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Functional diversity of Mediterranean coastal fishes differs across habitats

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Abstract:	The functional diversity of temperate coastal ecosystems is strongly influenced by environmental variability and habitat characteristics. The specific contribution of different marine habitats to the functional diversity of fish communities remains understudied, particularly in temperate regions such as the Mediterranean Sea. Herein, we use functional diversity indices to examine and compare the functional diversity and traits of fish communities in three major infralittoral Mediterranean habitats, sandy bottoms, rocky bottoms, and Posidonia oceanica meadows. The results revealed significant differences in functional diversity and traits among habitats, with variations in the ecological characteristics of fish communities. Specifically, functional traits such as the minimum depth and habitat preferences exhibited strong associations with particular habitats, influencing the functional structure of fish communities. Environmental factors such as seabed temperature, depth, and chlorophyll concentration significantly influence the functional composition of fish communities, shaping their structure. Moreover, functional diversity is unevenly distributed across habitats, underscoring the significance of sandy bottoms in preserving functional beta diversity—an aspect frequently neglected in conservation strategies. This study offers novel insights valuable for coastal biodiversity management, emphasising the complementary role of habitats in maintaining the ecological functionality of Mediterranean fish communities.

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To the Editor in Chief Professor Giovanni Zurlini and to the Editorial Board of Ecological Indicators,

Dear Editor,

Please consider our manuscript entitled “Functional diversity of Mediterranean coastal fishes differs across habitats” for publication as a Research Paper in Ecological Indicators.

Marine biodiversity loss and the degradation of coastal ecosystems are critical issues that compromise ecosystem functionality and resilience. While traditional taxonomic approaches have provided valuable insights into biodiversity, it is essential to integrate the functional dimension by focusing on the ecological roles of species within ecosystems to develop scientifically rigorous indicators for effective management and conservation. Notably, very few studies address functional traits and their ecological implications in temperate areas. Research filling this gap is therefore both timely and critically needed.

As a case study, we selected the Mediterranean Sea given the basin’s unique ecological characteristics and global importance as a biodiversity hotspot, and, specifically, the coasts of Calabria. The Calabria Region has coastlines extending for almost 800 km, covering a range of different marine habitats located in different subareas (Tyrrhenian Sea, Ionian Sea and Strait of Messina) encompassing two different ecoregions. Therefore, it represents an ideal case study where to investigate biodiversity and its variability related to potential environmental drivers.
Using underwater visual census with strip transects, we compiled a very large database about the diversity of coastal fish assemblage in 62 sites (for a total of 496 replicates) across three major coastal habitats—rocky bottoms, sandy bottoms, and *Posidonia oceanica* meadows along approximately 600 km. In addition, we built a database about traits for the 71 species recorded. Building on these data, we computed a robust suite of functional diversity indices and analyzed these with univariate and multivariate analyses (including pRDA and GAMLSS) to quantitatively assess the influence of key environmental variables (e.g., sea bottom temperature, depth, and chlorophyll concentration) on the functional structure of these communities.

Notably, our findings reveal significant habitat-specific differences and unexpectedly highlight the critical role of sandy bottoms in maintaining functional beta diversity. This result provides novel insights relevant to the development of ecological indicators and emphasizes the importance of integrating functional diversity into management strategies for temperate coastal ecosystems.

This study represents a methodological advancement compared to previous studies. For the first time, it expands the analysis to a broad spectrum of coastal

fish species' functional traits, usually studied individually, and evaluates functional variability across different habitat types.

In addition, in line with the journal's focus on methodological advancement and data sharing, we provide the comprehensive dataset of functional traits for the analysed species. This dataset integrates previously fragmented information from the literature, offering a complete and valuable resource for future indicator-based monitoring and management efforts.

We believe our research addresses critical knowledge gaps in temperate fish ecology and presents methodological advancements and applicable insights that will be of broad interest to the readership of Ecological Indicators.

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Sincerely, (on behalf of the co-authors)

Stefania Russo
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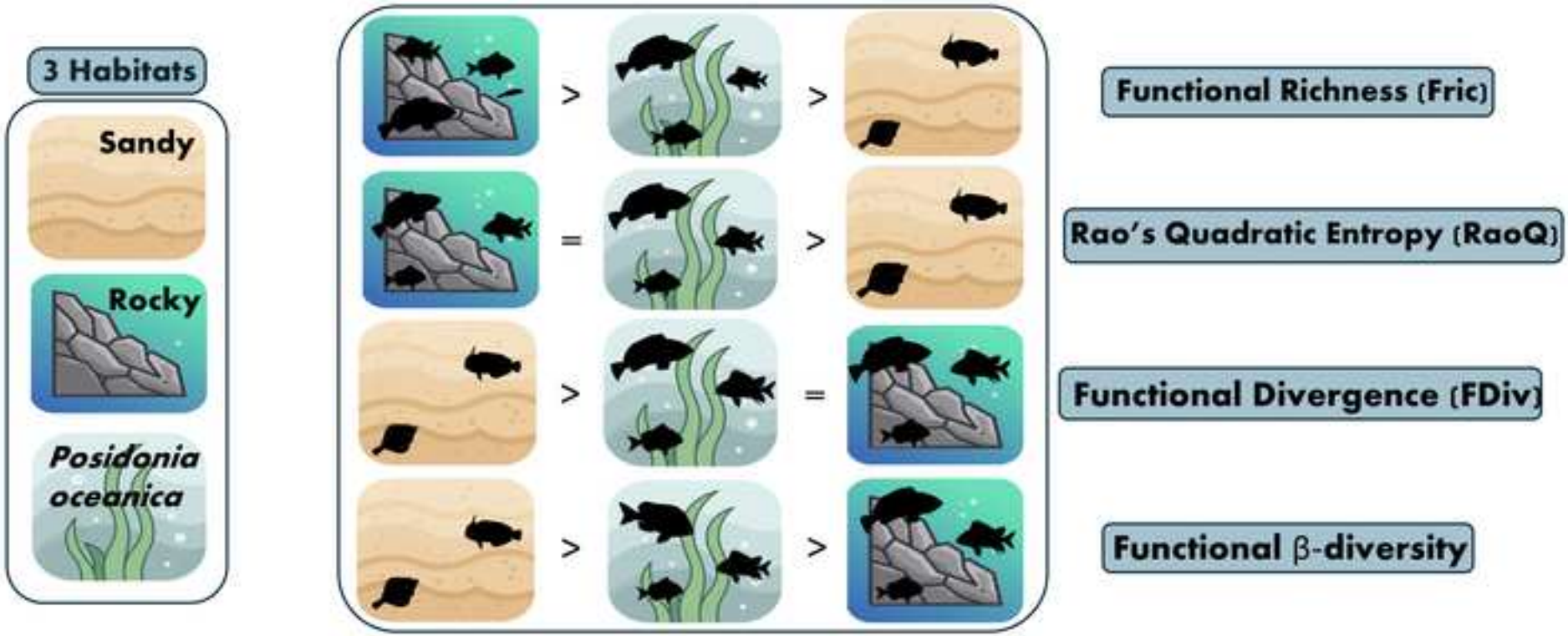
Graphical Abstract(for review)



Highlights:

- Functional and beta diversity of coastal fishes varies significantly among sandy, rocky, and *Posidonia* habitats.
- Community-weighted mean index highlights habitat-driven trait patterns.
- A trait-based approach reveals ecosystem functioning differences.
- Findings enhance understanding of Mediterranean coastal fish ecology.

Functional diversity of Mediterranean coastal fishes differs across habitats

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Abstract

The functional diversity of temperate coastal ecosystems is strongly influenced by environmental variability and habitat characteristics. The specific contribution of different marine habitats to the functional diversity of fish communities remains understudied, particularly in temperate regions such as the Mediterranean Sea. Herein, we use functional diversity indices to examine and compare the functional diversity and traits of fish communities in three major infralittoral Mediterranean habitats, sandy bottoms, rocky bottoms, and *Posidonia oceanica* meadows. The results revealed significant differences in functional diversity and traits among habitats, with variations in the ecological characteristics of fish communities. Specifically, functional traits such as the minimum depth and habitat preferences exhibited strong associations with particular habitats, influencing the functional structure of fish communities. Environmental factors such as seabed temperature, depth, and chlorophyll concentration significantly influence the functional composition of fish communities, shaping their structure. Moreover, functional diversity is unevenly distributed across habitats, underscoring the significance of sandy bottoms in preserving functional beta diversity—an aspect frequently neglected in conservation strategies. This study offers novel insights valuable for coastal biodiversity management, emphasising the complementary role of habitats in maintaining the ecological functionality of Mediterranean fish communities.

Keywords:

Beta diversity; Mediterranean Sea; Community-weighted mean (CWM); Functional diversity; Habitat variability; Temperate coastal fish; Trait-based approach.

1. Introduction

Biodiversity encompasses not only the number of species present within an ecosystem but also the distinct functional roles that each species fulfils (Naeem, 2002). Species contribute uniquely to ecological processes, and ecosystem stability and resilience rely on the diversity of ecological functions rather than solely on taxonomic richness (Hatton et al., 2024; Stuart-Smith et al., 2013). Functional diversity reflects the range of biological characteristics and roles of species in the ecosystem and has emerged as a significant metric for evaluating biodiversity in recent years (McGill et al., 2006; Mouillot et al., 2013a, 2013b; Violle et al., 2007). Functional diversity includes the variations in species' functional traits, which directly influence ecosystem dynamics and the capacity to respond to environmental changes. This perspective emphasises that not only the number but also the identity of the species, through diverse functional roles within a community, plays a key role in determining functional diversity and finally affecting ecosystem resilience (De Bello et al., 2021; Mouillot et al., 2013 b). For this reason, understanding functional diversity is key for formulating effective conservation strategies, as functional traits yield more informative insights into species responses to environmental changes than taxonomic diversity (D'Agata et al., 2014). The functional approach allows for a more nuanced comprehension of ecological functioning, including the analysis of species' roles (Kelley et al., 2018; Lam-Gordillo et al., 2021) and their relationships with environmental factors.

The diversity of marine fishes, encompassing numerous ecological functions, makes them valuable proxies for assessing changes in marine environments (Duffy et al. 2016; Stuart-Smith et al. 2013). The composition and diversity of fish communities within coastal habitats exhibit considerable variability, influenced by a multitude of environmental (e.g. temperature), ecological, and anthropogenic factors (e.g. fishing pressure) (Duffy et al., 2016; Maureaud et al., 2019; Mouillot et al., 2011; O'Hara et al., 2024; Stuart-Smith et al., 2013). In fact, many fish communities have experienced declines in both abundance and diversity over the past few decades in different marine regions, with studies reporting significant reductions in fish populations due to a number of stressors such as overexploitation, habitat destruction and climate change (Edgar et al., 2023).

The loss of species and essential ecological functions due to local and global environmental changes and human activities, can undermine the taxonomic and functional diversity of coastal marine ecosystems, ultimately reducing their resilience and ability to adapt to further disturbances (Albouy et al., 2015a; Keck et al., 2025; Kelley et al., 2018; O'Hara et al., 2023). The notion of "functional erosion" underscores it, describing how alterations in seawater temperature, ocean acidification, and

habitat degradation can modify the functional traits and the response of coastal marine ecosystems (Kelley et al., 2018; Receveur et al., 2024; Teixidó et al., 2024; Villéger et al., 2010).

Diversity also varies among habitats, with the physical structure of habitats significantly influencing resource availability, competitive interactions, and species distributions, leading to habitat-specific compositions and diversity of fish communities, both when considering taxonomics (Cecapolli et al., 2024; Harper et al., 2022; Sgarlatta et al., 2023) and functional aspects (Maciel et al., 2024; Sanabria-Fernandez et al., 2024). To this end, assessing the drivers of biodiversity is key to design evidence-based, sound conservation and management measures in marine ecosystems that preserve marine biodiversity and related functions and services (Miatta et al., 2021).

The Mediterranean Sea is widely recognised as a global hotspot for biodiversity (Coll et al., 2010), hosting more than 700 fishes (Kovačić et al., 2021), with many species playing crucial roles within the ecosystem (Prato et al., 2013). At the same time, the Mediterranean is subjected to considerable pressures, such as climate change, overfishing, and the loss of coastal habitats (Claudet & Fraschetti, 2010; Coll et al., 2010; Hilborn et al., 2020). Mediterranean coastal areas encompass a number of different marine habitats with associated fish assemblages. While several studies have explored the taxonomic diversity across habitats (e.g., Cecapolli et al., 2024; Giakoumi & Kokkoris, 2013; Guidetti, 2000), only a few focused on the functional traits of fish communities (Lattanzi et al., 2024; Papapanagiotou et al., 2020; Tzanatos et al., 2020).

Considering the limited knowledge available, this study aims to assess the functional diversity of coastal fish communities across different coastal habitats, testing the hypothesis that environmental drivers significantly influence the functional diversity patterns and shape the community, considering environmental variability and cumulative human impacts on marine ecosystems. Specifically, the research investigates how functional diversity metrics (e.g., Functional Richness, Evenness, and Divergence, see Tab. S1 sup. mat.) vary among sandy, rocky, and *Posidonia oceanica* habitats, building on evidence that these habitats contribute differently to overall biodiversity (Cecapolli et al., 2024). Additionally, we examine functional beta diversity to understand the extent of functional turnover among these habitats (Villéger et al., 2013).

2. Materials and methods

2.1 Study area and sampling design

Sampling was carried out along the Calabrian coasts (Southern Italy, Central Mediterranean Sea, Fig. 1) between June and July 2022. The Calabria Region has a peninsular shape with coastlines extending for almost 800 km, covering a range of different marine habitats located in different subareas (Tyrrhenian Sea, Ionian Sea and Strait of Messina) encompassing two different ecoregions (Spalding et al., 2007). Therefore, it represents an ideal case study where to investigate biodiversity and its variability related to potential environmental drivers. A set of 62 sites were sampled along the Calabrian coasts (Fig. 1), distributed to include a wide geographic range and capture the environmental variability of the region. This strategy aimed to represent the distributional range of values for a set of potential predictor variables (recorded at the site level) that could affect the biodiversity patterns along the Calabrian coastline.

The sites were selected to maximise habitat variability within a reduced spatial scale. The selection of potential sites was performed using QGIS software (version 3.24.2) with data sourced from the European Nature Information System (EUNIS) database, a comprehensive habitat classification system (http://eunis.eea.europa.eu/habitats.jsp, Montefalcone et al., 2021). The study area was divided into spatial units (i.e., cells) based on a grid with a resolution of ~4 km^2, as this best matched the environmental variables considered in our analysis and was consistent with the spatial division used by the Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu) for environmental data collection. Through this process, each site was associated with a specific habitat type.

2.2 Data collection

Fish diversity data were collected using Underwater Visual Census (UVC) surveys. Sampling operations were conducted at depths ranging from 3 m to 28 m. To maximise consistency in fish identification, the same team of trained scientific divers carried out UVCs at all sites.

Within each of the 62 sites, 8 replicates (from now on referred to as “transects”) were performed, for a total of 496 transects. Out of the total number of sites, 24 were rocky, 23 were sandy, and 15 were *Posidonia oceanica* meadows, with this distribution related to the natural coverage of the habitats. At each site, the actual habitat sampled (rocky, sandy, *Posidonia*) was recorded to confirm the EUNIS prediction via ground-truthing visually. Each site was assigned to the verified habitat category for the following analysis based on the coverage of the dominant habitat. Habitat coverage estimates were conducted visually for each replicate transect and averaged per site. Given the inherent heterogeneous nature of Mediterranean coastal habitats at the sampling scale, around 58% of them included more than one habitat, with the median coverage for the primary habitat being 96.1% and overall limited

coverage of the other habitats. The number of transects per site was adequate to assess taxonomic diversity. Secondary habitats in some sampling sites did not affect overall variability estimates, as described in Cecapolli et al. (2024).

Sampling was carried out along each transect according to the protocol described by Harmelin-Vivien et al. (1985), adopted widely in the Mediterranean (Di Franco et al., 2009; Di Lorenzo et al., 2020; Sala et al., 2012). We used strip transects of 25m×5m, with a total surface of 125 m^2. A trained diver operator using SCUBA equipment swam one way at a constant speed along each transect, covering the transect in approximately 6–8 min. The diver recorded all fish species, estimating the abundance and the size of all fishes encountered. The actual number of fishes encountered was recorded up to 10 individuals, whereas larger groups were recorded using categories of abundance (i.e., 11–30, 31–50, 51–200, 201–500, >500 ind.). Fish size (total length, TL) was recorded within 2 cm size classes for most of the species and within 5 cm size classes for large-sized species (maximum size > 50 cm) such as Epinephelinae (Bortone & Mille, 1999; Edgar et al., 2004; Mallet & Pelletier, 2014). Because of the cryptic nature of some benthic species in the Mediterranean assemblages (e.g., Blenniidae, Gobiidae, Scorpaenidae; Thiriet et al., 2016) on the way back to the starting point of each transect, the operator selectively looked for cryptic fish species under rocks, in crevices and other hidden portions of the sea bottom, to ensure a complete and consistent census of all species. Some individuals could not be identified at species level, so a higher taxonomic level has been adopted (e.g., Atherina sp., Pomatoschistus sp., Mugilidae, Sphyraena sp., Trachurus sp.), while the vast majority of fishes (96.4 %) were identified at the species level. The diver also recorded the habitat coverage (in percentage, as previously described), starting and ending depths, then averaged to obtain a mean depth for each transect.

For all species identified, we combined data from multiple existing databases on Mediterranean coastal fish species to retrieve information on their functional trait composition. Functional traits information was primarily sourced from Albouy et al. (2015b), obtaining a total of 13 functional traits, which we then expanded with additional data extracted from FishBase, implementing the rfishbase package in R (Boettiger et al., 2012), and reaching a total of 16 functional traits. From the obtained species × traits matrix, the remaining NAs were filled using different sources (see Tab. S2 sup. material). Whenever trait data were unavailable for a given species, we assigned a trait value belonging to the nearest congeneric species (Catford et al., 2014; Swenson, 2014).

A comprehensive set of environmental variables potentially influencing coastal fish functional diversity (Cecapolli et al., 2024) (see complete in sup. material, Tab. S3) was retrieved from the

Copernicus Marine Service (CMEMS) online database. Further, a compound index obtained through a cumulative impact model representing human impacts on marine ecosystems in the Mediterranean Sea (Micheli et al., 2013) was also used as a possible driver shaping fish functional diversity. All the variable values were associated with each site. Data exhibiting temporal variability were managed by averaging the annual values of the year preceding the sampling.

2.3 Data analyses

Fish biomass (i.e., wet weight, in g) was estimated from size data using length-weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible from FishBase (Froese & Pauly, 2023). Biomass per species and total biomass for each transect (i.e., community biomass, Cardinale et al. 2013) were then computed.

For each transect, we calculated the community-weighted mean (CWM), i.e., the average of species traits in a community weighted by the species biomass (De Bello et al., 2021). CWM per transect was computed as follows:

$$CWM = \sum_{i=1}^{N} b_i x_i / B$$

With *N*, the number of species found in the transect, b_i is the biomass of species *i* in that community, x_i is the trait value of species *i*, and B is the total biomass of the transect. All biomasses have been log-transformed prior analyses to reduce the effect of very abundant species.

A partial redundancy analysis (pRDA) was performed to investigate the relationship between the CWM and environmental variables. pRDA was preferred over standard RDA to account for the conditional effect of spatial random factors (i.e., site) on the response variables.

The pRDA model was developed in three stages. First, to exclude multicollinearity issues, Variance Inflation Factor (VIF) was calculated for all environmental variables before running the pRDA (Zuur et al., 2010). A stepwise procedure was applied to sequentially remove highly collinear environmental variables with VIF > 2 from the analysis (Table 2 sup. materials). Then, all the remaining environmental variables were included as predictors, with "site" as a conditioning factor. Finally, a forward stepwise selection procedure, based on the Akaike Information Criterion (AIC) and F-tests for model comparison, was applied to identify the key environmental variables that best explained the observed variation in the CWM.

After performing the pRDA, only the traits significantly and strongly correlated with the axis were included in the final ordination plot. By focusing on these, the plot shows the functional characteristics crucial in shaping community composition while minimising the visual impact of less relevant traits.

An ANOVA-like permutation test (based on 999 permutations) was implemented to assess the overall statistical significance of constraints (i.e., the predictors included) and the statistical significance of RDA axes.

A multiple comparison test was performed using RDA to assess differences in species' functional traits among the three habitats. The analysis uses the Bray-Curtis distance to compare the CWM structure across habitat types. The RDA model was specified with habitat as the explanatory variable and was constrained to maximise the variation in functional trait composition explained by habitat differences (Legendre & Gallagher, 2001).

A Similarity Percentage (SIMPER) analysis (Clarke, 1993) was conducted to identify which functional traits contributed most to habitat differentiation. The SIMPER analysis allowed to assess the percentage contribution of individual traits to the overall dissimilarity between pairs of habitats, helping to pinpoint key traits that distinguish the functional composition across habitat types.

To quantify the diversity of functional traits within the fish assemblages sampled, we calculated a set of functional diversity indices using the *FD* package (Laliberté et al., 2014) in R (for a summary of the indices used, see the supplementary materials Tab. 1). The set of functional diversity indices computed included Functional Richness (FRic), Functional Dispersion (FDis), Functional Divergence (FDiv), Functional Evenness (FEve), and Rao's Quadratic Entropy (RaoQ). These indices capture complementary aspects of functional diversity, offering insights into how species differ in ecological roles and functions. This is essential for understanding ecosystem processes, community assembly, and responses to environmental changes (Mouillot et al., 2013 b).

More specifically, FRic measures the extent of functional trait space occupied by the community, considering only species presence and not their abundance; higher values of FRic correspond to greater functional diversity. FDis quantifies species spread across the functional trait space, weighted by relative species biomass; higher FDis values represent more evenly dispersed species relative to the centre of the functional space. FDiv reflects the proportion of the total biomass that corresponds to species with the most extreme functional traits (i.e., far from the centre of the functional space filled by the community); a high FDiv value indicates a greater degree of specialisation. FEve indicates how evenly species abundance is distributed along the functional trait gradient and can also be defined as the regularity of the distribution and relative abundance of species in functional space for a given community. Finally, RaoQ combines species composition with functional or phylogenetic differences to capture trait diversity and biomass information, with high values indicating functionally diverse communities. Functional diversity was calculated using a species-by-trait matrix

and species biomass data. Log-transformed biomass data were used to reduce the influence of dominant species and ensure that all traits and abundance values were comparably scaled.

To examine the relationships between habitat type, environmental variables and each diversity index (FRic, FDis, FDiv, FEve, and RaoQ), we applied Generalized Additive Models for Location, Scale and Shape (GAMLSS) (Rigby & Stasinopoulos, 2005). Each diversity index was modelled as a function of habitat type and environmental predictors that were not highly correlated, as identified by VIF analysis. The environmental variables included in the models were habitat type, sea bottom temperature (SBT), sea surface temperature (SST), chlorophyll concentration (chl), cumulative human impact, and mean depth. We specified a random effect for "site" to account for spatial dependency across sampling sites.

The most parsimonious model was selected using the stepGAIC function, which iteratively evaluates models based on the Akaike Information Criterion (AIC). This process allowed for the identification of the optimal combination of environmental variables and the explanation of variations in each diversity index (Akaike, 1974). This modelling approach enabled us to assess the influence of both habitat type and environmental variables on functional diversity, accounting for site-level variability and potential non-linear effects of environmental factors. A likelihood ratio test (LRT) was also implemented for each GAMLSS model to calculate the overall P-value of the habitat factor.

To identify habitats with distinct functional trait compositions and assess their contribution to overall functional beta diversity, we computed the Local Contribution to Beta Functional Diversity (LCBD) for each transect. This analysis involved normalising the Community Weighted Mean (CWM) matrix, standardising trait values on a scale from 0 to 1, and calculating functional beta diversity using the "Hellinger" distance metric. Statistical significance was evaluated through 999 permutations. The resulting LCBD values quantify the uniqueness of each habitat functional traits, highlighting areas that contribute disproportionately to beta diversity across the examined habitats.

To assess the influence of environmental gradients and habitat types on LCBD, we implemented a GAMLSS with a Gamma distribution due to the strictly positive and heavily skewed LCBD data. The model, also in this case, included habitat type (factor), SBT, SST, chl, cumulative human impact, and mean depth as predictors. The site was included as a random effect.

The most parsimonious model was selected using the stepGAIC function based on the AIC. The R^2 was calculated using the Cragg-Uhler metric. The influence of habitat was evaluated through an LRT by comparing the full model to a reduced model, excluding the habitat factor.

All the analyses were performed using R and facilitated by RStudio (R Core Team, 2023; RStudio Team, 2023).

3. Results

A total of 72 fish taxa were observed across the 62 sites considered. "Catadromous" is the only trait unique to a habitat (rocky), while all the others differ among habitats in their occurrence (see Fig. S1).

The selected pRDA model explained approximately 22% of the total variability in the CWM. The first two pRDA axes (RDA1 and RDA2) captured 19% and 3.0%, respectively.

Among the functional traits analysed, minimum depth ($R^2 = 0.91$), benthic and demersal traits ($R^2 = 0.87$ for both) and maximum depth and no reversal ($R^2 = 0.67$ and $R^2 = 0.66$ respectively) exhibited the highest R^2 and were statistically significant (p-value = 0.001).

The minimum depth, benthic and demersal traits exhibited strong correlations with specific environmental variables. Sea bottom temperature, mean depth, and chlorophyll concentration contribute substantially to the CWM compositional variation (Fig. 2).

The sandy habitat was associated with the minimum depth and demersal traits. The rocky habitat was found to be linked to benthic species. The relatively tight clustering of points within the rocky habitat polygon may indicate more uniform environmental conditions across those sites. In contrast, the *Posidonia* habitat showed weaker associations with environmental variables and functional traits, overlapping with rocky sites.

The ANOVA-like Permutation Tests for terms and axis confirmed that habitat, bottom temperature, mean depth, and chlorophyll significantly influenced species functional traits, with habitat showing the strongest effect (F-value: 59.51, $p < 0.001$, R^2: 18%), followed by bottom temperature (F-value: 14.91, $p < 0.001$, R^2: 2%) and mean depth (F-value: 9.88, $p < 0.001$, R^2: 1%). Chlorophyll also had a significant but weaker influence (F-value: 3.94, $p = 0.008$, R^2: 0.006%). Sea surface temperature did not significantly influence functional traits (F-value: 1.77, $p = 0.121$). Finally, the permutation test for axes indicated that only RDA1 and RDA2 explained a significant portion of the variance in the model (RDA1: Variance = 0.395, F-value = 121.88; RDA2: Variance = 0.063, F-value = 19.50; $p < 0.001$ for both axes). Significant differences among the three habitats were detected ($p < 0.001$ for all comparisons) in terms of functional trait compositions. SIMPER showed the functional traits that contributed most significantly to habitat differentiation. The minimum and maximum depth traits contributed the most to the differences between the sandy habitat and the other habitat types. The two

traits that had the greatest impact in differentiating rocky and *Posidonia* habitats were the protogynous trait and minimum and maximum depth (Sup. materials. Tab. 3).

GAMLSS model for FRic ($R^2 = 0.72$; see Supplementary Material Fig. S2 for model diagnostics, including residual plots for all six GAMLSS models) showed significant differences among habitat types (likelihood ratio test $p < 0.001$). Specifically, rocky habitat displayed significantly higher FRic than sandy one (Fig. 3). Also SST ($t = 4.6$, $p < 0.001$), chlorophyll concentration ($t = 1.9$, $p > 0.05$), and cumulative impact ($t = -4.7$, $p < 0.001$), significantly improved the model fit (Fig. 3 for plot habitat and other statistically significant predictors).

GAMLSS for FDis ($R^2 = 0.70$) indicated no significant effects from the predictor variables included in the model. The intercept was significant ($p < 0.001$), providing a constant baseline for FDis across the dataset. Also, for FEve ($R^2 = 0.73$), the predictors had no significant effects.

The model for FDiv ($R^2 = 0.68$) showed a marked difference between the sandy habitat and the other two, even if the overall habitat effect was marginally non-significant ($p = 0.06$). Among the environmental covariates, chlorophyll concentration had a significant negative effect on FDiv ($t = -2.26$, $p < 0.05$), while mean depth had a significant positive effect ($t = 3.2$, $p = 0.001$) (Fig. 4).

The RaoQ model ($R^2 = 0.65$) results revealed the significant effect of habitat types ($p = 0.01$). Sandy habitats exhibited the lowest level of functional diversity among the habitats examined. A negative correlation was observed between sea bottom temperature (SBT) and RaoQ ($t = -3.1$, $p < 0.01$; Fig. 5), sites with higher SBT tended to exhibit lower RaoQ values. In contrast, cooler environments promoted a wider array of functional traits within the community.

The GAMLSS model for LCBD ($R^2 = 0.64$) highlighted significant variability among habitat types ($p = 0.03$; Fig. 6). Sandy habitats exhibited the highest LCBD values, followed by *Posidonia* and rocky habitats.

4. Discussion

This study investigated the functional diversity of coastal fish communities across the three most common habitats—sandy, rocky, and *Posidonia oceanica* meadows— found in the infralittoral zone of the Mediterranean Sea. By integrating functional traits, functional diversity indices, and beta diversity analysis, we identified significant differences and patterns among these habitats, especially when comparing sandy habitats to the other two habitat types. The findings presented herein underscore the pivotal role of habitat types in shaping the functional structure of coastal fish communities, confirming previous evidence about environmental gradients influencing community functional structure through trait filtering (e.g., Mouillot et al., 2013 b; Stuart-Smith et al., 2013; De Bello et al., 2013).

Recent studies indicated that shifts in coral composition, rather than coral cover, are strongly correlated with changes in reef fish diversity patterns (González-Barrios et al., 2025). This highlights how modifications in habitat structure, rather than just habitat availability, can drive functional reorganization in marine communities. Similar dynamics have been observed in Mediterranean coastal ecosystems, where changes in habitat complexity and composition influence the fish species diversity (Garcia-Charton et al. 2004) and as demonstrated herein the functional diversity of fish assemblages.

Rocky habitats in the Mediterranean Sea are highly diverse and complex (Bevilacqua et al. 2021), and are often characterised by high fish species diversity (Guidetti 2000; Giakoumi and Kokkoris 2013; Cecapolli et al. 2024). This study demonstrated that these habitats also support higher functional richness (FRic) compared to sandy and seagrass habitats, suggesting that their natural higher structural complexity could provide a wider array of ecological niches, fostering a broader range of functional adaptations. Furthermore, elevated RaoQ values in the rocky habitat underpin significant functional diversity and dissimilarity within this habitat type, reinforcing the importance of rocky bottoms in maintaining ecosystem functionality. These findings are consistent with prior research conducted across diverse marine ecosystems on species richness, including tropical seascapes, thereby highlighting the significance of structural complexity among and within habitat types (Hall & Kingsford, 2021). Relations between within-habitat complexity and fish functional diversity have also been observed in temperate regions regarding diverse macroalgal habitats, influencing fish functional diversity, redundancy, and richness across temperate marine realms (Sanabria-Fernández et al., 2024). A recent study on functional diversity (Sgarlatta et al., 2023) related to habitat complexity recommended considering small-scale spatial drivers when aiming to

understand how habitat characteristics link with functional diversity. Our study aimed at comparing different habitat types, and did not consider within-habitat complexity. Future research could implement small-scale analyses within habitats, following approaches similar to Fernández et al. (2024), to verify intra-habitat differences. These findings highlight the complex relationships between habitat characteristics and fish communities, emphasising the importance of considering multiple aspects of habitat complexity in ecological studies and conservation efforts.

In contrast, the wide distribution of sandy replicates in the pRDA analysis suggested that this habitat exhibits high environmental and trait variability. Sandy bottoms also displayed the highest functional divergence (FDiv) values, with fish communities occupying more specialised niches and species performing distinct roles within the community. While sandy areas are commonly regarded as homogeneous, they are, in fact, subject to continuous physical changes related to hydrodynamic patterns, which contribute to increased habitat complexity and heterogeneity with an impact on diversity indices (Júnior et al., 2023). The results of beta diversity analyses further indicated that the sandy habitat type contributes disproportionately to functional turnover, hosting distinct species compositions that vary significantly from those found in rocky bottoms and *Posidonia oceanica* meadows. Despite the lower richness, sandy bottoms significantly contribute to overall coastal fish β-diversity, in line with the significant contribution previously highlighted in terms of taxonomic diversity (Cecapolli et al., 2024). This turnover is a key component of beta diversity, as Whitaker (1960) defined, and reflects species replacement driven by environmental filtering, spatial and historical factors, and constraints. Such dynamics provide valuable insights into community assembly processes applied to taxonomic and functional diversity (Hernández-Mendoza et al., 2024).

The pRDA results highlight the key role of habitat type and environmental factors, such as bottom temperature, mean depth, and chlorophyll concentration, in shaping variations in species' functional traits, with the most pronounced differences emerged between rocky and sandy habitats. The absence of significant effects from the predictor variables on the functional dispersion (FDis) indicates that the species in all habitats were evenly distributed within the functional space and that the functional composition within each habitat is similar in terms of species differences. The stability of the functional evenness (FEve) values across different environmental gradients suggests a consistent functional distribution of species across habitats. This uniformity implies that each habitat supports a relatively even distribution of functional traits among the fish community, regardless of the environmental factors.

The negative relationship between sea bottom temperature (SBT) and RaoQ highlights the influence of temperature in driving functional similarity among species in warmer environments (Herrera et al., 2023). Long-term data analysis of other systems reveals that climate change has altered fish trait compositions, resulting in an overall decrease in functional diversity over time (Souza et al., 2023).

The functional traits composition of fish communities in *Posidonia* meadows presented similarities to those of the rocky habitat. Previous studies investigating the taxonomic fish diversity among habitats also found overlap in the species composition of these two habitats (Guidetti 2000; Giakoumi and Kokkoris 2013; Cecapolli et al. 2024). This study suggests that species composition in *Posidonia* sites is shaped by factors not fully captured by the RDA axes, indicating that this seagrass habitat may host communities with weaker environmental constraints. The fish composition in *Posidonia* meadows resulted in more generalist communities and were not strongly associated with specific environmental gradients. This finding suggests that this habitat may provide a refuge for species less constrained by environmental conditions, in addition to being nursery grounds for many fish species (Díaz-Gil et al. 2017).

Overall, our analyses highlight that habitat type plays a crucial role in shaping the functional diversity of fish communities, with significant implications for managing and conserving marine biodiversity. Currently, conservation efforts have been targeting mainly rocky habitats and *Posidonia* meadows as these are considered "richer habitats", hosting species of conservation interest (e.g., *Pinna nobilis* and *Lithophaga lithophaga*) and supporting important ecosystem services (Giakoumi et al., 2013; Cecapolli et al., 2024). Conversely, the ecological relevance of Mediterranean sandy habitats and the need to protect them has been overlooked. The unique contribution to taxonomic (Cecapolli et al. 2024) and functional (as highlighted in the present study) beta diversity of sandy habitats warrants further attention to safeguarding their role in maintaining regional biodiversity. Our findings also underscore the importance of incorporating functional diversity metrics into biodiversity assessments and conservation plans to capture ecological dynamics more comprehensively than taxonomic richness alone. This is particularly significant in regions like the Eastern Mediterranean Sea, where non-native species have occupied the ecological niches of native species whose populations have locally declined due to climate warming. In such regions, the conservation focus should be the maintenance of functional diversity rather than native species diversity (Giakoumi et al., 2016; Rilov et al., 2020), with the aim of ensuring ecosystem functioning and productivity (Wan et al., 2024).

By addressing habitat-specific patterns and environmental influences on functional diversity, our work provides a foundation for targeted conservation strategies that can help mitigate anthropogenic

411 pressures and climate change impacts, focusing on habitat type. Future research could build on this
412 effort by exploring the temporal dynamics of functional diversity and expanding the geographic scope
413 to better understand ecosystem resilience under changing environmental conditions. As highlighted
414 in the Global Biodiversity Framework, future conservation efforts should not only target species and
415 habitat protection but ensure that ecosystem functions are maintained and restored, accounting for
416 ecological integrity and connectivity.

417

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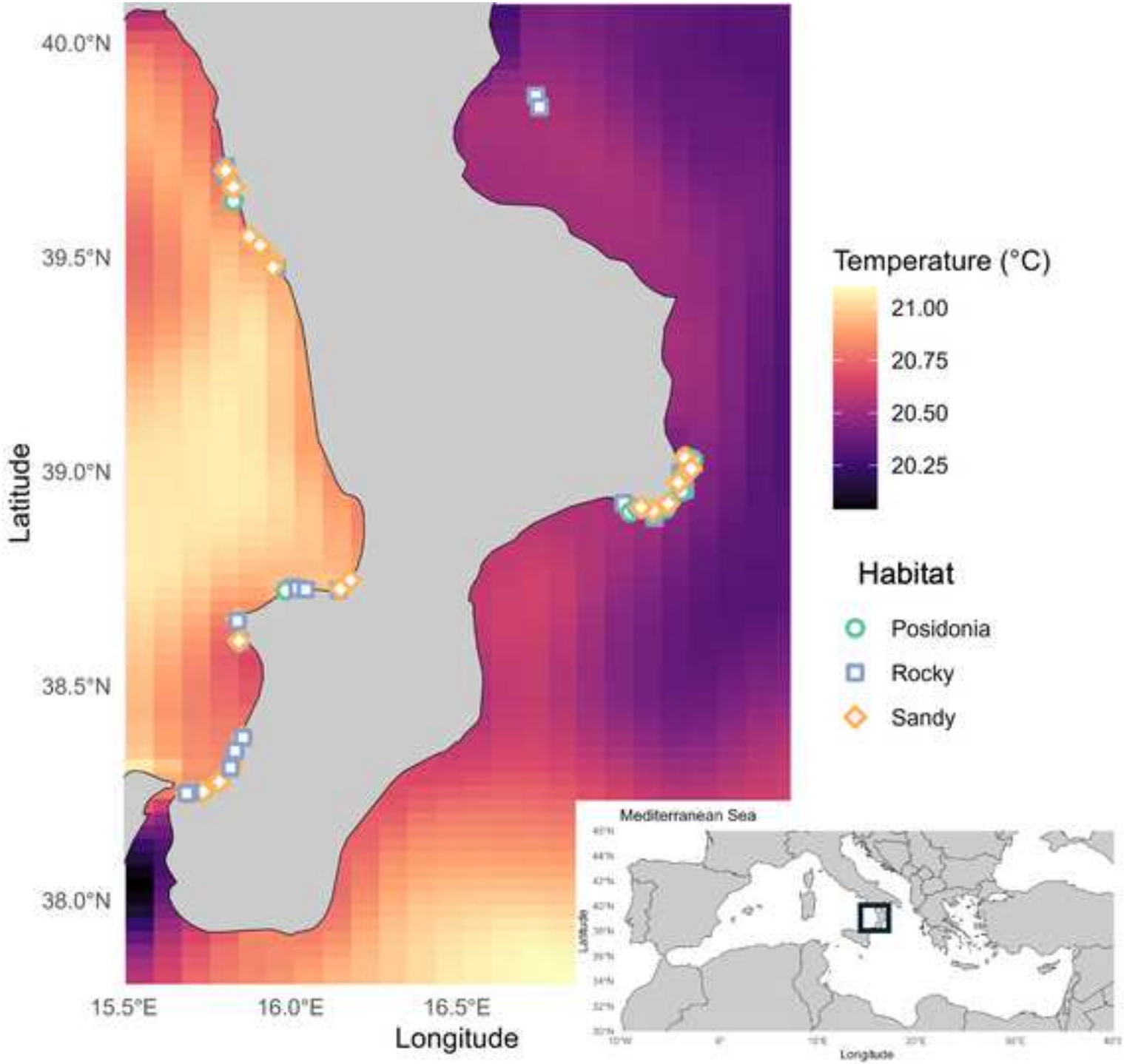

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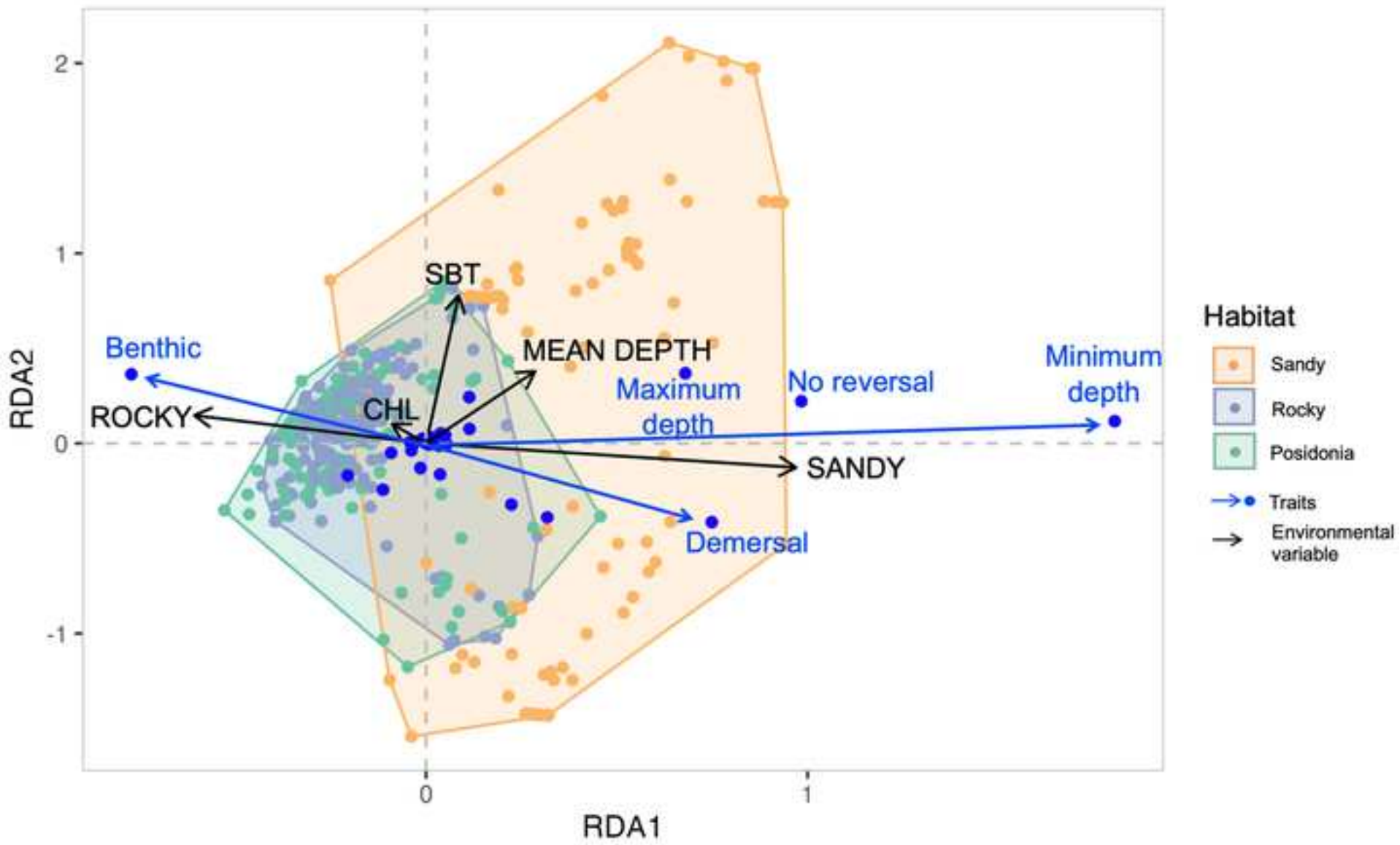

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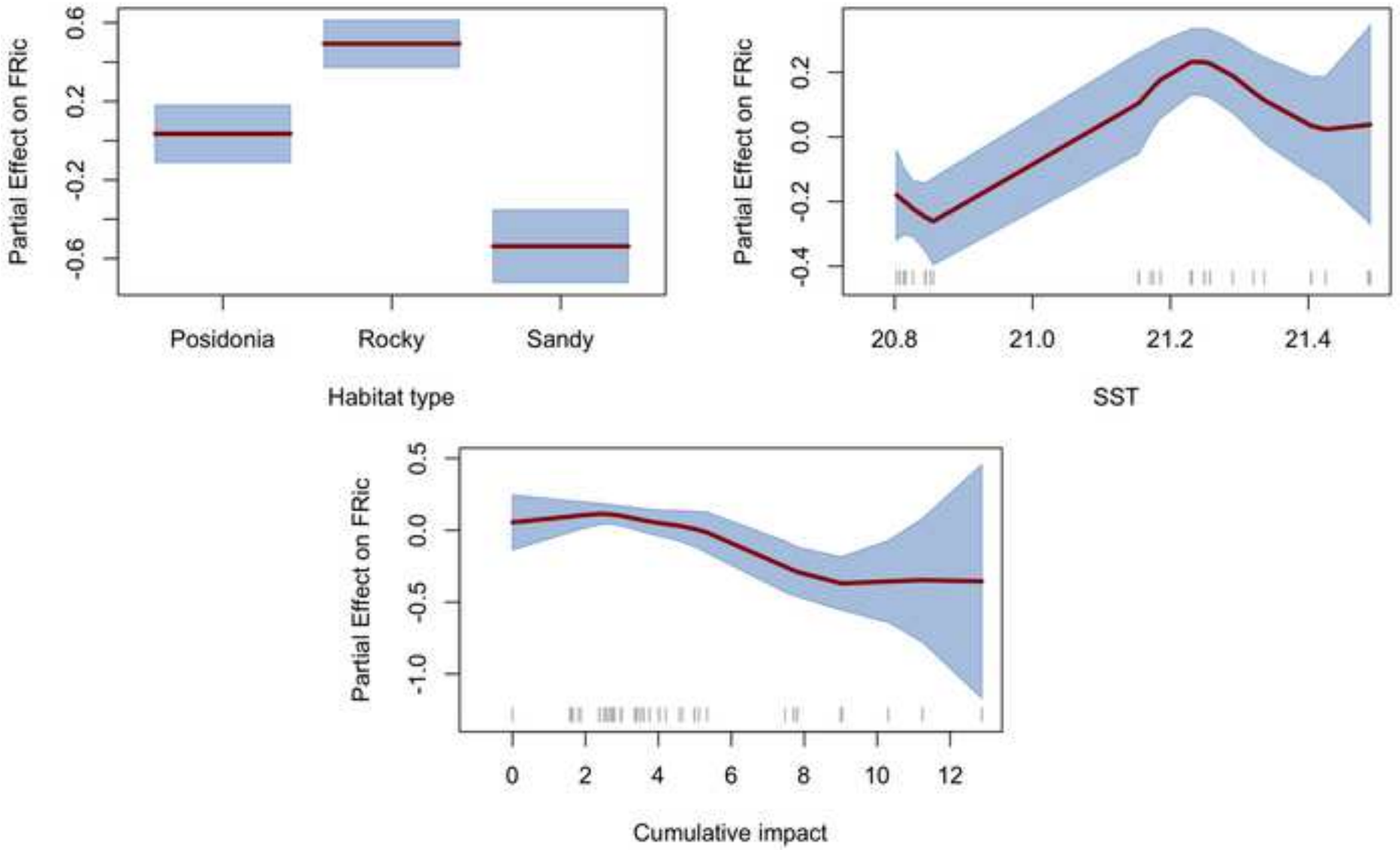

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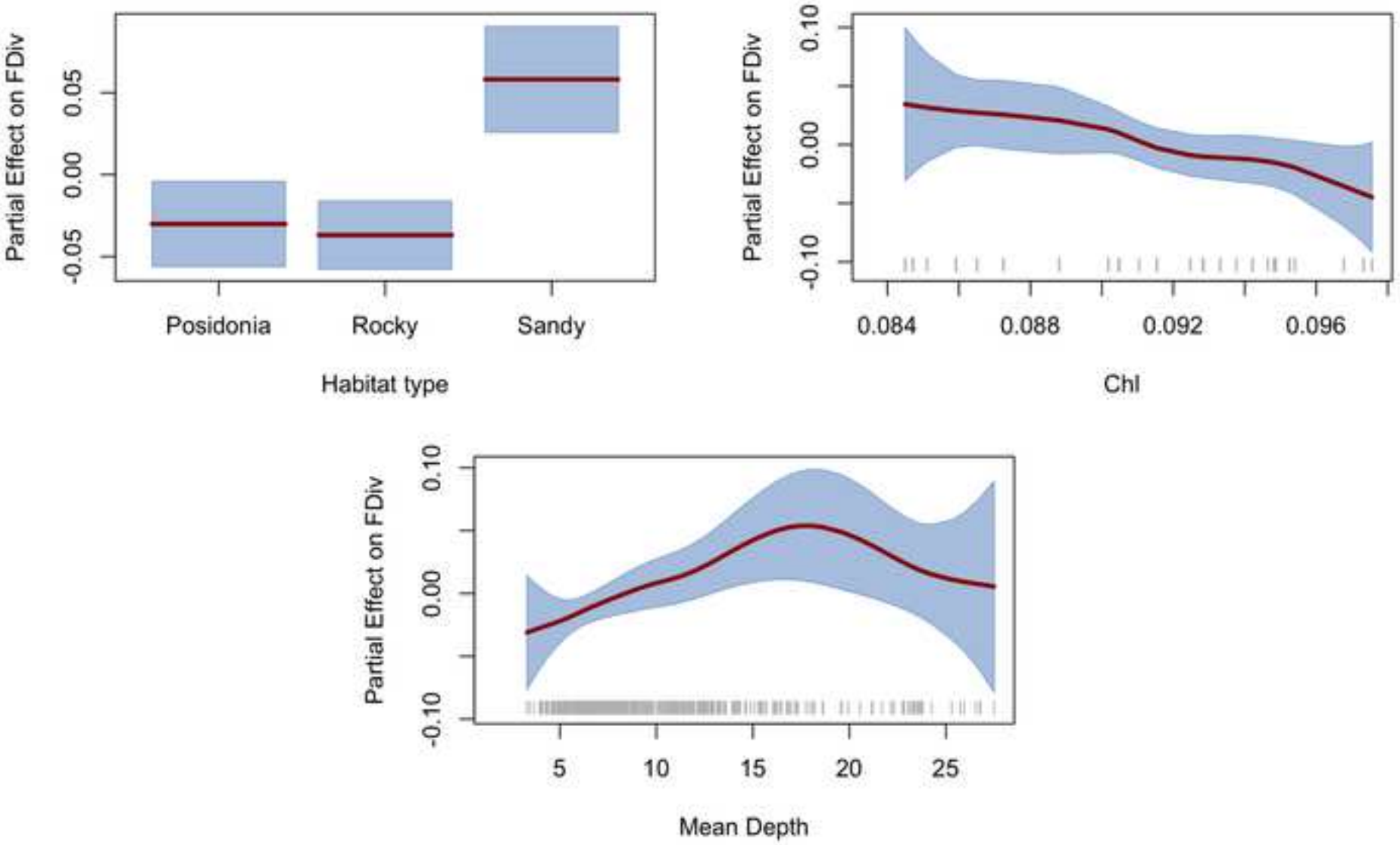

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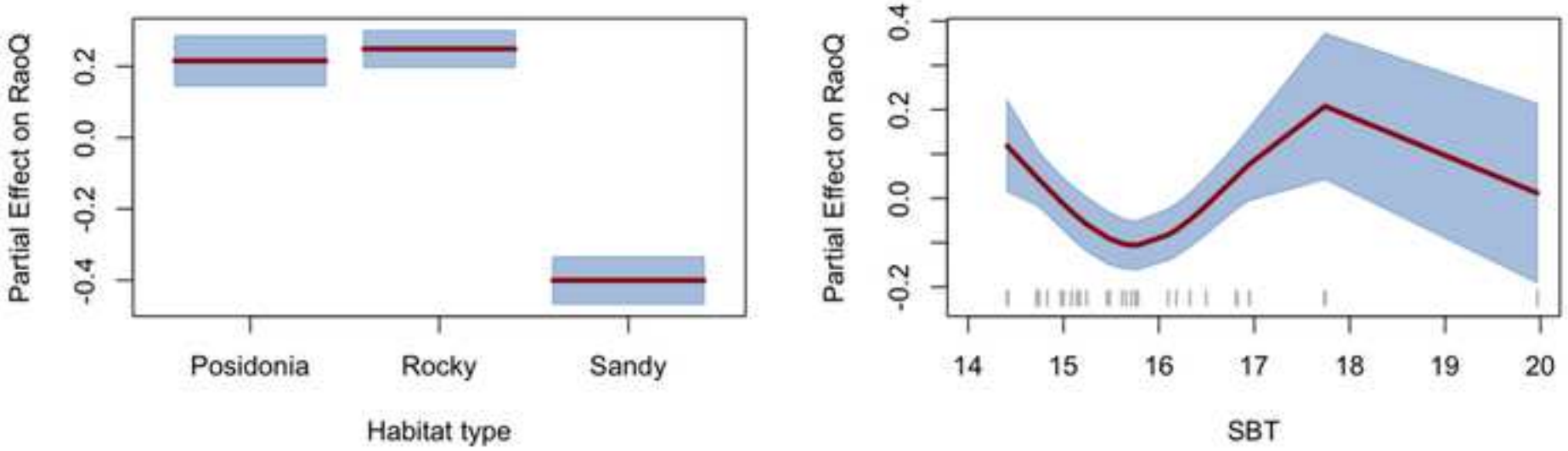

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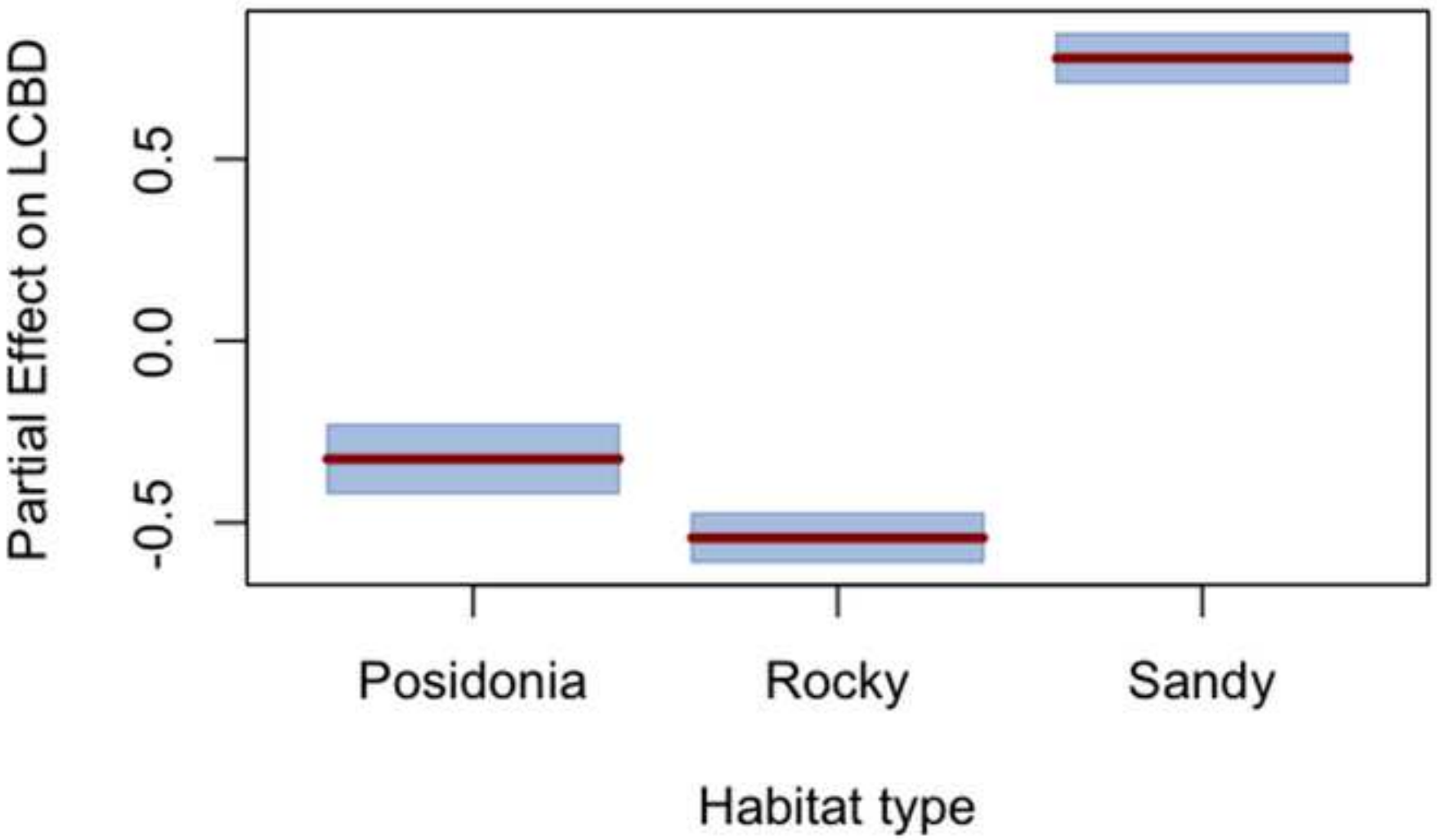


Figure captions

Figure 1- Sampling sites location for each habitat and Mean annual sea surface temperature of the study area.

Figure 2 - pRDA plot showing the relationship between functional traits and environmental variables in the three habitats.

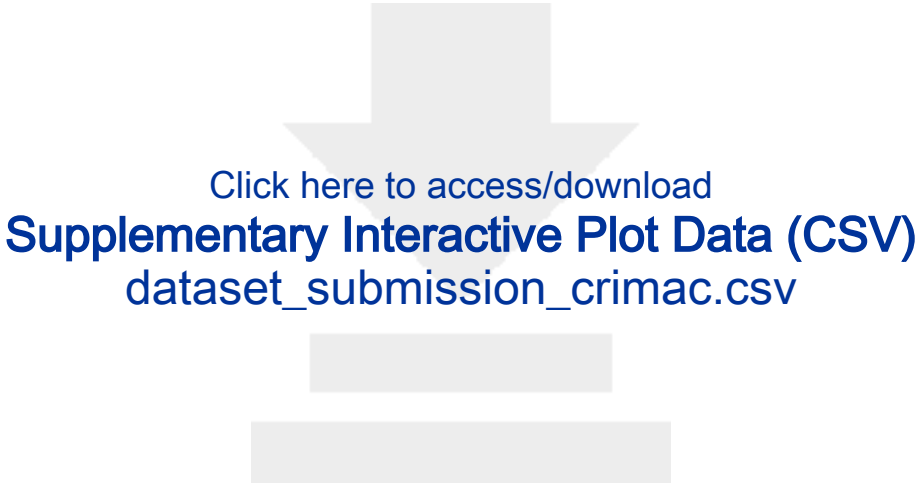
Figure 3 - Partial effects of the significant explanatory variables on functional richness (FRic). The plot displays the effects of habitat type, sea surface temperature (SST) and cumulative impact on FRic values.

Figure 4 - Partial effects of the significant explanatory variables on functional divergence (FDiv). The plot displays the effects of habitat type, chlorophyll concentration (chl) and mean depth on FDiv values.

Figure 5 - Partial effects of the explanatory variables on Rao's Quadratic Entropy (RaoQ). The plot illustrates the effects of habitat type and sea bottom temperature (SBT) on RaoQ values.

Figure 6 - LCBD partial effect for each habitat type.

species-by-traits matrix



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Supplementary Interactive Plot Data (CSV)

dataset_submission_crimac.csv

Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: