase with latitude (Lin and Costello 2023), while temperature, hydrological connectivity and estuary size shape trait composition at regional scales (Henriques et al. 2017). Functional diversity may increase with depth but decrease with latitude in some temperate systems (Myers et al. 2021) and morphological adaptations often reflect energetic constraints in extreme environments (Myers et al. 2019). Large-scale analyses show that functional diversity is not always congruent with species richness (Denis et al. 2018; Diamond and Roy 2023), with trait turnover responding strongly to environmental, physiological and biotic drivers (Wang et al. 2024; Fisher et al. 2010).

Within Macaronesia, taxonomic patterns suggest a decline in species richness from south (Cabo Verde, Canary Islands) to north (Madeira, Azores) (Freitas et al. 2019a). Yet it remains unclear whether this latitudinal gradient is mirrored by differences in functional traits or functional diversity (Burrows et al. 2019). Key ecological traits—including body size (Olden et al. 2007; Trindade-Santos et al. 2022), trophic category (Friedlander and DeMartini 2002; Albouy et al. 2019), habitat affinity (Burkepile and Hay 2008), milieu (Beukhof et al. 2019; Madigan et al. 2021) and climatic zone (Cheung et al. 2009; Fogarty et al. 2017)—are expected to influence colonisation capacity, persistence and community assembly in isolated marine systems. Trait-based biogeography suggests that environmental gradients across Macaronesia should leave detectable signatures on assemblage structure (Beukhof et al. 2019; Mason et al. 2008; Myers et al. 2019).

Despite progress in terrestrial island trait-based studies (Cadotte et al. 2011), functional perspectives on marine assemblages across oceanic archipelagos remain limited (Bender et al. 2013). Functional diversity approaches are increasingly recognised as essential for understanding ecosystem functioning and guiding conservation in vulnerable island systems (Costa et al. 2023; Henriques et al. 2025; McKinley et al. 2023). Yet we still lack a clear understanding of how functional traits and community-level functional diversity jointly shape coastal fish assemblages at the scale of large insular regions.

To address these gaps, we integrated species-level functional traits with community-level functional diversity indices to characterise coastal fish assemblages across the four Macaronesia archipelagos. Our study was guided by the following questions: (1) how do taxonomic and functional compositions of coastal fish assemblages vary across the Macaronesian archipelagos; (2) which functional traits best predict species occurrences across the region's environmental and biogeographic gradients; (3) do functional diversity indices (e.g., FRic, FEve, FDis, RaoQ) provide additional explanatory power beyond species-level traits when modelling species occurrences; and (4) does functional richness follow the latitudinal gradient observed for species richness in Macaronesia.

Based on biogeographic theory and previous empirical studies, we predicted that as follows: (i) species richness and functional richness would increase towards lower latitudes (Freitas et al. 2019a); (ii) body size and habitat affinity would be the strongest trait-level predictors of occurrence, reflecting dispersal and habitat-filtering processes (Mouillot et al. 2014; Trindade-Santos et al. 2022); and (iii) functional diversity indices would enhance species-occurrence models by capturing emergent community-level structure (Mason et al. 2008).

2 | Material and Methods

2.1 | Methods

2.1.1 | Species Assemblage Data

This study examined coastal fish assemblages across the four Macaronesia archipelagos: the Azores, Madeira (including the Selvagens Islands), the Canary Islands and Cabo Verde. Together, these archipelagos span a pronounced latitudinal gradient from approximately 15° N to 40° N, encompassing tropical, subtropical and temperate marine environments (Figure 1). Coastal species were defined as those typically occurring at depths shallower than 200 m, following established ecological and fisheries conventions (Palomares and Pauly 2019).

Species lists were compiled from the most comprehensive and up-to-date sources available for each region. For the

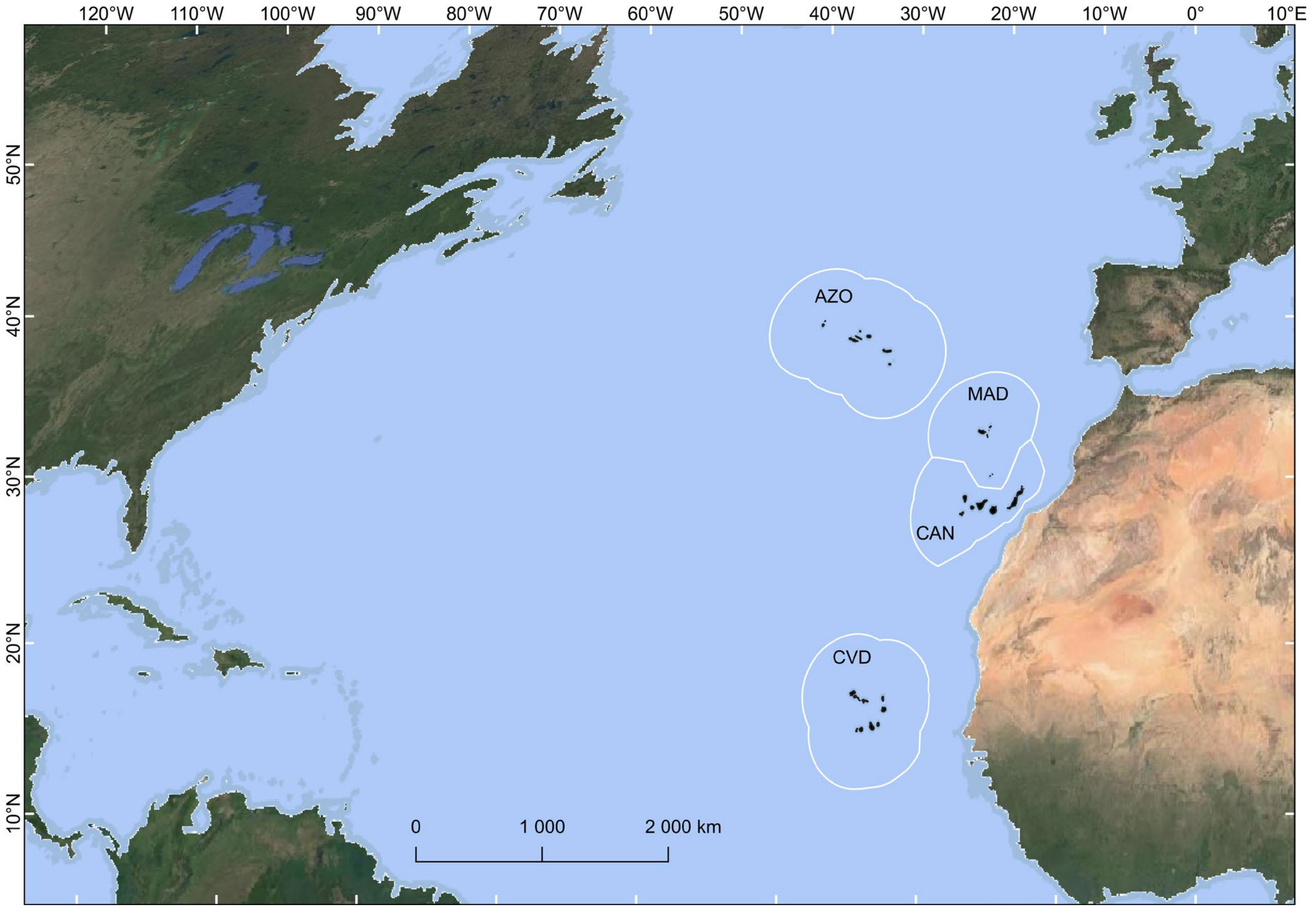

FIGURE 1 | Location of the Macaronesia archipelagos in the North Atlantic: Azores (AZO), Madeira (MAD), Canary Islands (CAN) and Cabo Verde (CVD). Boundaries represent Exclusive Economic Zones (EEZs). Map projection: Mollweide (ESRI: 54009). Basemap: Google Satellite imagery; Ocean layer: Global Oceans and Seas v1 (VLIZ).

Azores, these included Barcelos et al. (2021a, 2021b), Carneiro et al. (2019), Froese and Pauly (2024) and Porteiro et al. (1999). Records for Madeira were sourced from Biscoito et al. (2018), Wirtz et al. (2008) and GBIF occurrences. Data for the Canary Islands were obtained from the das Canárias (2024), whereas Cabo Verde species were compiled from Barcelos et al. (2025).

All records were cross-validated to retain only well-documented resident species; vagrants, transient pelagic visitors and taxa of uncertain identity were excluded. The final dataset comprised 682 coastal fish species distributed across three classes: Petromyzonti, Elasmobranchii and Actinopteri.

2.1.2 | Functional Traits

Each species was characterised by five ecologically meaningful functional traits selected for their relevance to community structure, resource use and biogeographic filtering in island systems (Table S1): Size Category (body size)—reflecting ecological dominance, life-history strategy and trophic interactions; Trophic category—feeding guild; Habitat affinity—types of substrate and habitat used by species; Milieu—vertical habitat domain (water column layers and habitat associations); Climatic affinity—thermal preference (geographic and climatic zones where species are found).

Trait information was compiled from FishBase (Froese and Pauly 2024), FAO identification guides (Carpenter and De Angelis 2014; Carpenter and De Angelis 2016a, 2016b, 2016c; Cohen et al. 1990; Heemstra and Randall 1993), the IUCN Red List (Gearty and Chamberlain 2025; IUCN 2025), GBIF (Chauvier et al. 2022) and regional literature. Missing trait entries were completed using information from congeneric species under the assumption of general ecological similarity.

We acknowledge that no null models were used to control for species-richness dependence in functional diversity metrics; potential implications are discussed in the Discussion.

2.1.3 | Functional Diversity Metrics

Functional diversity was quantified using five complementary indices describing different dimensions of trait structure: (Mouchet et al. 2010) functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao's quadratic entropy (RaoQ). All indices were computed with the fundiversity R package (Grenié and Gruson 2025).

A single multidimensional functional space was constructed from mixed trait types using Gower distances computed with daisy from the cluster package (Maechler et al. 2025), followed by a Principal Coordinates Analysis (PCoA) implemented in the ape package (Paradis and Schliep 2019) (ape::pcoa) with a Cailliez correction applied when required. Axes explaining $>80\%$ of cumulative variation were retained. Species coordinates in this functional space formed the basis for calculating all functional diversity indices at the archipelago level ($n=4$). Pairwise functional richness intersections (FRic_intersect) were also calculated to quantify the shared portion of functional space among archipelagos.

Species scores in the PCoA functional space are provided in Appendix S1, in PCoA_scores_species file.

2.1.4 | Data Analysis

2.1.4.1 | Trait-Based GLMs. We evaluated the influence of functional traits on species occurrence using generalised linear models (GLMs). The response variable was species presence–absence across archipelagos. Predictors were the five functional traits: size category, trophic category, habitat affinity, milieu and climatic affinity. Categorical predictors were treated as factors, and continuous variables were standardised (z-scores).

To avoid imposing a priori assumptions regarding error structure, we fitted all non-empty combinations of the five predictors under three alternative GLM families: binomial, Poisson and Gaussian (via the glm() function in base R). For each fitted model, we computed Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood and McFadden's pseudo-R^2. Within each family, the model with the lowest AIC was retained, and the overall 'best' model was defined as the one with minimum AIC across all families. Binomial GLMs consistently provided the best compromise between fit and interpretability and were therefore used for inference.

Multicollinearity among predictors was assessed using Variance Inflation Factors (VIF) from the car package (Fox and Weisberg 2019), which were <5 for all traits. Pairwise contrasts between trait levels were evaluated using the postHoc package (Labouriau 2020). Model discrimination was quantified via receiver operating characteristic (ROC) curves and area under the curve (AUC) values using the pROC package (Robin et al. 2011).

2.1.4.2 | Generalised Linear Mixed-Effects Models (GLMMs). To account for hierarchical structure and potential non-independence in the data, we fitted binomial generalised linear mixed-effects models (GLMMs) using the lme4 package (Bates et al. 2015), applying the same fixed-effect structure as the best AIC-selected binomial GLM. Given the nested and repeated-measures nature of the dataset, we included random intercepts for archipelago and species identity:

$$\text{Occurrence} \sim \text{traits} + (1|\text{archipelago}) + (1|\text{species}).$$

Models were fitted using the bobyqa optimiser with an increased maximum number of iterations ($\text{maxfun}=10^5$) to ensure stable convergence. For each model, we extracted AIC, BIC and log-likelihood values, as well as marginal and conditional R^2 using the MuMIn package (Barton 2024). Fixed-effect estimates were converted to odds ratios with 95% confidence intervals by exponentiating coefficients and their confidence bounds. ROC curves and AUC values were computed following the same procedure used for the GLMs.

GLMM results were used as a robustness check to confirm that accounting for random effects did not qualitatively alter the conclusions drawn from the GLM analyses. Full model comparisons and detailed outputs are provided in Appendix S1.

2.1.4.3 | Functional Diversity and Occurrence. To evaluate whether assemblage-level functional structure improved the prediction of species occurrence beyond species-level traits, we incorporated functional diversity indices into the occurrence–trait framework. Functional indices (FRic, FEve, FDiv, FDis and RaoQ), computed at the archipelago level, were merged with the species table via the archipelago identifier and subsequently included as predictors in a binomial GLM. Models were fitted and summarized using the same procedures applied to the trait-only GLMs.

We compared three model sets: (i) the best AIC-selected trait-only GLM, (ii) the best BIC-selected trait-only GLM and (iii) the GLM including functional diversity indices. This comparison allowed us to explicitly assess whether functional diversity metrics contributed additional explanatory power beyond individual species traits.

Finally, to explore whether functional richness followed a simple latitudinal gradient across archipelagos, we regressed FRic against the mean latitude of each archipelago ($n=4$) using a simple linear model (FRic ~ latitude). Because FRic was computed once per archipelago, classical group-comparison tests such as ANOVA or Kruskal–Wallis are not applicable. Instead, we assessed the significance of the slope using a permutation test with 9999 randomisations of FRic values across archipelagos.

2.1.4.4 | Taxonomic Overlap and Trait–Environment Structure. Patterns of shared taxa across archipelagos were visualised using UpSet plots from the ComplexUpset package (Krassowski 2020), based on pre-computed frequencies of classes, orders, families, genera and species across all combinations of the four archipelagos.

To examine the joint structure linking species composition, functional traits and archipelago identity, we applied RLQ analysis and Fourth-Corner tests using the ade4 package (Dray and Dufour 2007). The L table (sites × species), containing presence–absence data, was analysed using correspondence analysis (CA; dudi.coa). The Q table (species × traits) consisted entirely of categorical functional attributes and was therefore analysed using multiple correspondence analysis (MCA; dudi.acm). The R table (sites × groups) contained a single categorical descriptor—archipelago identity—which was internally expanded into dummy variables as required by MCA. Row weights of R and Q were constrained to match the site and species weights derived from L, following the requirements of RLQ methodology.

The significance of the RLQ ordination was assessed via Monte Carlo permutation tests (randtest, 999 permutations). Global trait–environment relationships were evaluated using Fourth-Corner analysis (fourthcorner, $\text{modeltype}=6$), with p-values adjusted for multiple testing using Holm's method. RV coefficient permutation tests (RV.rtest) quantified the strength of association between the L–R and L–Q matrices. Full outputs (eigenvalues, RLQ axes, Fourth-Corner statistics, adjusted *p*-values and RV tests) are provided in Tables S17–S23.

3 | Results

The Macaronesia region hosts a total of 682 coastal fish species, spanning three taxonomic classes (Petromyzonti, Elasmobranchii and Actinopteri), 45 orders, 159 families and 377 genera. Species richness followed a clear latitudinal trend, increasing from the Azores (315 species) to Madeira (392) and peaking in the Canary Islands (416), while Cabo Verde supported 393 species (Figure 2; Table S2).

Despite its larger coastal perimeter, Cabo Verde was not the most species-rich archipelago. Only Madeira contained representatives of all three fish classes, whereas the remaining archipelagos comprised Elasmobranchii and Actinopteri. Taxonomic uniqueness was high: 39 orders, 95 families, 200 genera and 273 species were exclusive to a single archipelago. Conversely, 145 species occurred across all four archipelagos; 130 species were shared by two archipelagos and 135 by three (Table 1; Figures S1–S5).

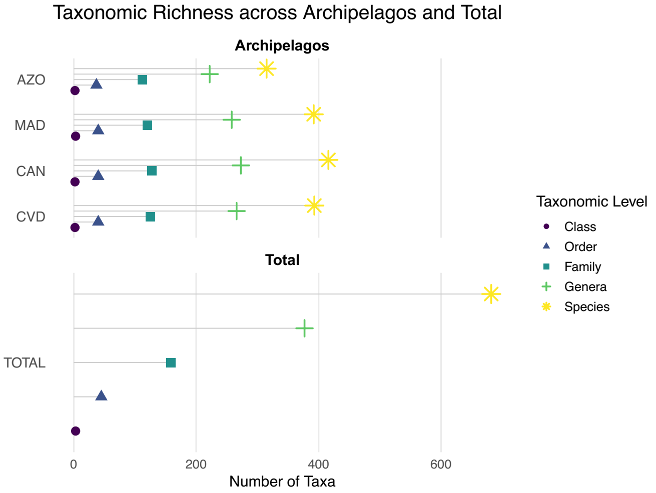

FIGURE 2 | Taxonomic richness of marine fishes across the Macaronesia archipelagos. Number of classes, orders, families, genera and species recorded in the Azores (AZO), Madeira (MAD), Canary Islands (CAN) and Cabo Verde (CVD), along with total richness across the region.

Functional trait composition differed across regions (Table S3; definitions in Table S1). Small-bodied species (< 10 cm) were consistently scarce, while very large species (> 60 cm) represented > 40% of the fauna in all archipelagos. Medium-sized species (30–45 cm) showed stable representation throughout the region, whereas large-bodied species (45–60 cm) reached their highest proportional abundance in Cabo Verde. Trophic structure was dominated by macro-carnivores—particularly in the Azores, where they accounted for 65% of the assemblage. Herbivores and omnivores were generally rare, although slightly more common in Cabo Verde. Macro-invertebrate feeders increased towards southern latitudes, whereas planktivores displayed relatively consistent proportions across all archipelagos.

Habitat affinity exhibited a pronounced spatial gradient. Water-column-associated species prevailed in the northern archipelagos (Azores and Madeira), while reef-associated taxa were more common in the Canary Islands and Cabo Verde. Species linked to unconsolidated substrates also increased towards the south, whereas the proportion of taxa without a defined affinity (NHA) remained relatively even across regions. A comparable pattern was observed for Milieu traits: demersal species dominated all assemblages and were particularly abundant in Madeira. Epipelagic and pelagic species were more common in northern archipelagos, whereas reef-associated species increased towards the south. Mesopelagic and bathypelagic species were consistently rare throughout the region.

A Principal Coordinates Analysis (PCoA), based on Euclidean distances among species' traits, revealed extensive functional overlap among the four archipelagos (Figure 3). However, centroid positions and confidence ellipses showed subtle but consistent displacement, indicating weak but detectable regional differentiation in functional trait structure. Figure S13 provides a species-level ordination with detailed trait distributions in the functional space.

Climatic affinities followed a marked latitudinal gradient. Cabo Verde was dominated by tropical-affinity species, Madeira and the Canary Islands by subtropical taxa and the Azores by temperate species; the latter was the only archipelago to include boreal-affinity species (Figures S6–S10).

Functional diversity indices varied substantially among archipelagos (Table 2). The Azores exhibited the highest functional richness (FRic = 412.44), functional evenness (FEve = 0.46), functional dispersion (FDis = 2.71) and Rao's quadratic entropy

TABLE 1 | Taxonomic overlap across Macaronesia archipelagos.

	Class	Order	Family	Genus	Species
Unique to 1	1	6	31	104	273
Shared by 2	0	1	13	47	129
Shared by 3	0	3	32	83	135
Shared by 4	2	33	83	143	145

Note: Number of taxa (classes, orders, families, genera and species) that are unique to a single archipelago or shared among two, three or all four archipelagos.

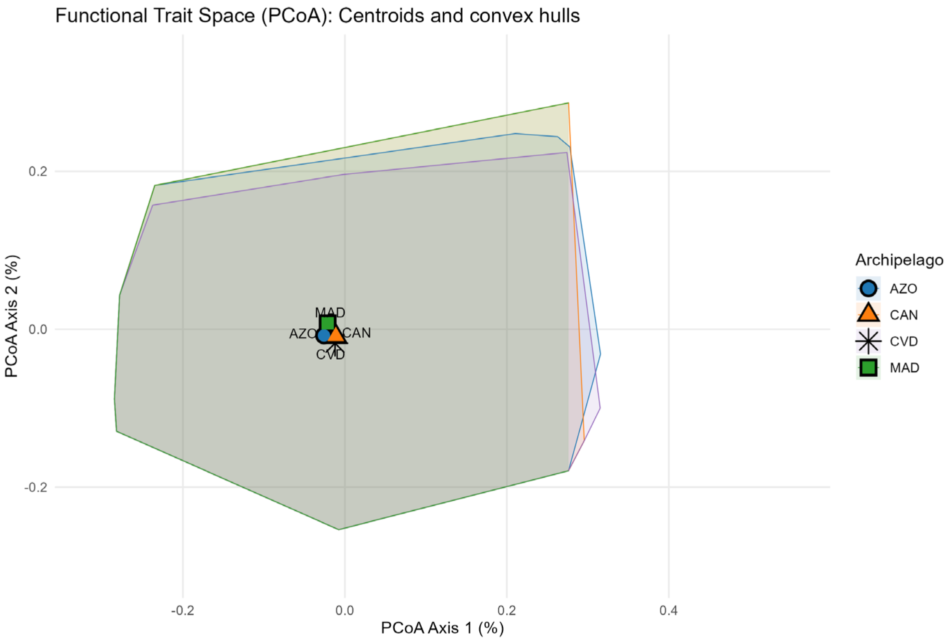

FIGURE 3 | Functional trait space (PCoA) for coastal fish assemblages across the four Macaronesia archipelagos. Convex hulls show the total functional extent of each archipelago and centroids summarise their multivariate trait structure. Axis labels indicate the variance explained. Colours and shapes identify the archipelagos: Azores (blue circles), Madeira (green squares), Canary Islands (orange triangles) and Cabo Verde (purple stars).

TABLE 2 | Functional diversity metrics (FRic, FEve, FDiv, FDis, RaoQ) for coastal fish assemblages in each Macaronesia archipelago.

Site	FRic	FEve	FDiv	FDis	RaoQ
AZO	412.44	0.46	0.87	2.71	3.73
MAD	380.69	0.41	0.86	2.61	3.59
CAN	373.6	0.4	0.86	2.65	3.63
CVD	371.25	0.44	0.86	2.55	3.52

Note: Values reflect within-archipelago functional structure.

TABLE 3 | Coefficients of the best-supported GLMs based on AIC and BIC. Size category and habitat affinity had the strongest effects.

	AIC coefficients	BIC coefficients
Intercept	3.25	2.83
size_cat	1.25	1.24
H_affinity	1.11	—
Milieu	0.74	0.75
clim_Z	0.89	—

(RaoQ = 3.73). Madeira and the Canary Islands displayed intermediate levels of functional diversity, whereas Cabo Verde showed the lowest FRic (371.25), FDis (2.55) and RaoQ (3.52). Pairwise intersections of functional richness were greatest between the Azores and Madeira (362.85) and lowest between the Canary Islands and Cabo Verde (315.50) (Tables S4 and S5). To evaluate whether functional richness follows a simple latitudinal gradient, FRic values (one per archipelago) were regressed against mean latitude. FRic increased towards higher latitudes, but this trend was not statistically significant (slope = 1.63 ± 0.88 FRic units per degree latitude, $R^2 = 0.63$, $p = 0.20$). A permutation test (9999 randomisations) confirmed that the relationship was not significant (permutation $p = 0.20$), and the latitudinal pattern is therefore considered suggestive rather than conclusive (Table S6).

Generalised Linear Models (GLMs) identified body size and habitat affinity as the strongest predictors of species occurrence across Macaronesia. Models containing these two traits consistently showed the lowest AIC and BIC values (Table 3) and the highest pseudo-R^2. The best-performing GLM included body size, habitat affinity, milieu and climatic affinity, with a McFadden pseudo-R^2 of 0.0340 (Table S7). Trophic category contributed minimally. Post hoc comparisons confirmed the dominant influence of body size and habitat affinity, with smaller but statistically significant effects for milieu and climatic affinity (Table S8A,B).

Multicollinearity was negligible, with all VIF values < 1.05 (Table S9), confirming that the functional traits used as predictors were largely independent. ROC curves showed low discriminatory ability, performing only marginally above random expectation (Figures S11 and S12).

To account for the hierarchical structure of the dataset, we additionally fitted Generalised Linear Mixed Models (GLMMs) with random intercepts for archipelago and species identity. These models demonstrated markedly improved discrimination (AUC = 0.801; Figures S13 and S14), indicating that hierarchical structure captures important non-independence among observations. However, improvements in AIC were modest, BIC values exceeded those of the GLMs, and marginal R^2 remained low (Table S10), with most explanatory power attributed to random effects. Fixed-effect odds ratios confirmed strong and consistent influences of body size and habitat affinity (Tables S11 and S14 for fixed effects; Tables S12 and S15 for random-effect variances), whereas random-effect variances highlighted substantial species-level heterogeneity (Tables S12 and S14). Full model summaries are provided in Tables S13 (extended model) and S16 (minimal model), and ROC curves for both models are shown in Figures S18 and S19. GLMMs therefore served as a robustness check and supported the direction and magnitude of the trait–occurrence relationships recovered by the GLMs, which remained the primary inferential framework.

Integrating functional diversity (FD) indices into GLMs did not improve model performance (Table 4). Functional richness (FRic) was the only significant FD predictor and exhibited a negative relationship with occurrence probability, indicating that greater functional richness was not associated with higher likelihood of species presence (glm_fd_comparison.csv). However, FD-augmented models yielded lower explanatory power than trait-only models (Table S7), suggesting that assemblage-level FD metrics provide limited additional explanatory value at the regional scale.

The RLQ analysis revealed a strong overall co-structure between functional traits and environmental variables, with the first axis explaining 91.7% of the projected inertia and separating archipelagos along a clear environmental gradient (total inertia = 0.08168; Figure S14). Axes 2 and 3 accounted for 4.23% and 4.06% of inertia, respectively (Table S18). A global Monte-Carlo randomisation test (Model 4) confirmed significant RLQ structure ($p = 0.001$), whereas Model 2 was non-significant ($p = 0.849$) (Table S23). RLQ site, species and trait scores are provided in Tables S19–S21.

RV-based permutation tests indicated a strong and significant association between functional traits and species composition (RV(Q, L) = 0.72; $p = 0.001$; Figure S17, Table S22). In contrast, the environment–species RV test (RV(R, L)) yielded a degenerate permutation distribution, characterised by minimal variation across permutations and thus preventing statistical inference. The observed RV was high (~0.93), but the lack of a usable null distribution renders the test non-diagnostic (Figure S16).

Fourth-Corner analyses detected no significant trait–environment associations after Holm correction for multiple testing (all adjusted $p = 1.0$). Several unadjusted correlations were modest in magnitude (e.g., climatic affinity in Cabo Verde $r = 0.204$; habitat affinity in Madeira $r = -0.066$), but none remained significant after correction. In combination, these results suggest that, although RLQ identifies a strong global trait–environment co-structure, individual trait–environment relationships are weak and not statistically robust when accounting for multiple comparisons (Table S17).

TABLE 4 | AIC and BIC values for the best GLMs (trait-based) and the model including functional diversity indices. Lower values indicate better fit.

Model	AIC	BIC
Best GLM (AIC)	3635.765	3665.329
Best GLM (BIC)	3645.852	3663.59
GLM with FD	3726.673	3750.324

4 | Discussion

This study provides a comprehensive assessment of coastal fish assemblages across the Macaronesia archipelagos, revealing the central roles of species richness, functional traits and environmental context in shaping community structure. Our findings confirm a clear latitudinal gradient in species richness, increasing from the Azores to Madeira, the Canary Islands and Cabo Verde. This pattern is consistent with biogeographic expectations (Macpherson 2002; Trindade-Santos et al. 2022; Willig et al. 2003; Tuya and Haroun 2009) and reflects the influence of warmer waters, higher habitat diversity—particularly reefs—and proximity to continental species pools (Almada et al. 2013; Azzurro et al. 2019; Freitas et al. 2019a).

Among the four archipelagos, the Canary Islands exhibited the highest species richness, likely reflecting their favourable biogeographic position, extensive reef systems and the considerable research effort that has expanded the regional ichthyofauna inventory in recent decades (Biscoito et al. 2018; Canárias 2024; Falcón et al. 2023). Madeira, despite its similar latitude, supported fewer species, probably due to both ecological factors and comparatively limited sampling, suggesting that additional inventory initiatives may reveal greater diversity (Appeltans et al. 2012; Costello and Chaudhary 2017; Mora et al. 2008).

Although the Azores hosted the lowest species richness, they displayed the highest functional diversity, supporting a disproportionately broad range of ecological roles (Freitas 2014; Freitas et al. 2019a). This pattern aligns with the expectation that isolated or peripheral systems may harbour functionally diverse assemblages due to relaxed biotic constraints, environmental heterogeneity or greater niche availability (Mouillot et al. 2014; Stuart-Smith et al. 2013). Oceanographic processes—such as complex current systems, variable thermocline structure and diverse seafloor topography—likely generate ecological opportunities that promote functional complementarity in the Azores (Almada et al. 2013; Borges et al. 2010). Lower levels of human pressure relative to the southern archipelagos may further support the persistence of functionally unique species (Bozec et al. 2015; Edgar et al. 2014).

Functional richness showed a modest increase towards higher latitudes, with the Azores and Madeira holding the broadest functional spaces. However, this pattern lacked statistical support—neither the linear model nor the permutation test detected a significant FRic—latitude relationship. This indicates that the apparent gradient is better interpreted as a biogeographic tendency rather than a formal latitudinal effect. The strong functional overlap between the Azores and Madeira reinforces the view of these islands as a transitional zone where temperate and subtropical faunas converge (Almada et al. 2013; Freitas et al. 2019a), a pattern further supported by the functional trait ordinations.

Among the functional traits examined, body size emerged as the strongest predictor of species occurrence. Larger-bodied species were more likely to occur across archipelagos, probably reflecting their greater mobility, broader environmental tolerances and enhanced dispersal potential (Bradbury et al. 2008; Lin and Costello 2023; Olden et al. 2007; Bailey et al. 2018). These findings support island biogeography theory, which predicts that species with higher dispersal capacity are more successful colonisers in remote archipelagos (Bowen et al. 2013; Cunha et al. 2017; Tosetto et al. 2024).

Habitat affinity was the second most influential trait. Habitat availability and structural complexity strongly shaped species presence across the region (Kaiser 1999; Munday 2004; Sangil et al. 2018; Jackson-Bué et al. 2024; Sgarlatta et al. 2023; Darling et al. 2017; Hall and Kingsford 2021). Reef-associated species dominated in the Canary Islands and Cabo Verde, reflecting the ecological importance of reef systems in these southern archipelagos (Biscoito et al. 2018; Freitas, Mendes, et al. 2019b). Cabo Verde supported particularly specialised tropical reef-associated assemblages, consistent with its proximity to equatorial biogeographic provinces (Briggs and Bowen 2012; Cunha et al. 2017; Koivunen et al. 2025). Conversely, pelagic and epipelagic species predominated in the Azores and Madeira, in line with their more oceanic and reef-poor characteristics (Menezes et al. 2006; Porteiro et al. 1999; Morato et al. 2016).

Integrating functional diversity indices into occurrence models yielded limited explanatory gain. Functional richness (FRic) was statistically significant, but FD-augmented GLMs performed worse than trait-only models, indicating that species-level traits captured the primary functional signal structuring assemblages (Cadotte et al. 2011; Lefcheck and Duffy 2015). Community-level metrics may provide less predictive value because functional space is already well represented by individual traits, or because key functional axes saturate quickly with increasing richness (Micheli and Halpern 2005; Mouillot et al. 2014).

Methodologically, RLQ and Fourth-Corner analyses helped address structural concerns raised by reviewers. Unlike GLMs, which evaluate trait effects independently and may struggle with complex trait–environment relationships (Cushman et al. 2024; Kumar et al. 2021), RLQ and Fourth-Corner jointly assess the multivariate structure linking species composition (L), environmental context (R) and species traits (Q) (Bowen et al. 2013; Dray et al. 2013; Dray and Dufour 2007). The significant global RLQ result indicates strong co-structure among these three components (Bosch et al. 2022; Beukhof et al. 2019), with the dominant RLQ axis explaining 91.7% of the projected inertia. This axis reflects the broad biogeographic gradient captured in our GLMs and GLMMs, particularly the influence of body size and habitat affinity. In contrast, the Fourth-Corner analysis revealed no individually significant trait–environment associations after Holm correction (Braga et al. 2018). This suggests that although global co-structure is strong, no single trait–environment pairing dominates once species turnover and multiple comparisons are considered. This interpretation also agrees with the modest explanatory power of the GLMs, reinforcing the importance of avoiding over-interpretation of isolated pairwise effects.

Patterns in climatic affinities also reflect processes operating across multiple spatial and historical scales. The predominance of temperate and boreal-affinity species in the Azores corresponds to their position at the northern fringe of the subtropical North Atlantic (Amorim et al. 2017). Conversely, Cabo Verde hosted primarily tropical species, consistent with the influence of warm West African currents and proximity to equatorial biogeographic regions (Cunha et al. 2017; Freitas et al. 2019a; Burgoa et al. 2021). Madeira and the Canary Islands displayed intermediate profiles, reinforcing their transitional roles (Almada et al. 2013; Freitas et al. 2019a).

Several limitations should be acknowledged. Presence—absence data may underestimate the influence of abundance and biomass on trait structure and ecosystem functioning (Friedlander and DeMartini 2002; Aguilar-Medrano and Calderon-Aguilera 2016; Nash et al. 2017). Incomplete trait information—particularly for trophic attributes—may also have restricted model performance (Carrington et al. 2021; da Silva et al. 2019). We did not apply null models to isolate the effects of species richness on functional diversity (Mason et al. 2005; Swenson 2011), nor did we incorporate phylogenetic relationships despite known phylogenetic signals in fish traits (Pavoine et al. 2009; Morlon 2014; Lin and Costello 2023). Future research should integrate phylogenetic, environmental and historical information to more fully explore the eco-evolutionary processes underlying trait–environment patterns (Almada et al. 2013; Bowen et al. 2013; Freitas et al. 2019a).

From a conservation perspective, the dominance of reef-associated species in the southern archipelagos raises concerns, as these assemblages may be particularly vulnerable to warming waters, habitat degradation and other climate-related stressors (Alvarez-Filip et al. 2015; Doney et al. 2012). In contrast, the high functional richness and dispersion observed in the Azores highlight their importance as reservoirs of functional strategies and potential climate refugia (Aparecido et al. 2023; Campanyà-Llovet et al. 2023). Madeira's transitional role reinforces its significance for maintaining connectivity and functional continuity across the region (Freitas et al. 2019a).

5 | Conclusion

This study demonstrates that body size and habitat affinity are the principal determinants of coastal fish assemblage structure across the Macaronesian archipelagos (Bosch et al. 2022; Letessier et al. 2024). While functional diversity indices provide valuable ecological context (Aparecido et al. 2023; Nemani et al. 2024), they did not substantially improve occurrence models beyond trait-based predictors. Together, these findings offer a robust framework for understanding and forecasting how functional structure in oceanic island systems may respond to environmental change (Bosch et al. 2022; Barneche and Morais 2023; Waechter et al. 2022).

Author Contributions

L.M.D.B.: Designed the study and developed the methodological framework, collected and assembled the data, compiled the functional trait database, carried out the analyses and wrote the first draft of the manuscript. A.B.A.: Provided ecological and biogeographical expertise, contributed to the validation of statistical analyses and interpretation of results and participated in manuscript revisions. R.F.: Contributed ecological and biogeographical expertise, participated in the collection

and validation of occurrence data and assisted in manuscript revisions. J.P.B.: Provided the conceptual framework and scientific coordination of the study, contributed to the development of methods and analytical strategy, supervised all stages of the research and critically revised the manuscript. All authors approved the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo DOI: 10.5281/zenodo.17882987 at https://zenodo.org/.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Functional traits and corresponding categories used to classify coastal fish species across the Macaronesia. The table lists all trait groups, abbreviations and definitions. These categories were used in all functional analyses. **Table S2:** Number of taxa recorded in each archipelago and in the full Macaronesian region. Counts are provided for classes, orders, families, genera and species. **Table S3:** Percentage of species belonging to each functional trait category across the four archipelagos. Trait abbreviations follow those defined in Table S1. **Table S4:** Pairwise intersections of functional richness (FRic) between Macaronesian archipelagos. Values indicate the proportion of FRic shared between each pair of regions. **Table S5:** Summary of the GLM relating species occurrences to the five functional diversity indices (FRic, FEve, FDiv, FDis and RaoQ). Estimates, standard errors and significance values are shown. **Table S6:** Functional richness (FRic) values for each archipelago and results of a permutation test assessing whether FRic varies with latitude. No significant latitudinal trend was detected. **Table S7:** Summary of all GLMs fitted to species occurrences using different combinations of functional traits. Model family, AIC, BIC, log-likelihood and McFadden's pseudo-R^2 are reported. **Table S8:** (A) Pairwise comparisons of functional traits based on estimated values and 95% confidence intervals. Lower-triangle cells show *p*-values and letters indicate statistically distinct groups. (B) Pairwise comparisons restricted to size category and milieu. Estimates, confidence intervals and statistical groupings are provided. **Table S9:** Variance Inflation Factors (VIFs) for functional trait predictors included in the best-supported GLMs. All values remained below accepted thresholds for collinearity. **Table S10:** Comparison of performance metrics for GLM and GLMM models. AIC, BIC, log-likelihood and pseudo-R^2 values are presented for each model formulation. **Table S11:** Fixed-effect odds ratios for the extended GLMM. Coefficients, standard errors, significance values and 95% confidence intervals are provided. **Table S12:** Random-effect variances for the extended GLMM. Standard deviations of random intercepts quantify unexplained variation at the site and species levels. **Table S13:** Summary of the extended GLMM, including fixed effects, random effects and model fit statistics. Scaled residuals and correlations among predictors are also shown. **Table S14:** Fixed-effect odds ratios for the minimal GLMM. Estimates, test statistics and confidence intervals are reported for all retained predictors. **Table S15:** Random-effect variances for the minimal GLMM. Variance components reflect species- and site-level effects after model reduction. **Table S16:** Summary of the minimal GLMM, including fixed and random effects. Model fit statistics and standard significance tests are provided. **Table S17:** Results of the fourth-corner analysis testing relationships between traits, environment and species composition. Observed test statistics, standardised values and corrected *p*-values are reported. **Table S18:** Eigenvalues and corresponding proportions of inertia for the first three RLQ axes. These values describe the major gradients in the combined trait–environment–species space. **Table S19:** RLQ species scores for the first two axes. Scores represent the positions of species assemblages from each archipelago in the RLQ space. **Table S20:** RLQ trait scores for the first two axes. Scores indicate how each functional trait contributes to the major RLQ gradients. **Table S21:** RLQ site scores for the first two axes. Values describe the relative placement of archipelagos within the combined environmental and functional trait structure. **Table S22:** Results of the RV permutation tests assessing correlations between environmental, species and trait matrices. Observed RV coefficients and permutation-based *p*-values are shown. **Table S23:** Global RLQ permutation test results for Models 2 and 4. Observed statistics and Monte-Carlo *p*-values evaluate the overall co-structure between matrices. **Figure S1:** Shared vertebrate classes across the four Macaronesian archipelagos. The UpSet plot shows class-level intersections among regions. **Figure S2:** Shared fish orders across the archipelagos. The UpSet plot illustrates overlap and unique orders per region. **Figure S3:** Shared fish families across the archipelagos. Intersections highlight family-level similarity and differentiation. **Figure S4:** Shared fish genera across the archipelagos. The plot visualises genus-level overlap among regions. **Figure S5:** Shared fish species across the archipelagos. Species-level intersections reveal patterns of regional uniqueness and shared diversity. **Figure S6:** Chord diagram showing the distribution of body-size categories across archipelagos. Link widths represent the relative contribution of each category to each region. **Figure S7:** Chord diagram showing the association between size categories and climatic zones. The plot illustrates how thermal regimes relate to body size. **Figure S8:** Chord diagram showing the association between size categories and habitat affinity. Links reflect the distribution of body sizes across habitat types. **Figure S9:** Chord diagram showing the association between size categories and milieu. Vertical and horizontal habitat domains are represented by link widths. **Figure S10:** Chord diagram showing the association between size categories and trophic groups. The diagram illustrates how body size aligns with feeding strategies. **Figure S11:** ROC curve for the best-supported GLM based on AIC. The model shows limited discriminatory power. **Figure S12:** ROC curve for the best-supported GLM based on BIC. Predictive performance is similar to that of the AIC-based model. **Figure S13:** Functional trait space (PCoA) for coastal fish species. Species scores and 68% confidence ellipses illustrate functional structure across archipelagos. **Figure S14:** RLQ ordination showing the joint structure among environmental, species and trait matrices. Axes summarise major multivariate gradients. **Figure S15:** Results of the global RLQ permutation test for Models 2 and 4. Histograms display the distribution of simulated statistics and the observed value. **Figure S16:** RV permutation test assessing the association between environmental variables and species composition. The observed statistic lies outside the null distribution. **Figure S17:** RV permutation test assessing the association between functional traits and species composition. Results indicate significant trait–composition relationships. **Figure S18:** ROC curve for the extended GLMM (GLMM_ext). The model displays strong discrimination with AUC = 0.801. **Figure S19:** ROC curve for the minimal GLMM (GLMM_min). Performance is comparable to the extended model with AUC = 0.801.