

Original Articles

Sandy bottoms play a key role in shaping coastal fish functional β -diversity in the Mediterranean Sea

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ARTICLE INFO

Keywords:

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

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 comparatively understudied in temperate regions such as the Mediterranean Sea. Herein, we use a multivariate approach along with functional diversity indices to examine and compare the functional diversity and traits of fish communities in the three most abundant 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 vertical distribution exhibited strong associations with particular habitats, influencing the functional structure of fish communities. Environmental drivers such as seabed temperature, depth, and chlorophyll concentration significantly influenced the functional composition of fish communities, as identified by partial redundancy analysis (pRDA). Among these, seabed temperature and depth explained the largest share of variation. No difference in functional redundancy was detected among habitats. Functional diversity is unevenly distributed across habitats, underscoring the significance of sandy bottoms in preserving functional beta diversity—an aspect often underrepresented in current 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.

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 the functional structure and resilience of ecosystems in recent years (McGill et al., 2006; Mouillot et al., 2013a,b; Violle et al., 2007). Functional diversity includes the variations in species' functional traits, which directly influence ecosystem dynamics and determine the capacity of communities to respond to both environmental variability and anthropogenic pressures. This perspective emphasises that the diversity of functional roles within a community is key to determining functional structure and supporting ecosystem resilience (De Bello et al., 2021; Mouillot et al.,

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<https://doi.org/10.1016/j.ecolind.2025.114226>

Received 1 April 2025; Received in revised form 11 September 2025; Accepted 16 September 2025

Available online 15 October 2025

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2013b). Reflecting this shift, international policy frameworks—including the EU Marine Strategy Framework Directive (2008/56/EC) (European Commission, 2008) and the Convention on Biological Diversity (including the Kunming-Montreal Global Biodiversity Framework), are increasingly recognizing the value of trait-based indicators to guide assessments of ecosystem status and conservation progress. For this reason, understanding functional diversity is key for formulating effective conservation strategies, as it allows inference about ecosystem properties such as resilience and stability (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 functional diversity of marine fishes, encompassing numerous ecological roles, makes them valuable proxies for assessing marine ecosystem changes (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 (e.g. predator-prey interactions), 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 multiple stressors including overexploitation, habitat destruction and climate change (Edgar et al., 2023). These losses may compromise the ecological functions, ultimately affecting the functional diversity and stability of marine ecosystems, reducing their resilience and ability to adapt to disturbances (Albouy et al., 2015a; Keck et al., 2025; Kelley et al., 2018; O'Hara et al., 2023). The notion of “functional erosion” underscores this process, describing how alterations in seawater temperature, ocean acidification, and habitat degradation can modify the functional traits and responses of coastal marine ecosystems, removing species with specialised trait combinations and leading to functional homogenisation and reduced redundancy within communities (Kelley et al., 2018; Receveur et al., 2024; Teixidó et al., 2024; Villéger et al., 2010).

Functional and taxonomic diversity also varies among habitats, with the physical structure of habitats shaping both the taxonomic and the functional-trait structure of fish communities. Numerous studies have documented habitat-specific changes in species composition (Cecapolli et al., 2024; Harper et al., 2022; Sgarlatta et al., 2023), while a few and more recent works have revealed parallel differences in functional aspects (Maciel et al., 2024; Sanabria-Fernández et al., 2024). To this end, assessing the drivers of biodiversity is key to designing 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 fish species (Kovacic et al., 2021), with many functional 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 and 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 and Kokkoris, 2013; Guidetti, 2000), only a few focused on the functional traits of Mediterranean fish communities (Lattanzi et al., 2024; Papapanagiotou et al., 2020; Tzanos et al., 2020). Existing work has either focused on single habitats, such as seagrass meadows (Lattanzi et al., 2024), or on region-specific modelling (Papapanagiotou et al., 2020) and trait cataloguing to support monitoring (Tzanos et al., 2020). A field-based, multi-habitat comparison of functional diversity across habitats at a regional scale is still lacking. Such a trait-based lens is particularly pertinent in the

Mediterranean Sea, a region with relatively detailed taxonomic inventories but still limited insight into how functional attributes underpin ecosystem functioning.

In light of this gap, our study assesses 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 multivariate traits diversity, and a set of complementary univariate functional diversity metrics (e.g., Functional Richness, Evenness, Divergence and Redundancy) vary among sandy, rocky, and *Posidonia oceanica* habitats, building on evidence that these habitats contribute differently to overall biodiversity (Cecapolli et al., 2024). Among the mosaic of shallow-water habitats that typify Mediterranean coasts, we focused on these habitats, due to their dominance in the infralittoral and occurrence from the western to the eastern basin (Bevilacqua et al., 2021; Furlani et al., 2014; Panayiotis et al., 2020). We also account for the potential effect of a set of environmental and anthropic variables (e.g. temperature, salinity, human pressures, among others) that could affect functional patterns. Finally, we assess the functional beta diversity to quantify turnover and identify the relative contribution of each habitat to regional-scale functional variation (Villéger et al., 2013).

2. Materials and methods

2.1. Study area and sampling design

We carried out sampling along the Calabrian coasts (Southern Italy, Central Mediterranean Sea, Fig. 1) between June and July 2022. This region represents an ideal case study for exploring biodiversity and its responses to environmental drivers. Its coastline extends for almost 800 km, encompassing habitat heterogeneity and spanning two distinct marine ecoregions: the Western Mediterranean and the Ionian Sea (Spalding et al., 2007), thus allowing generalization beyond the local scale.

We sampled 62 sites (Fig. 1), covering a wide geographic range to capture the environmental variability. 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.

We selected the sites to maximise habitat variability within a reduced spatial scale. We used QGIS software (version 3.24.2 QGIS.org, 2022) to select potential sites with data sourced from the European Nature Information System (EUNIS) database, a comprehensive habitat classification system (<https://eunis.eea.europa.eu/habitats.jsp>, Montefalcone et al., 2021). From the habitat maps with a resolution of approximately 100 m, we divided the study area into spatial units (i.e., cells) based on a grid with a resolution of $\sim 4 \text{ km}^2$, 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, <https://marine.copernicus.eu>) for environmental data collection. Through this process, we associated each site with a specific habitat type. We selected maximum one site per habitat within each spatial unit, in order to maximize spatial distribution and variability in associated environmental variables.

2.2. Data collection

We collected fish-diversity data using Underwater Visual Census (UVC) surveys with strip transects of $25 \text{ m} \times 5 \text{ m}$ (125 m^2), following the protocol described by Harmelin-Vivien et al. (1985), widely adopted in the Mediterranean (Di Franco et al., 2009; Di Lorenzo et al., 2020; Sahyoun et al., 2013; Sala et al., 2012). Scientific divers 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

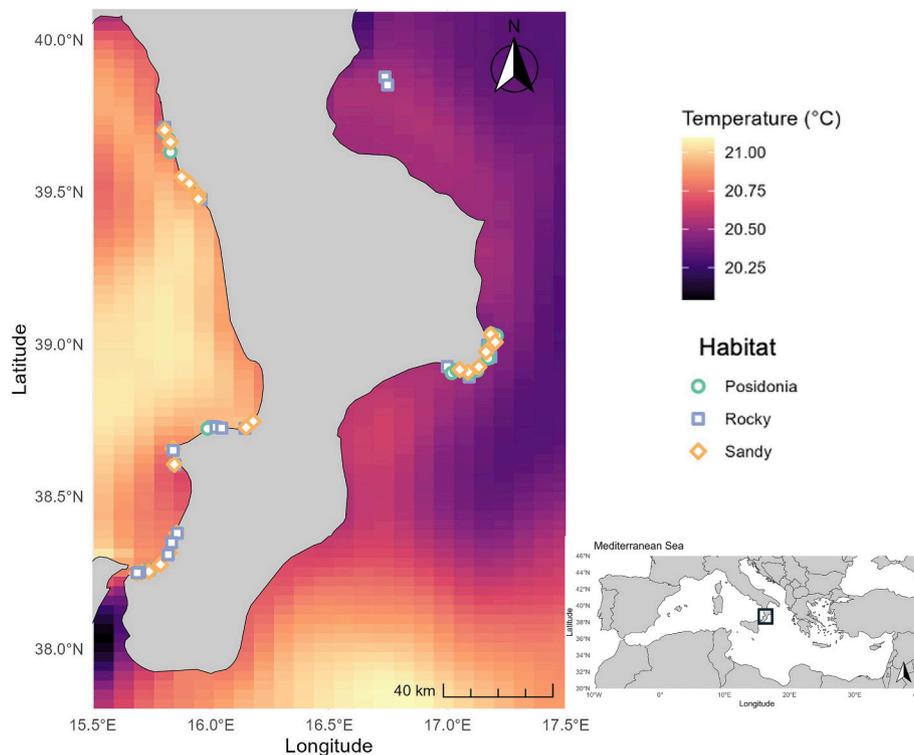


Fig. 1. Sampling sites location for each habitat and Mean annual Sea surface temperature of the study area.

the abundance and the size of all fishes encountered. We recorded the exact number of fishes encountered up to 10 individuals, while when over 10 we recorded the groups using categories of abundance (i.e., 11–30, 31–50, 51–200, 201–500, >500 ind.). We recorded fish size (total length, TL) 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 and Mille, 1999; Edgar et al., 2004; Mallet and 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. This additional effort helped reduce trait-based sampling bias, particularly for benthic-associated traits. Some individuals could not be identified at the species level, so we adopted a higher taxonomic level (e.g., *Atherina* sp., *Pomatoschistus* sp., Mugilidae, *Sphyræna* sp., *Trachurus* sp.), while the vast majority of fishes (96.4 %) were identified at the species level. We subsequently converted all size classes to biomass using the same midpoint-based procedure described in the Data Analyses section, ensuring equal treatment in biomass estimation. The divers also recorded the habitat coverage (in percentage, as previously described), starting and ending depths, then averaged to obtain a mean depth for each transect. Sampling was conducted at depths ranging from 3 m to 28 m, and the recorded depth variation was included as an environmental predictor in subsequent analyses (see details below). To maximise consistency in fish identification and size estimate, the same team of trained and intercalibrated scientific divers conducted all surveys.

Within each of the 62 sites, we performed 8 replicate transects (from now on referred to as transects), 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, we recorded the actual habitat sampled (rocky, sandy, *Posidonia*) to confirm the EUNIS prediction via ground-truthing visually. We assigned each site to the verified habitat category for the following analysis based on the coverage of the

dominant habitat. We visually estimated habitat coverage 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.

For all species identified, we combined data from multiple existing databases on Mediterranean coastal fish species to retrieve information on their functional trait composition. We primarily sourced functional-trait information 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. For categorical traits, each ordered level represents a distinct functional group. From the obtained species \times traits matrix, we filled the remaining NAs using different sources (see Table S1 sup. material for sources and full coding scheme). 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). The full traits dataset (functional trait values per species) is provided as Supplementary File S1 (Excel format). To explore the relationships between functional traits, we computed pair-wise Spearman correlations with *rcorr()* (package *Hmisc*), retaining the associated p-values to assess significance (summary in Fig. S1). We selected a comprehensive set of environmental variables (mean depth, Sea surface temperature, Sea bottom temperature, Oxygen, chlorophyll, pH, Sea surface salinity, Zooplankton, Phytoplankton) potentially influencing fish assemblages as suggested by studies in the Mediterranean and from other areas (Cecapoli et al., 2024; Di Lorenzo et al., 2022; Edgar et al., 2014; see complete in sup. material, Table S2). We retrieved these variables from the Copernicus Marine Service (CMEMS) online database. Further, we used a compound index developed by Micheli et al. (2013), obtained through a cumulative impact model representing human impacts on marine ecosystems in the Mediterranean Sea, which integrates 22 anthropogenic drivers (e.g., trawling, coastal population density, hypoxia, among others), and was used as a possible driver shaping fish functional diversity. We used these

variables to control for all related sources of variability and estimate the genuine effect of habitat on functional diversity. We associated all the variable values with each site. We averaged temporally variable data from the year preceding the sampling.

2.3. Data analyses

We estimated fish biomass (i.e., wet weight, in g) from size data using length-weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible from FishBase (Froese and Pauly, 2024). We obtained coefficients referred to individuals identified at higher taxonomic levels using the mean of the coefficients for all congeneric species available in literature. Then we computed biomass per species and total biomass for each transect (i.e., community biomass, Cardinale et al., 2013).

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). We computed CWM per transect 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 log-transformed biomass of the transect. We log-transformed all biomasses before analyses to reduce the effect of very abundant species.

We performed a partial redundancy analysis (pRDA) to investigate the effect of habitats on trait composition and the relationship between the CWM and environmental variables (using the *vegan* package from Oksanen et al., 2022). This analysis provides an integrated view of how the entire traits composition responds to habitat identity and environmental gradients. We selected pRDA over standard RDA to account for the conditional effect of spatial random factors (i.e., site) on the response variables.

We developed the pRDA model in three stages. First, to exclude multicollinearity issues, we calculated Variance Inflation Factor (VIF) for all environmental variables before running the pRDA (Zuur et al., 2010). We applied a stepwise procedure to sequentially remove highly collinear predictor variables with VIF >2 from the analysis (Table S2, sup. materials), starting from the initial set of variables. Then, we included all the remaining variables (6 out of 11) as predictors, with “site” as a conditioning factor. The variables retained are habitat type, Sea bottom temperature (SBT, °C), Sea surface temperature (SST, °C), chlorophyll concentration (chl, mg m⁻³), cumulative human impact (dimensionless index), and mean depth (m). We selected these predictors because they capture key ecological constraints on coastal fish assemblages like thermal niches, chlorophyll concentration as proxy for primary production, human impact for anthropogenic stressors and depth as filtering along the infralittoral gradient (Maureaud et al., 2019; Guidetti, 2000; Cecapoli et al., 2024).

Finally, we applied a forward stepwise selection procedure, based on the Akaike Information Criterion (AIC) and F-tests for model comparison, to identify the key variables that best explained the observed variation in the CWM.

We conducted Moran’s I test (Moran, 1950) on the pRDA residuals aggregated by site, to verify the assumption of spatial independence in the residuals. We performed the test using k-nearest neighbour spatial weights ($k = 4$) to define the spatial neighbourhood structure among sampling sites, implemented using the *spdep* package (Bivand and Wong, 2018) in R. Moran’s I values close to zero and non-significant p-values (all $p > 0.05$) confirmed the absence of spatial autocorrelation in the model residuals.

We then implemented an ANOVA-like permutation test (based on 4999 permutations) to assess the overall statistical significance of constraints (i.e., the predictors included) and the statistical significance of pRDA axes.

We performed a multiple comparison test using RDA to assess differences in species’ functional traits among the three habitats. The analysis uses the Bray-Curtis dissimilarity to compare the CWM structure, calculated on biomass, across habitat types. We specified the RDA model with habitat as the explanatory variable, and we constrained it to maximise the variation in functional trait composition explained by habitat differences (Legendre and Gallagher, 2001).

We conducted a Similarity Percentage (SIMPER) analysis (Clarke, 1993) to identify which functional traits contributed most to habitat differentiation. Given that SIMPER can be sensitive to outliers and biased towards dominant traits, we performed the analysis on a CWM matrix based on log-transformed biomass data in order to mitigate these issues. The SIMPER analysis allowed us 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 (see Table S3 sup. Mat) using the *FD* package (Laliberté et al., 2014) in R. Following the framework of Mouillot et al. (2013b), we supplied normalized trait values and log-transformed biomass data to the ‘dbFD’ function, which constructs the functional trait space via Principal Coordinates Analysis. We constructed the Gower’s distance matrix using the ‘dbFD’ function, as our study examined not only continuous variables but also qualitative functional traits (Karadimou et al., 2016). The ‘dbFD’ function then returned Functional Richness (FRic), Functional Dispersion (FDis), Functional Divergence (FDiv), Functional Evenness (FEve), and Rao’s Quadratic Entropy (RaoQ). We also quantified functional redundancy (FRed) using the ‘uniqueness’ function (Ricotta et al., 2016). We computed Functional redundancy as $R = 1 - U$ ($U =$ uniqueness), which represents the overlap of traits among species in the community, a direct proxy for response diversity and potential resilience. 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., 2013b; Villéger et al., 2008).

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. We calculated functional diversity using a species-by-trait matrix and species biomass data. We used log-transformed biomass data to reduce the influence of dominant species and ensure that all traits and abundance values were comparably scaled. We also examined Spearman correlations between functional diversity indices to assess the degree of independence between different aspects of functional space and facilitate ecological interpretation of the results. We calculated pair-wise rank correlations with the base-R function `cor()` using method = “spearman” (R Core Team, 2023) and visualised with `ggcorr()` in the *GGally* package (Schloerke et al., 2021). Spearman correlations among the functional-diversity indices revealed a few highly correlated pairs (Fig. S2); All indices were nonetheless retained because each captures a distinct facet of functional space and helps to interpret the patterns highlighted in the

results.

To examine the relationships between habitat type, environmental variables and each diversity index (FRic, FDis, FDiv, FEve, RaoQ, and FRed), we applied Generalized Additive Models for Location, Scale and Shape (GAMLSS) (Rigby and Stasinopoulos, 2005). This univariate step complements the pRDA by pinpointing which facets of functional space drive the multivariate patterns identified in the previous section. Partial RDA on CWM, provides an integrated view of how the entire trait composition responds to habitat identity and environmental gradients. Univariate GAMLSS on six functional-diversity indices supply synthetic, facet-specific measures that are widely adopted to summarise richness, evenness, divergence, dispersion and redundancy of trait space (Mouillot et al., 2013b; Villéger et al., 2008).

We modelled each diversity index as a function of habitat type and environmental predictors, using the same set used for pRDA after VIF inspection. The models included habitat type as a categorical fixed factor, alongside continuous predictors.

We selected the most parsimonious model using the stepGAIC function, which iteratively evaluates models based on the Akaike Information Criterion (AIC). This process allowed us to identify the optimal combination of environmental variables and explain the variations in each functional 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. We also implemented a likelihood ratio test (LRT) 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. We evaluated statistical significance through 4999 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. We included site as a random effect.

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

We evaluated model diagnostics for all seven GAMLSS fits by inspecting residual distributions and diagnostic plots (see Supplementary Fig. S3 for residual and Q-Q plots). We did not further standardise or normalise the predictors selected via VIF.

Prior to all the analyses, we checked sample size adequacy (in our case the minimum number of UVC transects to be performed at each habitat) for properly discriminating habitats. Specifically, we implemented the package SSP (simulation-based sampling protocol) in R (Guerra-Castro et al., 2021), a suite of functions that uses the dissimilarity-based multivariate standard error (Anderson and Santana-Garcon, 2015) to evaluate the adequacy of different sampling efforts for testing hypotheses. SSP returns a range of sampling sizes for which sampling effort is considered 'suboptimal' and 'optimal'. In order to be as conservative as possible, we pooled all sites of a given habitat together, therefore not partitioning spatial variability. MultSE showed that a minimum of 6 (for *Posidonia* and Rocky) and 7 (for Sandy) transects were an 'optimal' sample size per habitat (Figs. S4–S6), numbers lower than the sample size we adopted at each site (and therefore much lower of the overall number of replicates performed at each habitat).

To assess the potential effect of the presence of secondary habitats in a site on the overall within-habitat dissimilarity, we calculated MultSE on subsets of the entire dataset for each habitat. Specifically, we calculated MultSE using only transects with $\leq 80\%$ of coverage of the main habitats (for *Posidonia* and Rocky), transects with 80–90 % coverage, and transects with coverage $\geq 90\%$ for the main habitats. Results did not indicate substantial differences among the subsets within each habitat, and an absence of clear directionality (Figs. S4–S6), suggesting that no particular differences were associated to the transects with different coverage of the main habitats we sampled. Based on this evidence, all the transects have been used for the analyses. We performed all analyses in R, using RStudio as interface (R Core Team, 2023; RStudio Posit Team, 2023).

3. Results

We analysed 16 functional traits across 72 fish taxa recorded in the 62 sites considered (67 identified to species level, 5 at higher taxonomic ranks). Among them, only the Catadromous trait was exclusive to a single habitat (rocky) due to the presence of Mugilidae that were recorded only on rocky habitat. All the other traits showed varying distributions among habitats (see Fig. S7).

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 (Fig. 2). Among the functional traits analysed (see Suppl. Table S1 for classification and levels), 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 (squared correlation coefficients from envfit of each trait onto the pRDA axes) 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: 14.9, $p < 0.001$, 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, $p = 0.121$). These R^2 values represent adjusted R^2 obtained via variance partitioning using vegan's varpart function. 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, emphasizing dominant contributors and complementing our multivariate pRDA results (see Suppl. Table S4 and Fig. S7). 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 Table S4).

GAMLSS model for FRic ($R^2 = 0.72$; see Supplementary Material Fig. S3 for model diagnostics, including residual plots for all seven

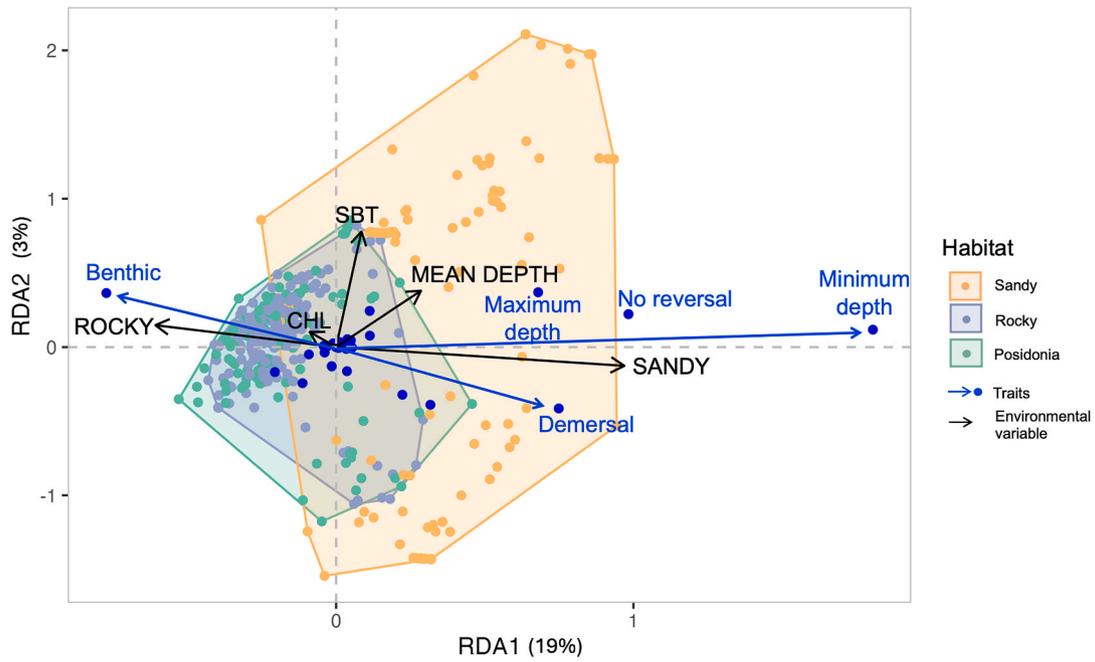


Fig. 2. pRDA plot showing the relationship between functional traits and environmental variables in the three habitats. Each point represents a sampling site, coloured by habitat. Polygons represent the convex hulls encompassing all sites within each habitat. Only environmental variables significantly correlated with the ordination axes ($p < 0.05$) are shown as vectors (in uppercase and black arrows). Functional traits are displayed as centroids (in lowercase and blue dots); labels are shown only for a subset of traits ($r > 0.6$) due to overlap near the origin of the ordination space. Percentages in parentheses indicate the proportion of variance explained by each axis.

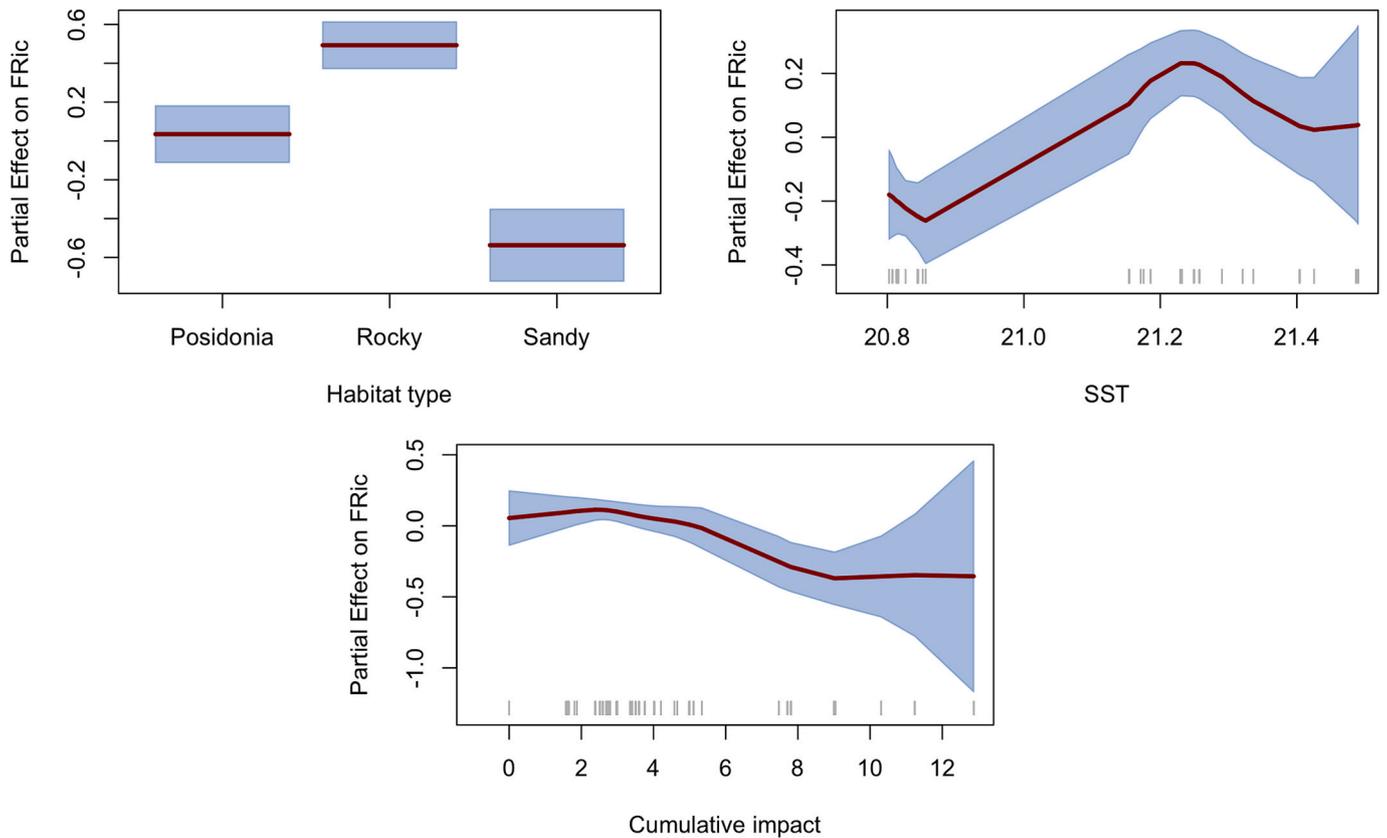


Fig. 3. Partial effects of the significant explanatory variables on functional richness (FRic). The plot displays the effects of habitat type, Sea surface temperature (SST) and cumulative impact on FRic values.

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 ($R^2 = 0.73$) and FRed ($R^2 = 0.20$), 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., De Bello et al., 2013; Mouillot et al., 2013b; Stuart-Smith et al., 2013). Importantly, this study is the first, to the best of our knowledge, to demonstrate that sandy habitats contribute disproportionately to functional beta diversity in Mediterranean infralittoral ecosystems.

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 (García-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 (Cecapoli et al., 2024; Giakoumi and Kokkoris, 2013; Guidetti, 2000). This study demonstrated that these habitats also support higher functional richness (FRic) compared to sandy and sea-grass 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.

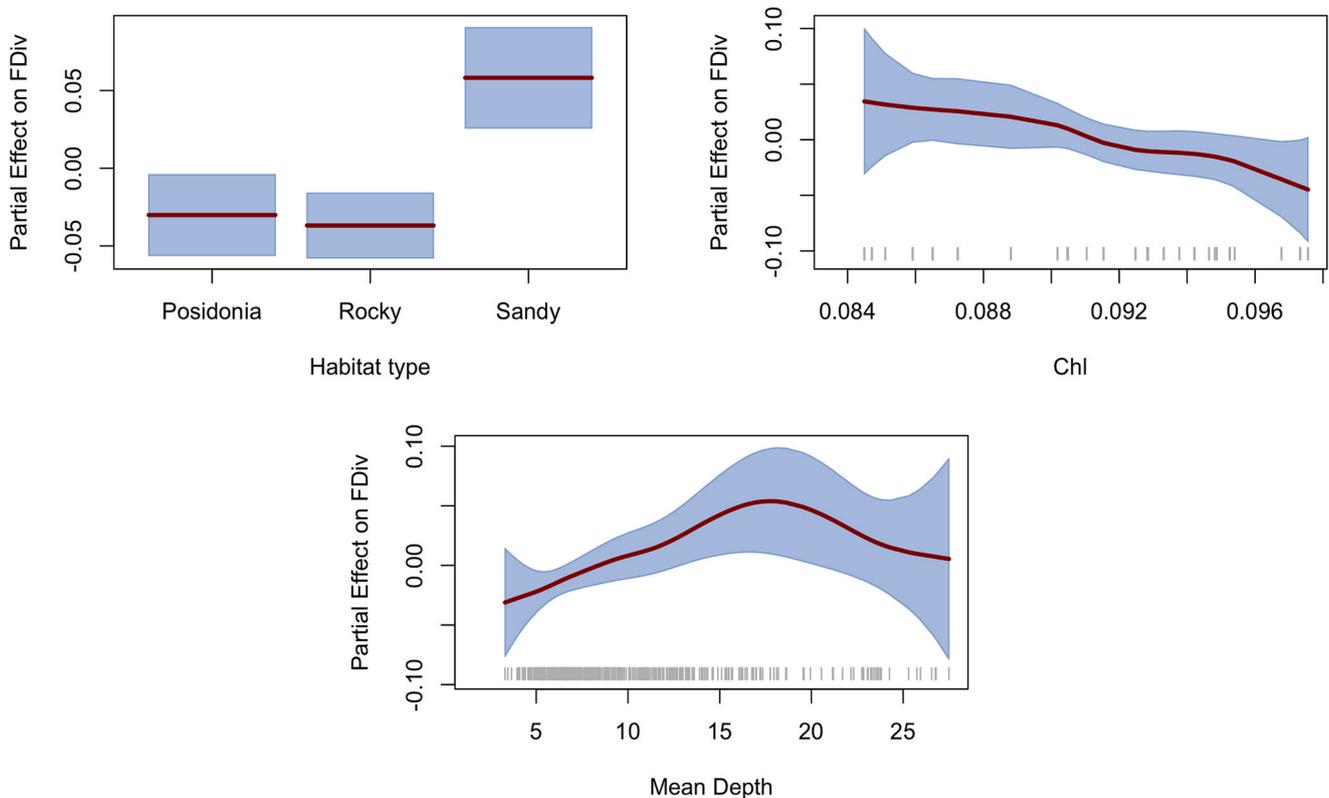


Fig. 4. Partial effects of the significant explanatory variables on functional divergence (FDiv). The plot displays the effects of habitat type, chlorophyll concentration (chl) and mean depth on FDiv values.

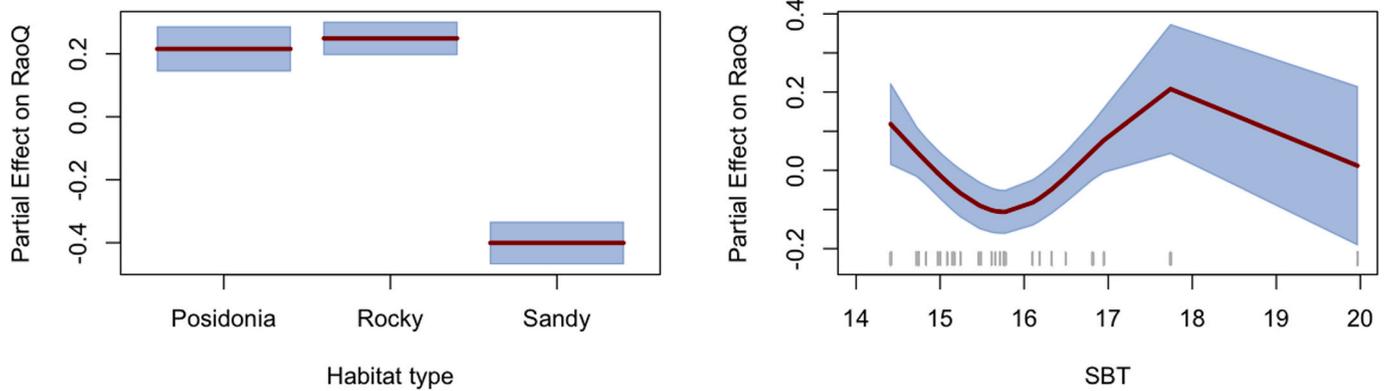


Fig. 5. Partial effects of the explanatory variables on Rao's Quadratic Entropy (RaoQ). The plot illustrates the effects of habitat type and sea bottom temperature (SBT) on RaoQ values.

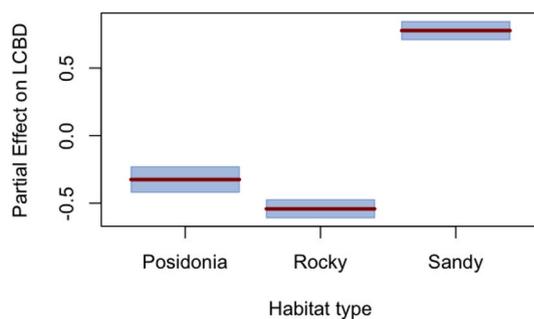


Fig. 6. LCBD partial effect for each habitat type.

In contrast, functional redundancy (FRed) did not show significant variation among habitats. This suggests that high functional diversity observed in rocky areas does not necessarily correspond to higher redundancy but rather reflects a broader range of distinct functional strategies with limited trait overlap. 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 and 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. Work in various systems has shown that habitat structure strongly influences fish population and functional diversity (Cheminée et al., 2017; Sanabria-Fernández et al., 2024). Examining intra-habitat heterogeneity and linking specific structural features to functional outcomes thus remains a pressing research need (Helder et al., 2022). These considerations 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. Future research should quantify microhabitat features (e.g., crevice density, substrate relief) through fine-scale surveys and assess their effect in structuring functional diversity.

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. Although often

perceived as homogeneous, sandy areas are subjected 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). Similar evidence comes from near-shore sandy ecosystems in the south-western Atlantic, where wave energy and productivity were shown to drive both taxonomic and functional diversity of fish assemblages (Shah Esmaeili et al., 2022). The results of beta diversity analyses further indicated that 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 their 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 Whittaker (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). This suggests that conservation strategies focusing only on structurally complex habitats may overlook essential functional variation provided by dynamic sandy systems.

The pRDA results highlight the dominant role of habitat type in shaping functional trait variations, with the most pronounced differences emerging between rocky and sandy habitats. Among the continuous environmental variables, sea bottom temperature was the most influential one, followed by mean depth and chlorophyll concentration. 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. FRed also showed no statistically significant response to any predictors, including the habitat type. This suggests that, across the infralittoral mosaic we surveyed, fish assemblages share a comparable "buffer" of ecological backup everywhere. However, recent evidence from freshwater systems indicates that high FRed alone may not be sufficient to prevent functional diversity declines (de Sá Ferreira Lima et al., 2025).

The negative relationship between 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). This trend suggests that climate warming could

reduce functional trait variance in coastal systems, potentially compromising ecosystem resilience.

The functional traits composition of fish communities in *Posidonia* meadows presented similarities to those of the rocky habitat. This overlap may reflect ecological similarities in structural complexity that support comparable trait assemblages. Previous studies investigating the taxonomic composition of fish communities also found overlap between these two habitats (Cecapoli et al., 2024; Giakoumi and Kokkoris, 2013; Guidetti, 2000), which is consistent with the functional similarity observed in our analysis. This study suggests that trait composition in *Posidonia* sites is shaped by factors not fully captured by the RDA axes, indicating that this seagrass habitat may host communities less structured by measured environmental gradients. 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).

While our study provides novel insights into how habitat types and environmental variables shape the functional diversity of coastal fish assemblages, it is important to acknowledge some limitations. Our analyses accounted for potential anthropogenic pressures through the cumulative impact index (Micheli et al., 2013). However, broader socioeconomic variables not captured by this index may also influence functional diversity. For example, Lazzari et al. (2020) showed that functional evenness and beta diversity of coastal fish communities were associated with socioeconomic indicators such as income per inhabitant, employment rate, and the presence of marine protected areas. Considering such social-ecological drivers could enrich future research, providing a more comprehensive framework for understanding the processes that shape functional diversity in coastal ecosystems.

Overall, our results highlight that habitat type plays a crucial role in shaping the functional diversity of fish communities, with significant implications for managing, conserving, and monitoring marine biodiversity. Based on our findings, we argue that the conservation value of a particular habitat cannot be assessed by structural complexity or species richness alone, but its contribution to safeguarding functional diversity at larger scales and ecosystem resilience should also be considered. Currently, conservation efforts in the Mediterranean Sea have been targeting mainly rocky habitats and *Posidonia* meadows as these are considered “richer habitats”, hosting species of European and Mediterranean conservation interest (e.g., *Pinna nobilis* and *Lithophaga lithophaga*) according to the EU Habitats Directive and the Barcelona Convention. Furthermore, these habitats, especially rocky reefs, are associated with recreational scuba dive tourism in MPAs and their high economic benefits (Cabral et al., 2025). Monitoring efforts have also mainly focused on seagrass beds, rocky reefs, coralligenous reefs, and sea caves for which dedicated indices have been developed (Bianchi et al., 2022). Conversely, the ecological relevance of Mediterranean sandy habitats and the need to protect (and monitor) them has been largely overlooked (Fraschetti et al., 2013). The unique contribution of sandy habitats to functional beta diversity, as highlighted in this study, aligns with previous findings on taxonomic turnover (Cecapoli et al., 2024) and warrants further attention to safeguarding their role in maintaining regional biodiversity. Explicitly targeting the conservation of sandy bottoms when designing new MPAs or generating broader marine spatial plans is therefore required. For example, Giakoumi et al. (2011) suggested specific protection targets for sandy habitats in the design of an MPA network in the Cyclades Archipelago. Similarly, Markantonatou et al. (2021) suggested setting conservation targets for all the habitats of Community importance (EU Habitats Directive), including sandy habitats, in marine spatial planning for the Aegean Sea. Although these two examples are academic spatial prioritisation exercises, they demonstrate a transparent way for considering all habitat types in spatial plans, including the overlooked sandy habitats.

Our findings also underscore the importance of incorporating

functional diversity metrics into biodiversity assessments to capture ecological dynamics more comprehensively than taxonomic richness alone. By supporting a wider range of ecological functions, higher functional diversity is expected to enhance the stability and resilience of fish communities under environmental change (De Bello et al., 2021; Mouillot et al., 2013b). 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 only native species diversity (Giakoumi et al., 2016; Rilov et al., 2020), with the aim of ensuring ecosystem functioning and productivity (Wan et al., 2024). This highlights the urgency of adapting conservation metrics to reflect ecosystem function rather than just historical species composition.

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 pressures and climate change impacts, focusing on habitat type. Future research could build on this effort by exploring the temporal dynamics of functional diversity and expanding the geographic scope to better understand ecosystem resilience under changing environmental conditions. As highlighted in the Global Biodiversity Framework, future conservation efforts should move beyond species and habitat protection alone and ensure that ecosystem functions are maintained and restored, accounting for ecological integrity and connectivity. Incorporating the full mosaic of habitat types, including often overlooked sandy bottoms, into marine spatial planning initiatives and coastal monitoring programmes could safeguard functional diversity and ecosystem resilience.

CRediT authorship contribution statement

Stefania Russo: Writing – original draft, Formal analysis, Data curation. **Enrico Cecapoli:** Writing – review & editing, Data curation. **Antonio Calò:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Sylvaine Giakoumi:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Manfredi Di Lorenzo:** Writing – review & editing, Methodology, Conceptualization. **Silvestro Greco:** Writing – review & editing, Funding acquisition. **Giacomo Milisenda:** Writing – review & editing, Formal analysis, Conceptualization. **Antonio Di Franco:** Writing – original draft, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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.

Acknowledgements

This research was funded by “Fondo per lo sviluppo e la coesione (FSC) – Centro Ricerche ed Infrastrutture Marine Avanzate in Calabria (CRIMAC) – CUP C64I20000320001”. Many thanks also to Emilio Sperone and his team for the logistic support in the realization of the sampling operations. We thank the National Recovery and Resilience Plan, Mission 4 Component 2 Investment 1.4 – Call for tender no. 3138 (16/12/2021) rectified by decree no. 3175 (18/12/2021) of the Italian Ministry of University and Research funded by the NextGenerationEU; project CN_00000033, concession decree no. 1034 (17/6/2022) adopted by the Italian Ministry of University and Research, CUP B73C22000790001, project “National Biodiversity Future Center-NBFC”. We are also grateful to the anonymous reviewers whose constructive comments and suggestions greatly improved an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.114226>.

Data availability

The dataset supporting this study is provided as [Supplementary File](#).

References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Autom. Control* 19 (6), 716–723. https://doi.org/10.1007/978-1-4612-1694-0_16.
- Albouy, C., Leprieur, F., Le Loc'h, F., Mouquet, N., Meynard, C.N., Douzery, E.J., Mouillot, D., 2015a. A. Projected impacts of climate warming on the functional and phylogenetic components of coastal Mediterranean fish biodiversity. *Ecography* 38 (7), 681–689. <https://doi.org/10.1111/ecog.01254>.
- Albouy, C., Lasram, F.B.R., Velez, L., Guilhaumon, F., Meynard, C.N., Boyer, S., Benestan, L., Mouquet, N., Douzery, E., Aznar, R., Troussellier, M., Somot, S., Leprieur, F., Le Loc'h, F., Mouillot, D., 2015b. FishMed: traits, phylogeny, current and projected species distribution of Mediterranean fishes, and environmental data. *Ecology*. <https://doi.org/10.1890/14-2279.1>.
- Anderson, M.J., Santana-Garcon, J., 2015. Measures of precision for dissimilarity-based multivariate analysis of ecological communities. *Ecol. Lett.* 18 (1), 66–73. <https://doi.org/10.1111/ele.12385>.
- Bevilacqua, S., Airoldi, L., Ballesteros, E., Benedetti-Cecchi, L., Boero, F., Bulleri, F., Terlizzi, A., 2021. Mediterranean rocky reefs in the Anthropocene: present status and future concerns. *Adv. Mar. Biol.* 89, 1–51. <https://doi.org/10.1016/bs.amb.2021.08.001>.
- Bianchi, C.N., Azzola, A., Cocito, S., Morri, C., Oprandi, A., Peirano, A., Montefalcone, M., 2022. Biodiversity monitoring in Mediterranean marine protected areas: Scientific and methodological challenges. *Diversity* 14 (1), 43.
- Bivand, R.S., Wong, D.W., 2018. Comparing implementations of global and local indicators of spatial association. *Test* 27 (3), 716–748. <https://doi.org/10.1007/s11749-018-0599-x>.
- Boettiger, C., Lang, D.T., Wainwright, P.C., 2012. rfishbase: exploring, manipulating and visualizing FishBase data from R. *J. Fish Biol.* 81, 2030–2039. <https://doi.org/10.1111/j.1095-8649.2012.03464.x>.
- Bortone, S.A., Mille, K.J., 1999. Data needs for assessing marine reserves with an emphasis on estimating fish size in situ. *Naturalista Siciliana*.
- Cabral, R.B., Millage, K.D., Mayorga, J., et al., 2025. Marine protected areas for dive tourism. *Sci. Rep.* 15, 1923. <https://doi.org/10.1038/s41598-024-83664-1>.
- Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., Wilsey, B.J., 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* 94 (8), 1697–1707. <https://doi.org/10.1890/12-1334.1>.
- Catford, J.A., Morris, W.K., Vesk, P.A., Gippel, C.J., Downes, B.J., 2014. Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. *Divers. Distrib.* 20 (9), 1084–1096. <https://doi.org/10.1111/ddi.12225>.
- Cecapoli, E., Calò, A., Giakoumi, S., Di Lorenzo, M., Greco, S., Fanelli, E., Milisenda, G., Di Franco, A., 2024. Sandy bottoms have limited species richness but substantially contribute to the regional coastal fish β -diversity: a case study of the Central Mediterranean Sea. *Mar. Environ. Res.* 201, 106701. <https://doi.org/10.1016/J.MARENRES.2024.106701>.
- Cheminée, A., Pastor, J., Bianchimani, O., Thiriet, P., Sala, E., Cottalorda, J.-M., Dominici, J.-M., Lejeune, P., Francour, P., 2017. Juvenile fish assemblages in temperate rocky reefs are shaped by the presence of macro-algae canopy and its three-dimensional structure. *Sci. Rep.* 7, 14638. <https://doi.org/10.1038/s41598-017-15291-y>.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18 (1), 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>.
- Claudet, J., Fraschetti, S., 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biol. Conserv.* 143 (9), 2195–2206. <https://doi.org/10.1016/j.biocon.2010.06.004>.
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglià, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Voultsiadou, E., 2010. The biodiversity of the Mediterranean sea: estimates, patterns, and threats. *PLoS One* 5 (8), e11842. <https://doi.org/10.1371/JOURNAL.PONE.0011842>.
- D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D.R., Cinner, J.E., Vigliola, L., 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Curr. Biol.* 24 (5), 555–560. <https://doi.org/10.1016/j.cub.2014.01.049>.
- De Bello, F., Lavorel, S., Hallett, L.M., Valencia, E., Garnier, E., Roscher, C., Lepš, J., 2021. Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends Ecol. Evol.* 36 (9), 822–836. <https://doi.org/10.1016/j.tree.2021.05.001>.
- De Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F., Thuiller, W., 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography* 36, 393–402. <https://doi.org/10.1111/j.1600-0587.2012.07438.x>.
- de Sá Ferreira Lima, R.G., Soares, B.E., Cadotte, M., Albrecht, M.P., 2025. Freshwater fish functional diversity shows diverse responses to human activities, but consistently declines in the tropics. *Ecography*, e07746.
- Di Franco, A., Bussotti, S., Navone, A., Panzalis, P., Guidetti, P., 2009. Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. *Mar. Ecol. Prog. Ser.* <https://doi.org/10.3354/meps08051>.
- Di Lorenzo, M., Calò, A., Di Franco, A., Milisenda, G., Aglieri, G., Cattano, C., Milazzo, M., Guidetti, P., 2022. Small-scale fisheries catch more threatened elasmobranchs inside partially protected areas than in unprotected areas. *Nat. Commun.* 13 (1), 1–11. <https://doi.org/10.1038/s41467-022-32035-3>.
- Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A., Claudet, J., 2020. Assessing spillover from marine protected areas and its drivers: a meta-analytical approach. *Fish Fish.* <https://doi.org/10.1111/faf.12469>.
- Díaz-Gil, C., Smee, S.L., Cotgrove, L., Follana-Berná, G., Hinz, H., Marti-Puig, P., Catalán, I.A., 2017. Using stereoscopic video cameras to evaluate seagrass meadows nursery function in the Mediterranean. *Mar. Biol.* 164 (6), 137. <https://doi.org/10.1007/s00227-017-3169-y>.
- Duffy, J.E., Lefcheck, J.S., Stuart-Smith, R.D., Navarrete, S.A., Edgar, G.J., 2016. Biodiversity enhances reef fish biomass and resistance to climate change. *Proc. Natl. Acad. Sci.* 113 (22), 6230–6235. <https://doi.org/10.1073/pnas.1524465113>.
- Edgar, G.J., Barrett, N.S., Morton, A.J., 2004. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *J. Exp. Mar. Biol. Ecol.* <https://doi.org/10.1016/j.jembe.2004.03.004>.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506 (7487), 216–220. <https://doi.org/10.1038/nature13022>.
- Edgar, G.J., Stuart-Smith, R.D., Heather, F.J., Barrett, N.S., Turak, E., Sweatman, H., Bates, A.E., 2023. Continent-wide declines in shallow reef life over a decade of ocean warming. *Nature* 615 (7954), 858–865. <https://doi.org/10.1038/s41586-023-05833-y>.
- European Commission, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Off. J. Eur. Union* L 164, 19–40.
- Fraschetti, S., Guarnieri, G., Bevilacqua, S., Terlizzi, A., Boero, F., 2013. Protection enhances community and habitat stability: evidence from a Mediterranean Marine Protected Area. *PLoS One* 8 (12), e81838. <https://doi.org/10.1371/journal.pone.0081838>.
- Froese, R., Pauly, D. (Eds.), 2024. FishBase. World Wide Web electronic publication. Retrieved from <https://www.fishbase.org>, (10/2024).
- Furlani, S., Pappalardo, M., Gómez-Pujol, L., Chelli, A., 2014. The rock coast of the Mediterranean and Black seas. <https://doi.org/10.1144/M40.7>.
- García-Charton, J.A., Pérez-Ruzafa, A., Sánchez-Jerez, P., Bayle-Sempere, J.T., Reñones, O., Moreno, D., 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar. Biol.* 144, 161–182. <https://doi.org/10.1007/s00227-003-1170-0>.
- Giakoumi, S., Kokkoris, G.D., 2013. Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-Eastern Mediterranean Sea. *Mediterr. Marine Sci.* 14 (1), 58–68. <https://doi.org/10.12681/mms.318>.
- Giakoumi, S., Grantham, H.S., Kokkoris, G.D., Possingham, H.P., 2011. Designing a network of marine reserves in the Mediterranean Sea with limited socio-economic data. *Biol. Conserv.* 144 (2), 753–763.
- Giakoumi, S., Guilhaumon, F., Kark, S., Terlizzi, A., Claudet, J., Felling, S., Katsanevakis, S., 2016. Space invaders: biological invasions in marine conservation planning. *Divers. Distrib.* 22 (12), 1220–1231. <https://doi.org/10.1111/ddi.12491>.
- González-Barrios, F.J., Keith, S.A., Emslie, M.J., et al., 2025. Emergent patterns of reef fish diversity correlate with coral assemblage shifts along the Great Barrier Reef. *Nat. Commun.* 16, 303. <https://doi.org/10.1038/s41467-024-55128-7>.
- Guerra-Castro, E.J., Cajas, J.C., Simões, N., Cruz-Motta, J.J., Mascaró, M., 2021. SSP: an R package to estimate sampling effort in studies of ecological communities. *Ecography* 44 (4), 561–573. <https://doi.org/10.1111/ecog.05284>.
- Guidetti, P., 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuar. Coast. Shelf Sci.* 50, 515–529. <https://doi.org/10.1006/eecs.1999.0584>.
- Hall, A.E., Kingsford, M.J., 2021. Habitat type and complexity drive fish assemblages in a tropical seascape. *J. Fish Biol.* <https://doi.org/10.1111/jfb.14843>.
- Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Lasserre, G., 1985. Evaluation visuelle des peuplements et populations de poissons méditerranéens et problèmes. *Revue D'écologie* 40 (4), 467–539. <https://doi.org/10.3406/rev.1985.5297>.
- Harper, L.M., Lefcheck, J.S., Whippo, R., Jones, M.S., Foltz, Z., Duffy, J.E., 2022. Blinded by the bright: how species-poor habitats contribute to regional biodiversity across a tropical seascape. *Divers. Distrib.* 28 (11), 2272–2285. <https://doi.org/10.1111/ddi.13632>.
- Hatton, I.A., Mazzarisi, O., Altieri, A., Smerlak, M., 2024. Diversity begets stability: Sublinear growth and competitive coexistence across ecosystems. *Science* 383 (6688), eadg8488. <https://doi.org/10.1126/science.adg8488>.
- Helder, N.K., Burns, J.H.R., Green, S.J., 2022. Intra-habitat structural complexity drives the distribution of fish trait groups on coral reefs. *Ecol. Ind.* 142, 109266. <https://doi.org/10.1016/j.ecolind.2022.109266>.

- Hernández-Mendoza, L.C., Escalera-Vázquez, L.H., Vega-Cendejas, M.E., et al., 2024. Functional and taxonomic β diversity in fish assemblages is structured by turnover in a tropical coastal lagoon. *Environ. Biol. Fish* 107, 1219–1234. <https://doi.org/10.1007/s10641-024-01626-y>.
- Herrera, D.L., Navarrete, S.A., Labra, F.A., Castillo, S.P., Opazo Mella, L.F., 2023. Functional biogeography of coastal marine invertebrates along the south-eastern Pacific coast reveals latitudinally divergent drivers of taxonomic versus functional diversity. *Ecography* 2023 (12), e06476. <https://doi.org/10.1111/ecog.06476>.
- Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., De Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Ye, Y., 2020. Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci.* 117 (4), 2218–2224. <https://doi.org/10.1073/pnas.1909726116>.
- Júnior, A. da G.F.V., Lima Guedes, É.H., Brito, G.J.S., Pereira, J.A., Dolbeth, M., Pessanha, e.A.L.M., 2023. Do wave exposure and drifting algae drive the functional diversity of fishes in tropical ocean-exposed sandy beaches? *Estuar. Coast. Shelf Sci.* 287. <https://doi.org/10.1016/j.ecss.2023.108334>.
- Karadimou, E.K., Kallimanis, A.S., Tsiripidis, I., Dimopoulos, P., 2016. Functional diversity exhibits a diverse relationship with area, even a decreasing one. *Sci. Rep.* 6 (1), 35420. <https://doi.org/10.1038/srep35420>.
- Keck, F., Peller, T., Alther, R., et al., 2025. The global human impact on biodiversity. *Nature*. <https://doi.org/10.1038/s41586-025-08752-2>.
- Kelley, J.L., Grierson, P.F., Collin, S.P., Davies, P.M., 2018. Habitat disruption and the identification and management of functional trait changes. *Fish Fish.* 19 (4), 716–728. <https://doi.org/10.1111/FAF.12284>.
- Kovacic, M., Lipej, L., Dulčić, J., Iglesias, S.P., Goren, M., 2021. Evidence-based checklist of the Mediterranean Sea fishes. *Zootaxa* 4998 (1), 1–115. <https://doi.org/10.11646/ZOOTAXA.4998.1.1>.
- Laliberté, E., Legendre, P., Shipley, B., Laliberté, M.E., 2014. Package 'fd'. Measuring functional diversity from multiple traits, and other tools for functional. *Ecology* 1, 0–12.
- Lam-Gordillo, O., Baring, R., Dittmann, S., 2021. Taxonomic and functional patterns of benthic communities in southern temperate tidal flats. *Front. Mar. Sci.* 8. <https://doi.org/10.3389/fmars.2021.723749>.
- Lattanzi, A., Bellisario, B., Cimmaruta, R., 2024. A review of fish diversity in Mediterranean seagrass habitats, with a focus on functional traits. In: *Reviews in Fish Biology and Fisheries*. Springer Science and Business Media Deutschland GmbH. <https://doi.org/10.1007/s11160-024-09876-w>.
- Lazzari, N., Martín-Lopez, B., Sanabria-Fernandez, J.A., Becerro, M.A., 2020. Alpha and beta diversity across coastal marine social-ecological systems: Implications for conservation. *Ecol. Ind.* 109, 105786. <https://doi.org/10.1016/j.ecolind.2019.105786>.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. <https://doi.org/10.1007/s004420100716>.
- Maciel, E.B., Jovem-Azevedo, D., Lima, C.S.D.S., Pessanha, A.L.M., 2024. Multiple habitats drive the functional diversity of fish assemblages in a tropical estuary. *Mar. Environ. Res.* 195, 106379. <https://doi.org/10.1016/j.marenvres.2024.106379>.
- Mallet, D., Pelletier, D., 2014. Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research*. <https://doi.org/10.1016/j.fishres.2014.01.019>.
- Markantonatou, V., Giakoumi, S., Koukourouvlí, N., Maina, I., Gonzalez-Mirelis, G., Sini, M., Katsanevakis, S., 2021. Marine spatial plans focusing on biodiversity conservation: the case of the Aegean Sea. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 31 (8), 2278–2292.
- Maureaud, A., Hodapp, D., van Denderen, P.D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T., Beukhof, E., Lindegren, M., 2019. Biodiversity–ecosystem functioning relationships in fish communities: Biomass is related to evenness and the environment, not to species richness. *Proc. R. Soc. B Biol. Sci.* 286 (19189), 20191189. <https://doi.org/10.1098/rspb.2019.1189>.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21 (4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>.
- Miatta, M., Bates, A.E., Snelgrove, P.V., 2021. Incorporating biological traits into conservation strategies. *Ann. Rev. Mar. Sci.* 13 (1), 421–443. <https://doi.org/10.1146/annurev-marine-032320-094121>.
- Micheli, F., Halpern, B.S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Rosenberg, A.A., 2013. Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PLoS One* 8 (12), e79889. <https://doi.org/10.1371/journal.pone.0079889>.
- Montefalcone, M., Tunesi, L., Ouerghi, A., 2021. A review of the classification systems for marine benthic habitats and the new updated Barcelona Convention classification for the Mediterranean. *Marine Environ. Res.* <https://doi.org/10.1016/j.marenvres.2021.105387>.
- Moran, P.A., 1950. Notes on continuous stochastic phenomena. *Biometrika* 37 (1/2), 17–23. <https://doi.org/10.2307/2332142>.
- Mouillot, D., Albouy, C., Guilhaumon, F., Lasram, F.B.R., Coll, M., Devictor, V., Mouquet, N., 2011. Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Curr. Biol.* 21 (12), 1044–1050. <https://doi.org/10.1016/j.cub.2011.05.005>.
- Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Thuiller, W., 2013a. A rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol.* 11 (5), e1001569. <https://doi.org/10.1371/journal.pbio.1001569>.
- Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W., Bellwood, D.R., 2013b. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28 (3), 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>.
- Naem, S., 2002. Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. *Ecology* 83 (10), 2925–2935. [https://doi.org/10.1890/0012-9658\(2002\)083\[2925:DTIODO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2925:DTIODO]2.0.CO;2).
- O'Hara, C.C., Frazier, M., Valle, M., Butt, N., Kaschner, K., Klein, C., et al., 2024. Cumulative human impacts on global marine fauna highlight risk to biological and functional diversity. *PLoS One* 19 (9), e0309788. <https://doi.org/10.1371/journal.pone.0309788>.
- O'Hara, C., Frazier, M., Valle, M., Butt, N., Kaschner, K., Klein, C., Halpern, B., 2023. Cumulative human impacts on global marine fauna highlight risk to fragile functional diversity of marine ecosystems.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., ... Weedon, J., 2022. *vegan: Community ecology package (2.6-4)*. CRAN.
- Panayiotis, P., Sotiris, O., Vasilis, G., Vasilis, P., 2020. In: Anagnostou, C.L., Kostianoy, A. G., Mariolakos, I.D., Panayotidis, P., Soilemezidou, M., Tsaltas, G. (Eds.), *The Aegean Sea Environment. The Handbook of Environmental Chemistry*, 129. Springer, Cham. <https://doi.org/10.1007/978-2020-678>.
- Papapanagiotou, G., Tsagarakis, K., Koutsidi, M., Tzanatos, E., 2020. Using traits to build and explain an ecosystem model: Ecopath with Ecosim modelling of the North Aegean Sea (Eastern Mediterranean). *Estuar. Coast. Shelf Sci.* 236. <https://doi.org/10.1016/j.ecss.2020.106614>.
- Prato, G., Guidetti, P., Bartolini, F., Mangialajo, L., Francour, P., 2013. The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context. *Adv. Oceanogr. Limnol.* 4 (2), 176–193. <https://doi.org/10.1080/19475721.2013.841754>.
- QGIS.org, 2022. QGIS Geographic Information System – Version 3.24.2 Białowieża. QGIS Association.
- R Core Team, 2023. R: A language and environment for statistical computing. R foundation for statistical computing. <https://www.R-project.org/>.
- Receveur, A., Leprieux, F., Ellingsen, K.E., Keith, D., Kleisner, K.M., McLean, M., Méritot, B., Mills, K.E., Mouillot, D., Rufino, M., Trindade-Santos, I., Van Hoey, G., Albouy, C., Auber, A., 2024. Long-term changes in taxonomic and functional composition of European marine fish communities. *Ecography* 2024 (9), 861–875. <https://doi.org/10.1111/ecog.07234>.
- Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E., Pavoine, S., 2016. Measuring the functional redundancy of biological communities: a quantitative guide. *Methods Ecol. Evol.* 7, 1386–1395.
- Rigby, R.A., Stasinopoulos, D.M., 2005. Generalized additive models for location, scale and shape. *J. R. Stat. Soc. Ser. C. Appl. Stat.* 54 (3), 507–554. <https://doi.org/10.1111/j.1467-9876.2005.00510.x>.
- Rilov, G., Fraschetti, S., Gissi, E., Pipitone, C., Badalamenti, F., Tamburello, L., Katsanevakis, S., 2020. A fast-moving target: achieving marine conservation goals under shifting climate and policies. *Ecol. Appl.* 30 (1), e02009. <https://doi.org/10.1002/eap.2009>.
- RStudio Posit Team, 2023. RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL <http://www.posit.co/>.
- Sala, E., Ballesteros, E., Dendrinou, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S., Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., Zabala, M., 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. *PLoS One*. <https://doi.org/10.1371/journal.pone.0032742>.
- Sanabria-Fernández, J.A., Génin, A., Dakos, V., 2024. Unveiling functional linkages between habitats and organisms: macroalgal habitats as influential factors of fish functional traits. *Mar. Environ. Res.* 194, 106305. <https://doi.org/10.1016/j.marenvres.2023.106305>.
- Sahyoun, R., Bussotti, S., Di Franco, A., Navone, A., Panzalis, P., Guidetti, P., 2013. Protection effects on Mediterranean fish assemblages associated with different rocky habitats. *J. Mar. Biol. Assoc. U. K.* 93 (2), 425–435. <https://doi.org/10.1017/S0025315412000975>.
- Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., ... Crowley, J., 2021. GGally: Extension to 'ggplot2'. R package version 2.1. 2. GitHub Inc. Retrieved March, 10, 2022.
- Sgarlatta, M.P., Ramírez-Valdez, A., Ladah, L.B., Calderón-Aguilera, L.E., 2023. Fish functional diversity is modulated by small-scale habitat complexity in a temperate ecosystem. *Hydrobiologia*. <https://doi.org/10.1007/s10750-022-05061-x>.
- Shah Esmaili, Y., Corte, G.N., Checon, H.H., Bilatto, C.G., Lefcheck, J.S., Zacagnini Amaral, A.C., Turra, A., 2022. Revealing the drivers of taxonomic and functional diversity of nearshore fish assemblages: implications for conservation priorities. *Divers. Distrib.* 28 (8), 1597–1609.
- Souza, A.T., Dias, E., Antunes, C., Ilari, M., 2023. Disruptions caused by invasive species and climate change on the functional diversity of a fish community. *Neobiota* 88, 211–244. <https://doi.org/10.3897/neobiota.88.108283>.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57 (7), 573–583. <https://doi.org/10.1641/B570707>.
- Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501 (7468), 539–542. <https://doi.org/10.1038/nature12529>.
- Swenson, N.G., 2014. *Functional and Phylogenetic Ecology in R*, Vol. 639. Springer, New York.

- Teixidó, N., Carlot, J., Alliouane, S., Ballesteros, E., De Vittor, C., Gambi, M.C., Gattuso, J.P., Kroeker, K., Micheli, F., Mirasole, A., Parravacini, V., Villéger, S., 2024. Functional changes across marine habitats due to ocean acidification. *Glob. Chang. Biol.* 30 (1). <https://doi.org/10.1111/gcb.17105>.
- Thiriet, P.D., Di Franco, A., Cheminée, A., Guidetti, P., Bianchimani, O., Basthard-Bogain, S., Cottalorda, J.M., Arceo, H., Moranta, J., Lejeune, P., Francour, P., Mangialajo, L., 2016. Abundance and diversity of crypto- and necto-benthic coastal fish are higher in marine forests than in structurally less complex macroalgal assemblages. *PLoS One*. <https://doi.org/10.1371/journal.pone.0164121>.
- Tzanatos, E., Moukas, C., Koutsidi, M., 2020. Mediterranean nekton traits: distribution, relationships and significance for marine ecology monitoring and management. *PeerJ* 2020 (2). <https://doi.org/10.7717/peerj.8494>.
- Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages. *Glob. Ecol. Biogeogr.* 22 (6), 671–681. <https://doi.org/10.1111/geb.12021>.
- Villéger, S., Mason, N.W., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89 (8), 2290–2301. <https://doi.org/10.1890/07-1206.1>.
- Villéger, S., Ramos, M.J., Domingo, F.H., David, M., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* 20 (6), 1512–1522. <https://doi.org/10.1890/09-1310.1>.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos*. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Wan, Y., Zhang, C., Xu, B., Xue, Y., Ren, Y., Ji, Y., 2024. Which aspect of functional diversity shapes ecosystem functioning in exploited marine demersal fish community? *Ecol. Ind.* 163, 112083. <https://doi.org/10.1016/j.ecolind.2024.112083>.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou mountains Oregon and California. *Ecol. Monogr.* 30 (4), 407. <https://doi.org/10.2307/1948435>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1 (1), 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.