

RESEARCH ARTICLE OPEN ACCESS

Thriving Areas in Temperate Coastal Systems: Novel Insights for Marine Conservation

José A. Sanabria-Fernández^{1,2}  | Andrés Baselga³  | Natali Lazzari⁴  | Carola Gómez-Rodríguez⁵  | David Mouillot⁶  | Graham Edgar⁷  | Vasilis Dakos⁸ 

¹College of Science and Engineering, James Cook University, Townsville, Queensland, Australia | ²Department of Ecology and Evolution, Doñana Biological Station (EBD-CSIC), Sevilla, Spain | ³CRETUS - Department of Zoology, Genetics and Physical Anthropology, University of Santiago de Compostela, Santiago de Compostela, Spain | ⁴EqualSea Lab-CRETUS, University of Santiago de Compostela, Santiago de Compostela, Spain | ⁵CRETUS Department of Functional Biology (Area of Ecology), Universidade de Santiago de Compostela, Santiago de Compostela, Spain | ⁶MARBEC, Université de Montpellier, CNRS, IFREMER, IRD, Montpellier, France | ⁷Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia | ⁸ISEM, CNRS, Univ. Montpellier, IRD, EPHE, Montpellier, France

Correspondence: José A. Sanabria-Fernández (jose.fernandezsanabria@jcu.edu.au)

Received: 29 January 2025 | **Revised:** 8 September 2025 | **Accepted:** 13 September 2025

Editor: Vânia Proença

Funding: This work was supported by Fundación Biodiversidad, INBIOMAR - INBIOMAR II. European Union, MSCA Program, REVALSEA, 101146373. Consejería de Conocimiento, Investigación y Universidad, Junta de Andalucía, DGP_POST_2024_00757. Ministerio de Ciencia y Tecnología, Margarita Salas Postdoctoral Fellowship.

Keywords: Balearic Islands | decision-making | functional ecology | marine fish communities | resilience conservation

ABSTRACT

Aim: Resilience is a crucial property of ecosystems experiencing accelerated degradation in natural environments. While the functional characteristics of ecosystems play a significant role in shaping their resilience, the development of functional approaches in marine conservation has been largely overlooked. In light of this deficiency, we simultaneously consider the functional richness and redundancy of marine fish communities associated with rocky reefs to uncover and characterise the thriving and struggling areas.

Location: Five marine ecoregions in southern Europe.

Methods: We collected data on the density of reef-associated marine fish species using the Reef Life Survey's standardised protocol. Based on these data, we estimated the functional richness and redundancy using four key functional traits: dietary patterns, gregariousness, position in the water column, and substrate preference. Next, we applied a predictive approach by using the XGBoost algorithm to estimate these functional metrics across the study area, including areas where in situ data were unavailable. Subsequently, to identify threshold points in the predictions, we employed decision trees, enabling us to unveil thriving and struggling areas.

Results: Our results indicate that the proportion of thriving areas (26.7%) is similar to that of struggling areas (26.5%), and that their distribution is heterogeneous across the ecoregions. We also find that these thriving areas are distinguished by lower values of human density, fishing pressure, chlorophyll concentrations, and they also exhibit a higher protection status compared to struggling areas.

Main Conclusions: In the current context of declining resilience, it is essential to address the functional dimension of biodiversity to unveil thriving and struggling areas, thereby highlighting the regions that require prioritisation in conservation and restoration efforts. Our findings offer critical information for policymakers and governments at local, regional, and national levels, pinpointing priority areas to enhance marine resilience and prevent the ongoing loss of this vital ecosystem property.

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1 | Introduction

In light of the significant decline in resilience experienced by many of the world's ecosystems (Boulton et al. 2022; Forzieri et al. 2022; Rocha 2022; Smith et al. 2023), novel methodological approaches are needed to bolster and preserve resilience before ecosystems cross critical thresholds and become irreversibly degraded (GBF-CBD 2022). Following the framework of Walker et al. (2004), we define resilience as the capacity of a system to absorb disturbance and reorganise while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks. This capacity has been estimated in various ways, including by quantifying changing terrestrial vegetation cover (Ciemer et al. 2019) and variations in marine phytoplankton biomass over time (Wouters et al. 2015), the development of metrics that integrate data from biological, environmental, and management sources (Maynard et al. 2015; Sanabria-Fernández, Lazzari, and Becerro 2019), or through the assessment of dissimilarity between communities across different levels of protection (Sanabria-Fernández and Alday 2024). However, most of these approaches overlook the importance of the functions of co-existing species in biological communities, which are essential for ecosystems to maintain their capacity to adapt to changes and recover from disturbances (Mouillot et al. 2013; McLean et al. 2019; Auber et al. 2022). Functions such as nutrient cycling, which enhances soil fertility and supports plant growth; pollination, which is vital for the reproduction of plants; and predation, which helps regulate population sizes, are crucial for maintaining the full functioning of ecosystems and, consequently, their resilience (Huang et al. 2021; Ding et al. 2024; Olin et al. 2024). Community functions can be altered over time by factors such as coral reef bleaching (Graham et al. 2015) and fishing pressure (Pauly et al. 1998). Therefore, integrating the functional dimension in resilience studies should boost our understanding of this concept and enhance the development of measures to prevent ecosystem disruption.

The metrics functional richness (FRichness) and functional redundancy (FRedundancy) allow both a deeper understanding of community functional structures and also inform about the ecosystem's capacity to withstand disturbances and recover (Walker 1992; Walker 1995; Peterson et al. 1998; Allen et al. 2005; Fischer et al. 2007; Ricotta et al. 2023; McLean et al. 2019; Auber et al. 2022). Specifically, FRichness considers the diversity and breadth of functional traits present in a given community, informing about the range of functions performed by species in the ecosystem (Mayfield and Daily 2005; Wright et al. 2006). This metric is related to the insurance effect (Yachi and Loreau 1999; Carturan et al. 2022), a phenomenon where greater functional richness increases a system's capacity to adapt to stressors (Angeler et al. 2019) by increasing the probability of complementary functional responses (Elmqvist et al. 2003). Consequently, this mechanism promotes greater ecosystem resilience and the persistent maintenance of the system's functioning (Elmqvist et al. 2003). On the other hand, FRedundancy refers to a particular function being performed simultaneously by multiple species (Mouillot et al. 2014). While elevated FRedundancy can be interpreted as a buffer against the loss of functions, it is important to recognise that such values may also occur in scenarios with a limited number of functional traits, where multiple species converge on the same functions.

In other words, a community may exhibit high redundancy (FRedundancy) without necessarily being functionally diverse (FRichness). Thus, the simultaneous consideration of FRichness and FRedundancy is crucial as it can potentially provide more accurate insights into the resilience of communities by detecting whether redundancy supports a broad range of functions or alternatively masks their deficiency.

The concurrent assessment of these functional metrics is especially important in temperate coastal systems, where fish communities exhibit high functional diversity (Stuart-Smith et al. 2013; Trindade-Santos et al. 2022) while simultaneously facing elevated levels of threats (Williams et al. 2022). Considering both FRichness and FRedundancy simultaneously would allow consideration of contrasting scenarios, reflecting the distinct characteristics of each functional metric. For example, a system characterised by high levels of both FRedundancy and FRichness would represent areas of high resilience (Figure 1, thriving areas). This is because the variety of functions comprising FRichness acts as a backup mechanism by promoting complementary functional responses to stressors, thereby helping maintain the system's functioning (Carturan et al. 2022). Simultaneously, FRedundancy strengthens this resilience by providing a safety net through the presence of multiple species performing similar functions (Mouillot et al. 2014). Collectively, both FRichness and FRedundancy are essential elements underpinning resilience, positioning these resilient areas as a conservation priority. By contrast, a system characterised by low values of FRichness and FRedundancy (Figure 1, struggling areas) would represent areas with low resilience. These areas lack essential functions, hindering their ability to cope with disturbances, thus highlighting a need for restoration measures to extend the web of functions. However, research has largely overlooked resilience through both FRichness and FRedundancy, limiting our knowledge of key areas where conservation initiatives are urgently needed.

To address this knowledge gap, we aim to identify and characterise areas with high and low resilience—defined here as thriving and struggling areas, respectively—by simultaneously considering these two functional metrics. We estimated the FRichness and FRedundancy of reef fish communities based on four categorical traits that provide information on how species interact with their environment and perform ecological functions (Stuart-Smith et al. 2013; Mouillot et al. 2014; Villéger et al. 2017). Subsequently, we applied predictive models using environmental, physical, and anthropogenic variables to estimate functional metric values in areas not directly sampled, thereby enabling a spatially explicit assessment of ecological functioning across five temperate marine ecoregions in southern Europe. We classified the predictions of FRichness and FRedundancy into high and low categories by identifying the inflection point of each functional metric, and subsequently combined them to identify thriving and struggling areas. Our findings showed that 26.7% of the data represented thriving areas, which are a priority for conservation, while 26.5% indicated struggling areas requiring urgent restoration strategies to enhance functional attributes. Both thriving and struggling areas were present across all studied ecoregions; however, only two ecoregions, the Saharan and the Mediterranean, have shown a greater proportion of thriving areas compared to struggling areas

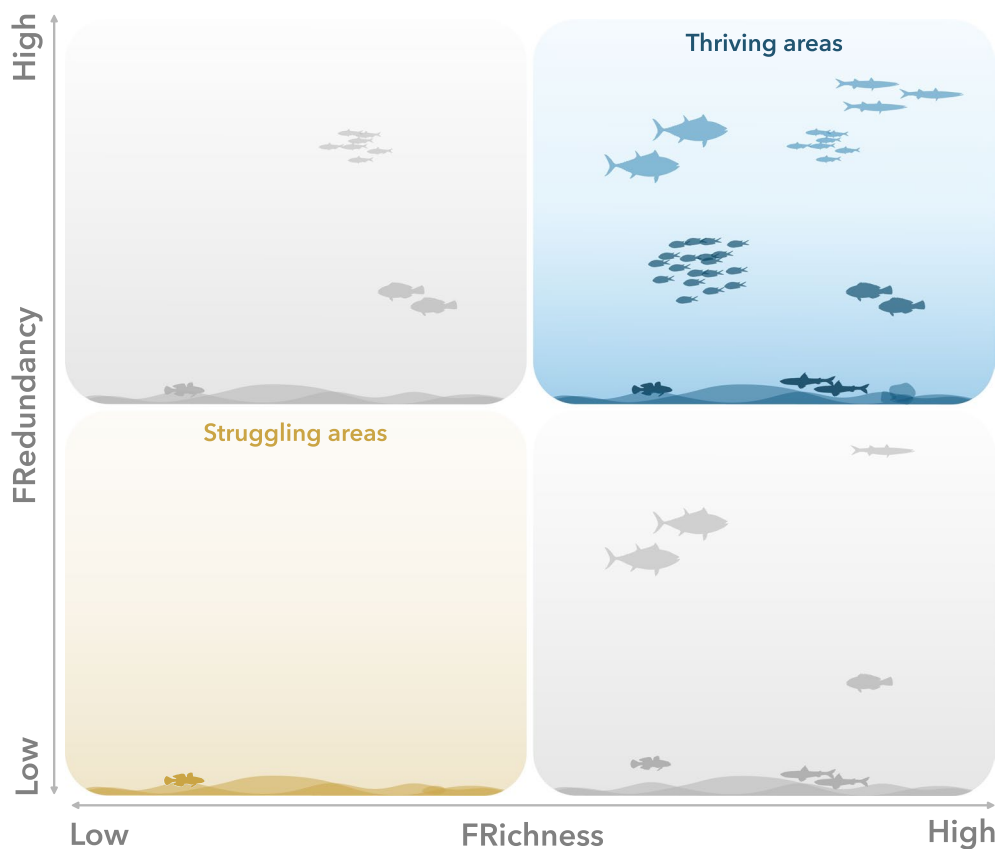


FIGURE 1 | Illustration of the four potential scenarios derived from the interaction between functional richness (FRichness) and functional redundancy (FRedundancy). The combination of high FRichness and high FRedundancy represents thriving areas, while the combination of low FRichness and low FRedundancy represents struggling areas. Transition scenarios also arise from the simultaneous consideration of both metrics; however, their analysis is also beyond the scope of this study.

(41% and 28%, respectively). Our study highlights the importance of identifying both thriving and struggling areas within temperate coastal systems, providing crucial insights for targeted conservation efforts and urgent interventions aimed at enhancing their functional resilience and long-term sustainability.

2 | Material and Methods

2.1 | Study Area

We conducted this study in European temperate coastal systems comprising five Marine Ecoregions of the World (Spalding et al. 2007): South European Atlantic Shelf, Azores, Canaries, Madeira, Saharan Upwelling, Alboran Sea, and Western Mediterranean (hereafter referred to as Atlantic, Canaries, Saharan, Alboran, and Mediterranean, respectively; see Figure 3d). Our research focused on these temperate areas because, in addition to hosting a rich gradient of functional diversity, they are experiencing multiple anthropogenic impacts (Coll et al. 2010; Alcorlo et al. 2023) and their resilience remains poorly investigated (Sanabria-Fernández and Lazzari 2025).

2.2 | Biological and Functional Characterisation

We surveyed 723 belt transects at 391 sampling locations using the Reef Life Survey protocol, a standardised quantitative

underwater visual census method (Edgar et al. 2020). At the belt transect level, we recorded reef fish species and their density within a 500 m² area (2×250-m² blocks). We characterised the functional strategy of each of the 123 fish species surveyed based on four categorical traits: dietary patterns, gregariousness, position in the water column, and substrate preference (Stuart-Smith et al. 2013; Mouillot et al. 2014; Villéger et al. 2017; Sanabria-Fernández et al. 2024), which were obtained from FishBase (www.fishbase.org; Froese and Pauly 2000) and the database used in Stuart-Smith et al. (2013). Dietary patterns were determined by assessing the primary food items consumed by each species, resulting in the identification of seven trophic categories: browsing herbivore, scraping herbivore, benthic invertevore, omnivore, piscivore, planktivore, and predator. Gregarious behaviour was categorised by preference for the number of nearby individuals of the same species: forming schools, paired, and solitary. The position in the water column was assessed based on where the species spend most of their time: benthic (sitting on the seabed), demersal (associated with seabed refuges but swimming above), and pelagic (wide-ranging). Substrate preference was categorised using the species' preference for two types of substrate: rocky bottoms or soft sediments. We did not account for intraspecific variability of traits across different life stages.

We quantified FRichness as the sum of distinct functional categories (Mouillot et al. 2014), and FRedundancy as 1-Functional diversity/Taxonomic diversity (De Bello et al. 2021). Functional

TABLE 1 | The thirty-six explanatory variables that were used to model FRichness and FRedundancy using the XGBoost algorithm.

[Chlo] Maximum, Mean, and Minimum chlorophyll concentration (mg m^{-3})	[Human density] (people/ km^2)
[Nitrate] Maximum, mean, and minimum nitrate concentration (mmol m^{-3})	[Fishing pressure] Fishing hours over a ten-year period (2013–2022) by fishing vessels
[Phosphate] Maximum, mean, and minimum phosphate concentration (mmol m^{-3})	[Dist_market] Distance to nearest market (km)
[Salinity] Maximum, mean, and minimum salinity concentration (PSS)	[Dist_coast] Distance to nearest coast (km)
[Silicate] Maximum, mean, and minimum silicate concentration (mmol m^{-3})	[Dist_to_plants] Distance to residual water treatment plants in the nearest 10 km
[Temp] Maximum, mean, and minimum sea surface temperature ($^{\circ}\text{C}$)	[Num_plants] Numbers of residual water treatment plants in the nearest 10 km
[Pp] Maximum, mean, and minimum primary production ($\text{g m}^{-3} \text{day}^{-1}$)	[Dist_to_outfalls] Distance to marine outfalls in the nearest 10 km
[Iron] Mean concentration dissolved iron (mmol m^{-3})	[Num_outfalls] Number of marine outfalls in the nearest 10 km
[Latitude] and [Longitude] (Decimal degrees $^{\circ}$)	[Dist_harbour] Distance to nearest harbour
[Slope] Sea bottom slope (degrees)	[Num_harbour] Number of harbours within the nearest 25 km
[Protection] Protection status (No-take, partially protected, and unprotected)	

Note: The name of the variable used is indicated within brackets [].

diversity was calculated using Rao's quadratic entropy based on Gower's dissimilarity distance, using the Rao() function (De Bello et al. 2021), while taxonomic diversity was estimated using the Simpson diversity index, applying the diversity() function from the R vegan package (Oksanen et al. 2024). Lastly, we calculated the values of FRichness and FRedundancy at each sampling location by averaging the values obtained from the belt transects.

2.3 | Modelling and Predicting Functional Metrics

We gathered information about 36 explanatory variables that are known to influence the functional dimension of marine biological communities in temperate coastal systems (Stuart-Smith et al. 2013; Herrera et al. 2023; McKinley et al. 2023; Luza et al. 2023). These variables were selected also for their potential to improve the predictive performance of models, given the complexity inherent in marine environments. Sea surface temperature, salinity, chlorophyll, phosphate, nitrate, iron, silicate concentration, and primary production were obtained from Bio-Oracle (Assis et al. 2018), using the coordinates of the sampling locations and applying the extract() function of the raster package (Hijmans et al. 2023). Additionally, the minimum, median, and maximum values of these variables were considered to encompass their full environmental range (Table 1). These variables were measured within a 5 arc-minute spatial resolution (Table 1). We also included the latitude and longitude of the sampling locations as explanatory variables. Physical variables, specifically the slope of the sea bottom and the distance to the nearest coast, were obtained from the Marspec database (Sbrocco and Barber 2013) (Table 1). Finally,

regarding anthropogenic pressures, we collected ten variables: human density and distance to the nearest market from the Yeager et al. (2017) database, which serve as proxies for the distance to the nearest city centre (Yeager et al. 2017); the number and distance of residual water treatment plants calculated as the distance from these residual water treatment plants to our sampling locations using the pointDistance() function of the Raster package (Hijmans et al. 2023); the number and distance to the nearest marine outfalls in coastal areas obtained from the European Environment Agency database (Table 1, Urban Waste Water Treatment Directive 2022); the number and distance of nearby harbours calculated as the distance from these harbours to our sampling locations using the pointDistance(). These last variables were important for assessing potential anthropogenic impacts on marine biodiversity and ecosystem health, including water quality degradation and habitat alteration (Mearns et al. 2019; Lazăr et al. 2021). We also considered the fishing pressure, measured as the average total fishing hours over a ten-year period (2013–2022) by fishing vessels, with a spatial resolution of 1 km^2 (Global Fishing Watch 2024). Lastly, we included the status of protection, obtained from the World Database on Protected Areas (UNEP-WCMC 2024).

To model the relationship between the functional metrics and the explanatory variables, we used the Extreme Gradient Boosting algorithm, applying the boost_tree() function, and set the engine to xgboost from the XGBoost package (Chen and Guestrin 2016; Chen et al. 2024). This machine learning technique offers significant advantages compared to other modelling methods because it has: (i) an inherent regularisation penalty to prevent model overfitting, (ii) the ability to handle high autocorrelation among explanatory variables without compromising the

model's accuracy, and (iii) the ability to capture non-linear relationships (Parsa et al. 2020). To train the models, we used 80% of the datasets from each ecoregion selected randomly, reserving 20% for the validation process. In this way, we ensure that our model considers all the ecoregions studied. The XGBoost algorithm requires the configuration of constituent hyperparameters, such as the number of trees, tree depth, and learning rate (Chen et al. 2024). These hyperparameters are combined in all possible ways to find the optimal combination that maximises the algorithm's performance on the training data. To validate this hyperparameter optimisation process, we employed cross-validation (Zhang et al. 2022). We chose this strategy because it ensures a comprehensive and robust evaluation of multiple hyperparameter configurations, helping us to avoid overfitting and to achieve an efficient and generalisable model (Geurkink et al. 2021; Zhang et al. 2022). We also evaluated the model's performance using the root mean squared error (RMSE) criterion. RMSE is an extensively employed metric for assessing the accuracy of regression and prediction models because it considers the average magnitude of errors between predicted values and original values (Wang et al. 2023). Finally, we used the selected models to predict the values of FRichness and FRedundancy in 5 arc-minute grid cells, utilising these predictions in subsequent steps.

To assess the importance of explanatory variables in the results of the FRichness and FRedundancy models, we relied on Shapley Additive Explanation values—SHAP (Futagami et al. 2021). These values represent an approach for interpreting machine learning models grounded in game theory (Parsa et al. 2020; Futagami et al. 2021). The fundamental premise of SHAP lies in providing a detailed understanding of how each variable contributes to the model's predictions. The SHAP value is computed by decomposing the prediction of the selected regression tree model into the sum of the individual contributions of each explanatory variable. This methodology quantifies the influence of the explanatory variable of interest on the model's output for a particular prediction, being expressed in the same units as the response variable (Lundberg et al. 2020; Vega García and Aznarte 2020). This allows for a direct interpretation of the relative importance of each variable within the model's framework. To compute the SHAP values, we utilised both the fastshap package (Greenwell 2024) and the inherent functions of the XGBoost package, ensuring a robust analysis of the contributions of each variable to the model's predictions.

2.4 | Unveiling Thriving and Struggling Areas

To categorise sites into thriving and struggling areas, we used min-max normalised predictions of FRichness and FRedundancy, ranked in ascending order. We determined the inflection point for the predictions of each functional metric using the recursive partitioning algorithm by applying the `rpart()` function of the Recursive Partitioning and Regression Trees package (Therneau et al. 2023). This algorithm is based on constructing decision trees that segment the functional metrics into subgroups, identifying the optimal point (i.e., the inflection point) where differentiation between subgroups is maximised (Strobl et al. 2009). This approach is particularly useful for detecting inflection points as it allows for a clear delineation of

boundaries within the data, thereby facilitating a more precise understanding of the transitions between different functional states. Thereafter, we used the inflection point to categorise the functional metrics into high and low classes. Sampling locations falling in the upper categories of both functional metrics (i.e., High FRichness—High FRedundancy) were denoted as thriving areas, as they exhibit functional attributes indicative of high resilience. On the other hand, sampling locations falling in the lower categories of both functional metrics (i.e., Low FRichness—Low FRedundancy) were identified as struggling areas, suggesting low resilience. Finally, we used radar charts to characterise thriving and struggling areas. We utilised the R programming language (R Core Team 2024) for data preparation, modelling, and visualisation.

3 | Results

3.1 | Functional Metrics: FRichness and FRedundancy

The FRichness predictions exhibited a range of values between 7 and 12, with the lowest value observed in the Atlantic ecoregion and the highest value identified in the Canaries ecoregion (Figure S1). The explanatory variables explained 60% variation in FRichness. Among these, the maximum and mean concentrations of silicate, the distance to the nearest residual water treatment plant, latitude, and the distance to the nearest market were the most influential variables (Figure 2a,b). The optimal configuration of the model's hyperparameters included 500 trees, a tree depth of 3, and a learning rate of 0.01. The inflection point that separated FRichness predictions into low and high categories was identified at 0.53 (Figure 3a).

The FRedundancy values ranged from 0.06 to 0.44, with the lowest and highest values observed in the Atlantic ecoregion (Figure S2). The explanatory variables explained 51% variation in FRedundancy. Of these variables, fishing pressure, mean concentration of iron, distance to the nearest market, and minimum primary production were identified as the most important (Figure 2c,d). The optimal configuration of the model's hyperparameters included 1000 trees, a learning rate of 0.01, and a tree depth of 1. The inflection point that separated FRedundancy predictions into low and high categories emerged at 0.40 (Figure 3b).

3.2 | Thriving and Struggling Areas

Simultaneous consideration of both functional metrics revealed that 26.7% of the values correspond to thriving areas, while 26.5% of the values were identified as struggling areas, both distributed heterogeneously across the studied ecoregions (Figure 3c,d). Only two ecoregions, the Saharan and the Mediterranean, showed a greater proportion of thriving areas compared to struggling areas (41% and 30%, respectively) (Figures 3d and 4). Within the Mediterranean ecoregion, it is particularly noteworthy that 72% of thriving areas are concentrated in the Balearic Islands, highlighting this archipelago as a stronghold of marine resilience (Figure 3d). In terms of their characterisation, these thriving areas are distinguished by higher protection levels,

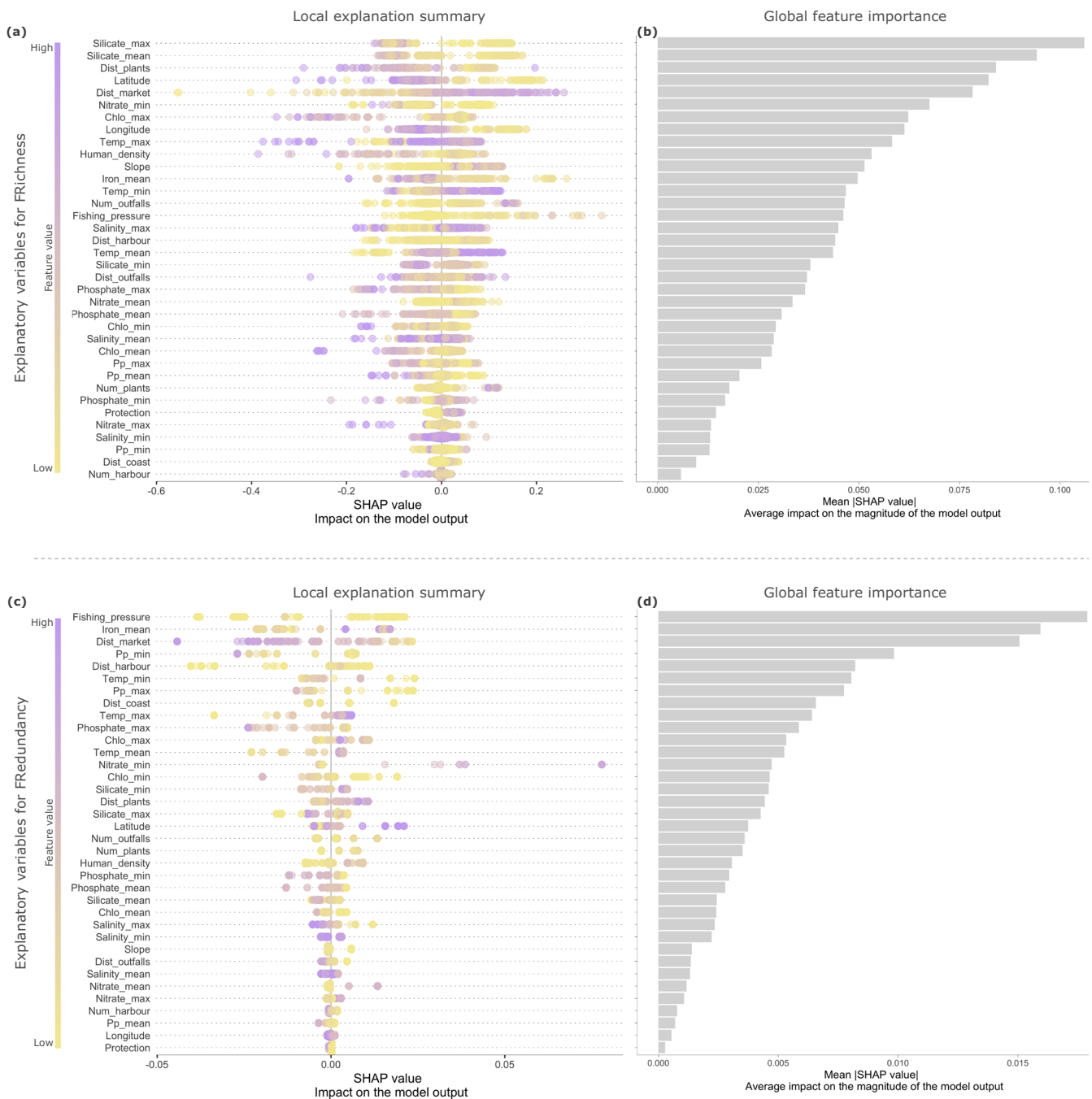


FIGURE 2 | The importance of explanatory variables is assessed based on SHAP values obtained from the XGBoost model for FRichness (a, b) and FRedundancy (c, d). Specifically, graphs (a) and (c) offer a summary of local explanations, illustrating the direction of the relationship between the explanatory variables and the model predictions. Positive SHAP values on the x-axis indicate that the explanatory variables increase the prediction to a higher level of the functional metrics. Conversely, negative SHAP values signify that the variables contribute to reducing the prediction of these metrics. The points represent the model output for each sampling location, with colour indicating a high (purple) or low (yellow) feature value. Graphs (b) and (d) present the mean absolute SHAP values for each explanatory variable, emphasising the overall importance of these variables within the models.

reduced fishing pressure, and lower concentrations of chlorophyll and nitrate relative to struggling areas. Additionally, they feature a steeper seabed slope and lower human density, with closer proximity to the nearest market (Figure 5).

Alboran, Atlantic, and the Canaries ecoregions exhibited high numbers of struggling than thriving ones (16%, 13%, and 6%, respectively) (Figures 3d and 4). Within the Canaries ecoregion,

86% of struggling areas were concentrated in the eastern islands of Fuerteventura and Lanzarote (Figure 3d). These struggling areas are characterised by upwelling, with high concentrations of nitrates, primary production, and chlorophyll compared to thriving areas. Additionally, they feature a high human population density, despite being farther from the nearest market and having a lower number of wastewater treatment plants (Figure 5).

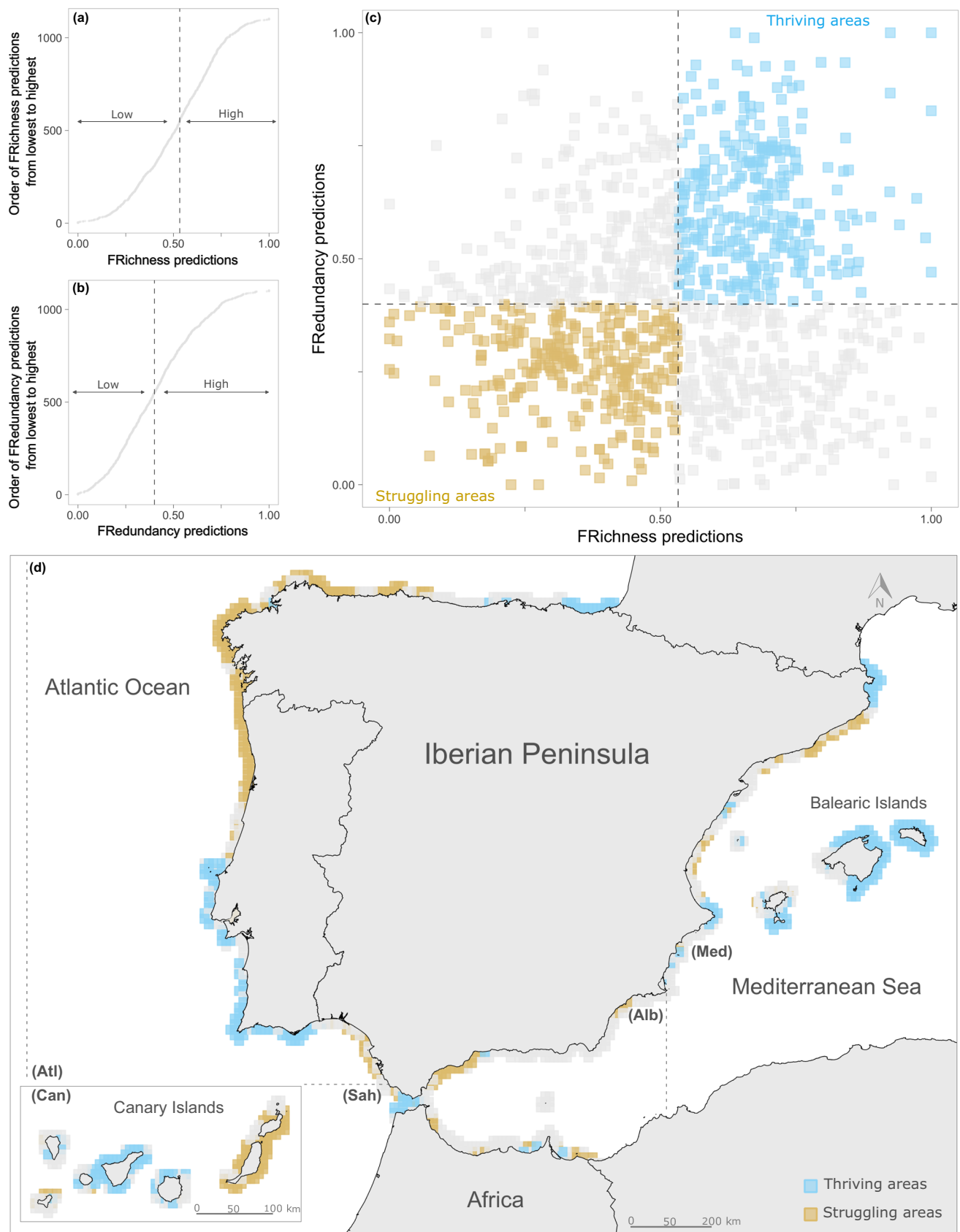


FIGURE 3 | Legend on next page.

FIGURE 3 | (a) Relationship between the predicted values of FRichness (x-axis) and their position in the ordered distribution from lowest to highest (y-axis). (b) Relationship between the predicted values of FRedundancy (x-axis) and their position in the ranked distribution from lowest to highest (y-axis). The dashed vertical lines represent the inflection points of each functional metric. (c) Scatterplot between FRedundancy and FRichness, where the squares represent the grid cells with a resolution of 5' arc-minutes. The dashed vertical line corresponds to the inflection point of FRichness, and the dashed horizontal line corresponds to the inflection point of FRedundancy. (d) Map depicting the classification of thriving and struggling areas across the study area. Dotted lines represent the boundaries of the five Marine Ecoregions of the World: (Atl) South European Atlantic Shelf, (Can) Azores Canaries Madeira, (Sah) Saharan Upwelling, (Alb) Alboran Sea, and (Med) Western Mediterranean (Spalding et al. 2007).

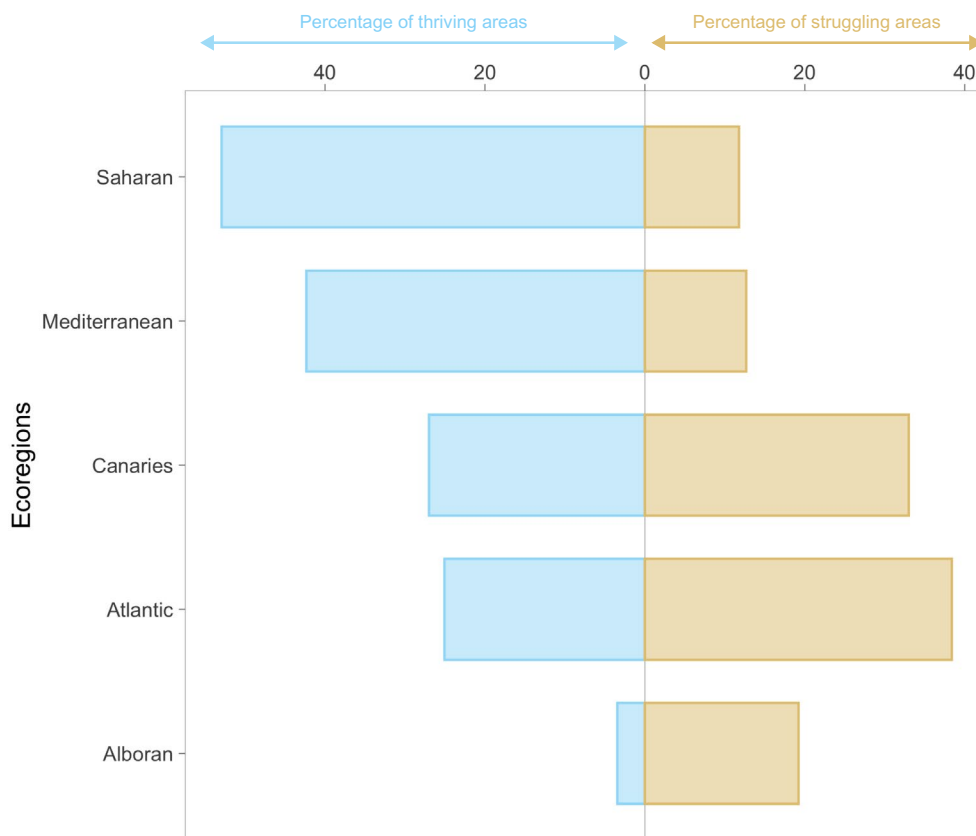


FIGURE 4 | Percentage of thriving and struggling areas (x-axis) by each ecoregion (y-axis). The ecoregions are sorted from highest to lowest percentage of thriving areas.

The ecoregional characterisation showed that, in four of the five studied ecoregions (Alboran, Atlantic, Mediterranean, and Saharan), thriving areas were associated with reduced levels of human impacts—notably including fishing pressure and population density—and exhibited a steeper seabed gradient (Figure S3). Conversely, struggling areas had higher levels of these anthropogenic impacts and showed increased primary productivity (Figure S3).

4 | Discussion

Resilience is a fundamental property of ecosystems. While the functional characteristics of ecosystems play a significant role in shaping their resilience, the development of functional approaches in marine systems has been limited. In light of this deficiency, this study used fish community data to model FRichness and FRedundancy based on the environmental, anthropogenic,

and physical characteristics of the sampling locations. The simultaneous consideration of both functional metrics revealed that 26.7% of the values correspond to thriving areas, while 26.5% of the values were identified as struggling areas, both distributed heterogeneously across the studied ecoregions. Recent investigations highlight the importance of integrating multiple functional metrics—such as richness, redundancy, evenness, and functional group response diversity—into a single indicator for assessing resilience (Flensburg et al. 2023). However, despite the advances made by Flensburg et al. (2023) in the North Sea, their focus on commercially targeted species overlooks an evaluation of the entire fish community, thereby limiting broader applicability. Indeed, relying solely on fishing data may result in an incomplete understanding of marine ecosystem resilience by neglecting the functional roles of non-commercial species, which nonetheless play a crucial role in maintaining the balance and functioning of the ecosystem (Simakova et al. 2022; Sablan et al. 2025).

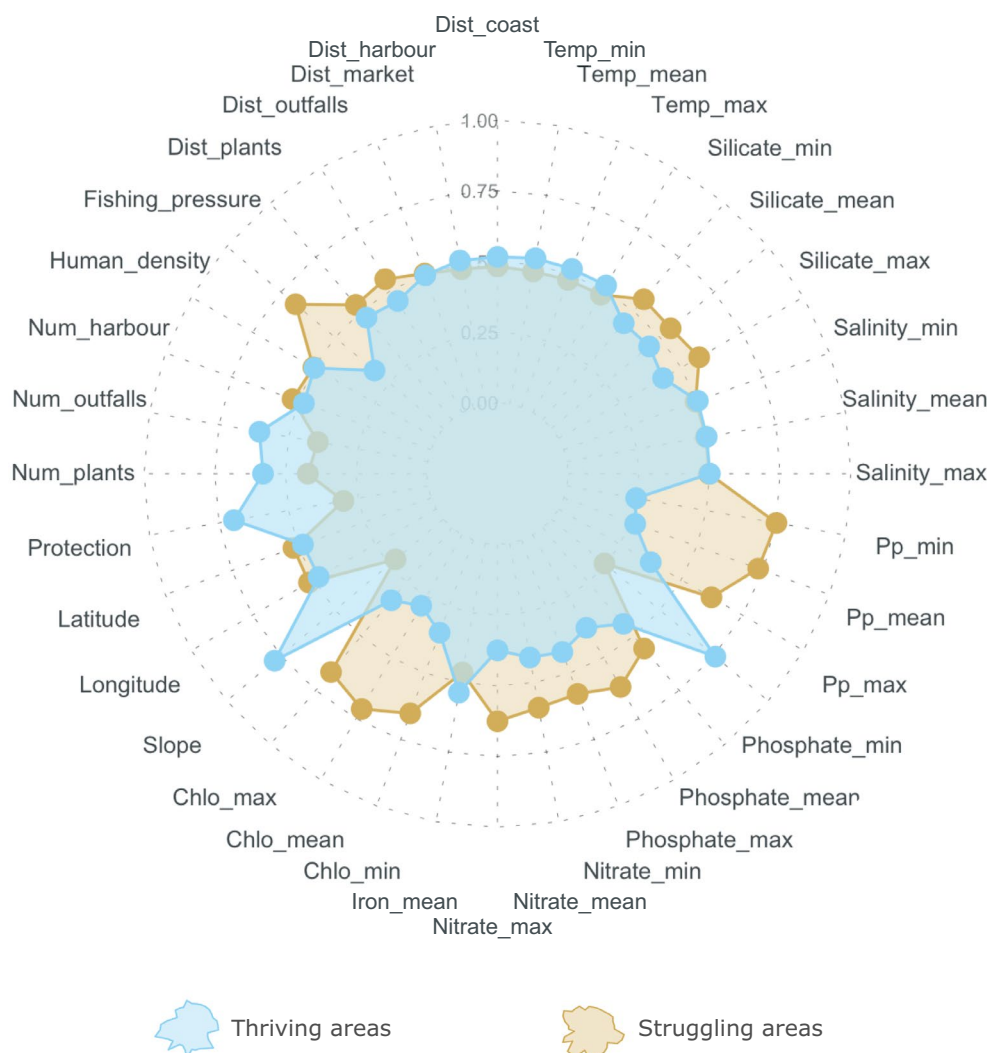


FIGURE 5 | Characterisation of thriving and struggling areas using environmental, physical, and anthropogenic variables employed to predict FRichness and FRedundancy.

Our study used the full reef community to estimate FRichness and FRedundancy. We developed a strategy that enabled the identification of both thriving and struggling areas by considering both metrics simultaneously. This revealed that Saharan and Mediterranean ecoregions showed a higher number of thriving areas than the Alboran, Atlantic, and Canary regions, which had more struggling areas than thriving ones (Figure 4). Balearic Islands emerged as a stronghold of marine resilience, hosting 72% of the thriving areas in the Mediterranean (Figure 3d). Two main reasons may explain these exceptional results. Marine conservation outcomes are probably important, as the islands contain 12 marine protected areas covering 67,420 ha (WDPA). These areas serve as natural refuges, promoting and preserving the biodiversity of marine communities by mitigating the negative impacts of human activities such as overfishing and environmental degradation (Sanabria-Fernández, Alday, et al. 2019). High resilience can also be attributed to the geographic isolation of the Balearic Islands from the mainland. Recently, Pichot et al. (2024) revealed that these islands function as a reservoir for threatened fish and elasmobranch species, largely due to lower fishing pressures and human population density compared to the mainland. In line with this, our findings indicate that thriving areas are characterised by

lower human population density, reduced fishing pressure, and a higher protection status compared to struggling areas. This finding underscores that human influence may affect ecosystem resilience and provides valuable insights for policy formulation aimed at preventing resilience loss. For example, regulating the use of infrastructure, such as roads or access routes to the coast, during specific periods may help to reduce human density and minimise the negative impact of unregulated human activities in the thriving areas (Sanabria-Fernández and Lazzari 2025). Such measures would contribute to preventing degradation and promoting the conservation of ecological functions and broader ecosystem resilience.

Preserving the exceptional thriving areas of temperate coastal systems is critical. However, with 26.5% of our data classified as struggling areas, it is equally important to focus on their improvement. Achieving this requires a detailed understanding of the causes of lower resilience values. For example, in the Canary ecoregion, our findings reveal that there are 6% more struggling areas than thriving ones. Specifically, 86% of these areas are concentrated in the two eastern islands, Fuerteventura and Lanzarote (Figure 3d). Consistent with our

findings, related research has revealed that these two islands exhibit greater social-ecological vulnerability compared to the rest of the Canary Islands (Fernández-Latorre and Diaz del Olmo 2011). This increased vulnerability is largely attributed to the low resilience of their marine fish communities and the elevated tourism pressure they experience (Fernández-Latorre and Diaz del Olmo 2011; Lazzari et al. 2019). Tourism pressure manifests through urbanisation, recreational fishing, increased population during peak season, and the development of ports and marinas (Mejjad et al. 2022). These can lead to a range of negative impacts on the marine ecosystem, including the degradation of critical habitats, such as seagrass beds, water pollution from discharges and waste via marine outfalls (Claudet and Frascchetti 2010), and biodiversity loss, often intensified by the introduction of artificial reefs (Sanabria-Fernández et al. 2018). Indeed, the introduction of artificial reefs can significantly alter the functional dimension of marine fish communities, leading to a reduction in specific trophic functional traits, such as planktivory (Cresson et al. 2019). Consequently, anthropogenic pressures can impact the functional dimension of marine fish communities, altering their structure and their capacity to maintain ecological balance (Henriques et al. 2014; Cresson et al. 2019; Trindade-Santos et al. 2022). Therefore, identifying these vulnerable areas is essential for guiding effective restoration efforts. As demonstrated by Sanabria-Fernández and Lazzari (2025), reducing human-induced pressures—such as pollution and fishing—can significantly enhance the resilience of these struggling areas, enabling targeted measures by policy-makers to promote their recovery.

Recognition of the significant role of environmental factors that influence and shape the functional dimension of marine communities is also crucial (Stuart-Smith et al. 2013; Herrera et al. 2023; McKinley et al. 2023; Luza et al. 2023). Consistent with our findings, Stuart-Smith et al. (2013) demonstrated that sea surface temperature and nutrient levels, such as phosphate concentration, critically vary with the functional attributes of fish communities globally. Similarly, Herrera et al. (2023) emphasised the importance of nitrate and chlorophyll concentrations in discriminating the functional richness and redundancy of marine invertebrate communities along the latitudinal gradient of the American South Pacific. Clearly, an understanding of the influence of environmental dimensions on functionality is needed in order to maximise effective management and conservation strategies aimed at maintaining functional integrity, while enhancing resilience in the context of ongoing climate change.

Given the significant decline in ecosystem resilience, new methodological approaches are necessary to halt their deterioration and maintain ecological integrity and functionality. In this study, we employed a combination of two functional metrics closely related to resilience—namely, FRichness and FRedundancy—to identify thriving and struggling areas. Our results indicate that the proportion of thriving areas is similar to that of struggling areas, and that their distribution is heterogeneous across the ecoregions. Specific regions, such as the Balearic Islands, emerge as a stronghold of resilience due to their high concentration of thriving areas. Conversely, the islands of Fuerteventura and Lanzarote in the Canary Islands host a high concentration of struggling areas, making their restoration a significant management challenge. Additionally, our results demonstrated that

these thriving and struggling areas exhibit distinct characteristics in terms of environmental conditions, physical attributes, and anthropogenic pressures. These findings represent a significant advance in identifying priority areas for conservation and restoration interventions from a functional perspective—an approach that has been only tentatively explored in marine environments. By conserving and promoting the restoration of functional dimensions, we enhance adaptability and recovery capacity in response to disturbances, thereby strengthening ecosystem resilience and contributing to long-term sustainability.

Author Contributions

José A. Sanabria-Fernández: conceptualization, data curation, formal analysis, funding acquisition, writing – original draft, writing – review and editing. **Andrés Baselga, Natali Lazzari, Carola Gómez-Rodríguez, David Mouillot, Graham Edgar, and Vasilis Dakos:** conceptualization, review and editing.

Acknowledgements

We extend our gratitude to the RLS divers, Ángel Orozco, Alberto Moreno, Domingo Borreguero, and Laura Palacín, for their invaluable support in data collection during the fieldwork. The development of this article has been made possible by the Margarita Salas postdoctoral fellowships of J.A.S.-F. and N.L., funded by the Universitat de Barcelona and the Spanish Ministry of Universities, the Recovery, Transformation, and Resilience Plan, and the NextGenerationEU. N.L. has been “Funded by the European Union, MSCA program”, REVALSEA, 101146373. Furthermore, J.A.S.-F. expresses gratitude for the Junta de Andalucía Postdoctoral Fellowship (DGP_POST_2024_00757). Finally, we acknowledge the Spanish Ministry of Defence for providing permits, transportation, and accommodation at the North African military bases. Additionally, we would like to express our appreciation for the insightful comments provided by the editor and anonymous reviewers, which have significantly enhanced the quality of this study. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

Disclosure

Research Team Biosketch: This multidisciplinary team comprises specialists in marine ecology and conservation, resilience, functional diversity analysis, and biogeography. The collective expertise of its members provides a comprehensive perspective on resilience in reef fish communities, with the objective of advancing knowledge from a functional standpoint and reinforcing conservation strategies.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.2fqz6132q>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Fig. S1.** Map illustrating the FRichness predicted. **Figure S2:** Map illustrating the FRedundancy predicted. **Figure S3:** Characterisation of thriving and struggling areas based on environmental, physical, and anthropogenic variables across ecoregions.