Marine Environmental Research 180 (2022) 105702

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

A mesoscale analysis of relations between fish species richness and environmental and anthropogenic pressures in the Mediterranean Sea

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ARTICLE INFO

Keywords:
Bayesian analysis
Fishery management
Spatial variability
Antropogenic pressures

ABSTRACT

Although there is a great knowledge about individual anthropogenic threats to different fish species in the Mediterranean Sea, little is known about how these threats accumulate and interact to affect fish species richness in conjunction with environmental dynamics. This study assesses the role of these threats in the fish richness component and identifies the main areas where the interaction between fish species richness and threats is highest. Our results show that fish richness seems to be higher in saltier and colder areas where the chlorophyll-a and phosphate concentrations are lower. Among the anthropogenic threats analyzed, the costal impact and the fishing effort seems to be the more relevant ones. Overall areas with high fish richness are mainly located along the western and northern shores, with lower values in the south-eastern regions. Areas of potential high cumulative threats are widespread in both the western and eastern basins, with fewer areas located in the south-eastern region. By describing the spatial patterns of the fish richness and which drivers explain these patterns we can also identify which anthropogenic activities can be managed more effectively to maintain and restore marine fish biodiversity in the basin.

1. Introduction

Evaluating the role of spatial dynamics of environmental processes in determining richness variation can provide insights into marine conservation and management planning (Menegotto and Rangel, 2018). Indeed, protecting as many species as possible instead of a single species under a single threat at a time is a first step toward an integrative ecosystem assessment (Fonseca et al., 2017). However, to achieve this objective a better understanding of the complexity and the multidimensionality of species richness is needed (Vilas et al., 2020).

Over the past three decades, numerous studies have demonstrated relationships between species richness and environmental variables that might reflect the availability of resources (Cumming, 2004; García-Charton and Pérez-Ruzafa, 2001; Sosa-López et al., 2007). At large geographical scales, the most used proxies for resource availability include net primary productivity (Kaspari et al., 2000), and temperature (Buckley et al., 2012). Environment-richness relationships have been shown to hold through time as well as across space, lending additional support to explanations based on top-down constraints (Hurlbert and Stegen, 2014).

Studies on how anthropogenic pressures influence the species richness are rare although it is only the anthropogenic component (human activities and resource use) that can be directly managed (Pennino et al., 2021). Therefore, identifying whether and where anthropogenic impacts affect the species richness, as well as the strength of this impact, is essential to inform more efficient conservation planning (Bellido et al., 2019).

The Mediterranean Sea, although representing a small part of the world's oceans, is inhabited by an unusually rich and diverse biota. It is home to approximately 17,000 species, representing 4–18% of the world's marine biodiversity, and includes temperate, cosmopolitan, subtropical, Atlantic and Indo-Pacific taxa (Bianchi and Morri, 2000;

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https://doi.org/10.1016/j.marenvres.2022.105702
Received 31 March 2022; Received in revised form 9 June 2022; Accepted 10 July 2022
Available online 5 August 2022

Coll et al., 2010). This high marine richness is due to different factors such as, among others, its geological history and the numerous climatic and hydrological events that led to the simultaneous existence of both temperate and subtropical species (Bianchi and Morri, 2000). Consequently, the Mediterranean Sea is considered a true biodiversity and richness hotspot (Bianchi and Morri, 2000; Coll et al., 2010), with an estimated 20–30% of endemic species (Boudouresque, 2004).

Nowadays, several anthropogenic pressures are affecting the Mediterranean coastal and marine ecosystems, such as habitat degradation, climate changes, coastal urbanization, overexploitation and the introduction of exotic species (Coll et al., 2010, 2012). As a result, the Mediterranean Sea has the highest proportion of threatened marine species in Europe (32%) with 21% listed as vulnerable and 11% as endangered (Lejeusne et al., 2010; Zenetos et al., 2012; Katsanevakis et al., 2013; Fuerst-Bjeliš, 2017).

In this study, we used Bayesian hierarchical spatial models to analyse the fish species richness along the Mediterranean sea. Differently to previous research studying species richness in Mediterranean marine ecosystems (Coll et al., 2010, 2012; Albouy et al., 2013; Corrales et al., 2018), we included in the modelling approach spatially-explicit information of anthropogenic variables, in addition to the environmental ones, in order to assess the role of these threats on the richness component. This is the first time that such an approach has been applied using this modelling methodology and complements previous studies aiming at explaining spatial patterns of fish species richness in the Mediterranean. In addition, the use of the Bayesian approach allowed quantifying and propagating the uncertainty through the entire modelling process. Indeed, underestimating uncertainty can lead to inefficient informed decision-making and management of natural resources (Schwartz, 2012). This is a fundamental issue in marine ecology, where the identification of priority areas is one of the most used tools in conservation and management to guarantee the long-term sustainability of species.

2. Material and methods

2.1. Study area

The Mediterranean Sea occupies a deep, elongated and almost landlocked irregular depression which extends between latitudes 30^o and 46^o N and longitudes 5^o 50' W and 36^o E (Gržetic et al., 2013). The Strait of Sicily divides the sea into two distinct basins, the western one (0.85 million km^2) and the eastern one (1.65 million km^2) (Coll et al., 2012).

The Mediterranean is an evaporation basin, i.e., average evaporation exceeds precipitation, which has important implications for the circulation and biogeochemistry of the sea. Its eastern surface is characterized by high salinity and warmer waters, while the relatively low salinity influx of Atlantic water through the Strait of Gibraltar dominates the western Mediterranean Sea, as well as colder waters (Tanhua et al., 2013). The basin is characterized by strong environmental gradients that make the eastern end more oligotrophic than the western end (Bianchi and Morri, 2000). Local characteristics enrich the coastal areas through changing wind conditions, temporary thermoclines, river flows and discharges, and municipal wastewater.

2.2. Fish species richness data

Fish species richness data were extracted from Coll et al. (2012), which collected an historical database (i.e., from 90s to 00s) of marine species in the Mediterranean Sea. The dataset includes species from coastal and open sea areas representing, benthic, demersal and pelagic habitats, and listed in Coll et al. (2010, 2012); Albouy et al. (2015)). The richness index was estimated as the sum of the species co-occurring in each cell into which we have divided all the study region, that is, the Mediterranean Sea. The grid cell was obtained by overlapping distribution maps at fine-scale resolution ($0.1 \times 0.1^\circ$). In particular, data on exotic fish species were collected from the Atlas of the "Commission Internationale pour l'Exploration Scientifique de la Méditerranée" (CIESM) and from Quignard and Tomasini (2000). Data for other fish species were available from the "Fishes of the Northern Atlantic and Mediterranean" (FNAM atlas; Whitehead (1984)) and were updated and integrated by Lasram and Mouillot (2009). This information is now freely available through SeaLifeBase (http://www.sealifebase.org; Palomares and Pauly (2010)), FishBase (http://www.fishbase.org; Froese and Pauly (2000)) and through the Sea Around Us project website (http://www.seaaroundus.org; Pauly (2007)), as discussed by Coll et al. (2012). The complete list of the 625 species used to generate the richness index can be found in supplementary materials.

The richness index presented an average of 170 species of fish per cell, varying with a minimum of 81 to a maximum of 372 species per cell (Fig. 1). Fig. 1 shows that this index has a longitudinal gradient from higher values in the western part of the basin, and lowest in the southern-eastern part.

2.3. Environmental variables

To model the distribution of fish richness species, a total of 30 physical and climatology variables (Table 1) were extracted from the Bio-Oracle (Tyberghein et al., 2012) (https://www.bio-oracle.org) and the MARSPEC (Sbrocco and Barber, 2013) (http://www.marspec.org) databases with a 5 arcmin spatial resolution (Fig. 2). In addition to these variables we also created a new bathymetry variable, "Bathy-cod", categorizing the bathymetry in two strata: "1" for the continental shelf and "0" for non-continental shelf.

2.4. Cumulative anthropogenic threats

Six different cumulative anthropogenic threats occurring in the Mediterranean Sea with a spatial resolution of $0.1 \times 0.1^\circ$ grid cells were extracted from previous data compilations (Coll et al., 2010, 2012). The generated variables accounted for the presence or absence of the different threats (expressed in a continuum between 0 and 1) at each grid cell (Fig. 3). Specifically, the threats used are:

- (1) Coastal-based impacts: cumulative effects from inorganic and organic coastal pollution, nutrient runoff, litter, hypoxia and presence of alien species.
- (2) Ocean pollution: deposition of heavy metals and inorganic nitrogen deposition.
- (3) Exploitation of marine resources by fishing: direct impacts of the exploitation of marine resources by industrial, semi-industrial and artisanal fisheries.
- (4) Climate change: cumulative effects from changes in sea water temperature, in the intensity of ultraviolet radiation and in water acidification.
- (5) Maritime activities: cumulative effects from maritime traffic due to shipping and other transport and the presence of oil rigs.
- (6) Trawling and dredging disturbances: cumulative (from 1950 to 2006) high disturbance on the sea floor by bottom fishing gear operations.

In addition to these variables we also added another layer representative of a the cumulative fishing effort. This layer was generated using Automatic Identification System (AIS) (Kroodsma et al., 2018) maps of trawlers, long liners and purse seiners from 2012 to 2017 from the Global Fishing Watch website (GFW: http://globalfishingwatch.org). Although there is a temporal mismatch between this anthropogenic variable and the species richness data, is still an approximation of where the impacts are at spatial level.

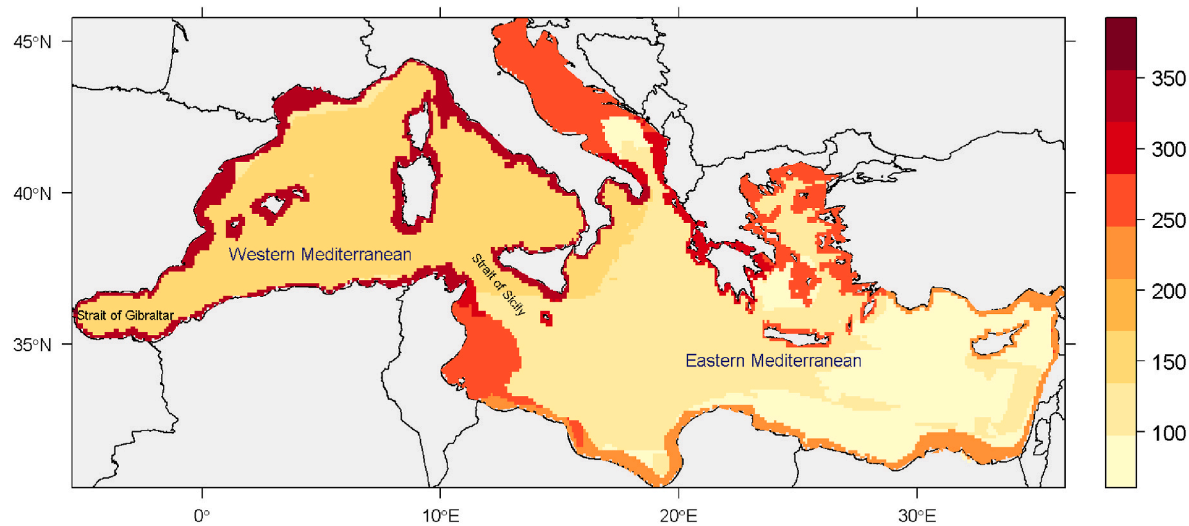

Fig. 1. Fish species richness index for the Mediterranean Sea.

2.5. Variables preparation and selections

In order to better interpret both the direction (positive or negative) and magnitudes (effect sizes) of the parameter estimates in relation to the others, all the explanatory variables, both environmental and anthropogenic predictors, were standardized, i.e. using a difference from the mean divided by the corresponding standard deviation (Gelman, 2008).

Data exploration techniques were used to identify any outliers and possible correlation between the explicative variables Zuur et al. (2010). In particular, outliers were detected with the Cleveland dotplot (Cleveland, 1993) with the ggplot2 package (Wickham, 2011) of the R software R Core Team (2021). Correlation among variables was checked by performing a Pearson's correlation test with the corrplot R-package (Wei et al., 2017). Variables with a correlation higher than $\widehat{\rho} = 0.70$ were removed from the analysis following ecological and biological criteria and bibliographic studies (Figures S1 and S2).

2.6. Modelling fish species richness

Fish species richness was modeled using a Poisson distribution, while the common logarithmic link function was used to relate the fish species richness expected value with the covariates and the underlying spatial effect. In particular, if Y_i denotes the value of the species richness in each cell of the grid (denoted by i), the relationship between Y_i and both the selected covariates and the spatial effect can be expressed as the following spatial Poisson regression model:

$$\begin{array}{lcl} Y_i & \sim & \text{Poisson}(\lambda_i) \\ \log(\lambda_i) & = & \boldsymbol{X}_i\boldsymbol{\beta} + u_i, \end{array}$$

where $\boldsymbol{X}_i$ is the vector corresponding to the i-th row of the design matrix (formed by the covariates and a first column of ones, the one multiplying the intercept β_0); and u_i corresponds to an area-specific random effect, which is modeled as spatially structured. In this study, we implemented the intrinsic conditional autoregressive model (ICAR, Besag, 1974) for $\boldsymbol{u} = \{u_1, \ldots, u_n\}$, in order to reinforce the idea that the richness of each location of the grid depends on the values of its neighbors.

More detailed, if we consider n areas, each characterized by a set of neighbors $\mathcal{N}(i)$, u_i is assumed to be the following random variable:

$$u_i|u_j, i \neq j, \tau \sim \text{N}\left(\frac{1}{\mathcal{N}_i}\sum_{i\sim j} u_j, \frac{1}{\mathcal{N}_i\tau}\right),$$

where $i \sim j$ denotes that j is a neighbor of j; $\frac{1}{\mathcal{N}_i}\sum_{i\sim j} u_j$ is the mean for the area i, which is depending of the number of neighbors of i ($\mathcal{N}_i$); and $\frac{1}{\mathcal{N}_i\tau}$ corresponds to the precision for the area i, which is also depending on the number of neighbors ($\mathcal{N}_i$). If an area has many neighbors then its precision will be bigger (and consequently, the variance will be smaller). In particular, the neighbourhood structure established was determined using the distance of 15 km, in other words, two locations are neighbors if the distance between them is less than 15 km. Other different distances (20, 30 and 40 km) were also used, but resulted in models with worst fit and predictive behavior.

The Bayesian approach was used to make inference and prediction in the previous model, as it provides a better quantification and propagation of the uncertainty through the entire modelling process. Within this approach, parameters are treated as random variables and so, prior knowledge (if available) can be incorporated using the corresponding prior distributions. In our case, default vague Gaussian distributions N($\mu = 0$, $\tau = 0.001$) were imposed for the parameters involved in the fixed effects (β_j), while in order to express the prior knowledge (or the lack of it) about hyperparameters, the default prior gamma(1,0.1) was used for φ. Finally, a penalized complexity prior (PC-prior) was established for the precision of the random effect τ according to Simpson et al. (2017). In our particular case, the PC-prior for τ was defined in terms of the square of its inverse, the standard deviation σ, such that $P(\sigma > 5) = 0.1$.

As usual in this context, performing analytical inference and prediction on the resulting Bayesian hierarchical spatial model is not an easy task. In our case, implementation was done using the integrated nested Laplace approximation (INLA) approach (Rue et al., 2009; Gómez-Rubio, 2020) and its corresponding R-INLA package.

3. Results

The final model with the uncorrelated variables retained as predictors: the sea surface chlorophyll-a (S-Chl-a), phosphate (S-Phos), temperature (SST), salinity (SSS), distance to the coast, the codified bathymetry, coastal impact, marine activities, exploitation of the marine resources, and fishing effort jointly with the spatial effect. Table 2 presents the posterior mean, standard deviation and 95% symmetric credible intervals for the parameters corresponding to the fixed effects.

Among the environmental variables, the bathymetry is the most relevant one (i.e. greater estimated coefficient). Results showed that continental shelf areas have higher fish richness values with respect to the non-continental shelf areas (reference level). The distance to the coast variable confirms this result showing a negative relationship with the richness index, reflecting that fish richness is higher in coastal waters. Chlorophyll-a and phosphate concentration show a negative

Table 1
Summary of the environmental covariates used in the study.

Variables	Description	Source
Bathymetry	average depth of the seafloor (meters)	MARSPEC
AspEW	East/West aspect of the seabed expressed (radians)	MARSPEC
AspNS	North/south aspect of the seabed expressed (radians)	MARSPEC
Curvature	Plan curvature of the seabed (divergent + convergent -)	MARSPEC
Distance	Distance to the coast (kilometres)	MARSPEC
Slope	Slope of the seabed (degree)	MARSPEC
Concavity	Concavity of the seabed (degree)	MARSPEC
Roughness	Complexity of the seabed (degree)	MARSPEC
S-Chl-a	Sea surface Cholorophyll-a concentration (mg.m-3)	Bio-Oracle
B-Chl-a	Bottom Cholorophyll-a concentration (mg.m-3)	Bio-Oracle
SSS	Sea Surface Salinity (PSU)	Bio-Oracle
BSS	Bottom Surface Salinity (PSU)	Bio-Oracle
SBT	Sea Bottom Temperature (C)	Bio-Oracle
SST	Sea Surface Temperature (C)	Bio-Oracle
S-Oxy	Sea surface dissolved oxygen in water (mol/m3)	Bio-Oracle
B-Oxy	Bottom dissolved oxygen in water (mol/m3)	Bio-Oracle
S-PP	Sea surface primary production (grams/m^2/day)	Bio-Oracle
B-PP	Bottom primary production (grams/m^2/day)	Bio-Oracle
S-Nitr	Sea surface nitrate concentration (mol/m3)	Bio-Oracle
B-Nitr	Bottom nitrate concentration (mol/m3)	Bio-Oracle
S-Phos	Sea surface phosphate concentration (mol/m3)	Bio-Oracle
B-Phos	Bottom phosphate concentration (mol/m3)	Bio-Oracle
Iron	Average molar concentration of iron (μg/m3)	Bio-Oracle
S-Sil	Sea surface silicate concentration (μmol/m^3)	Bio-Oracle
B-Sil	Bottom silicate concentration (μmol/m^3)	Bio-Oracle
S-Phy	Sea surface phytoplankton biomass (μmol/m3)	Bio-Oracle
B-Phy	Bottom phytoplankton biomass (μmol/m3)	Bio-Oracle
PAR	Photosynthetically available radiation (μE/m2/s)	Bio-Oracle
pH	Measurement of acidity or alkalinity of water	Bio-Oracle
CaCO3	Average concentration of calcite (mol/m3)	Bio-Oracle

association with the fish richness index, suggesting that fish species are likely to concentrate in less productive areas with lower phosphate concentration. Moreover, fish richness seems also to be higher in saltier and colder areas (Table 2).

Among the anthropogenic threats, coastal impact seems to have a relevant impact in the fish richness spatial distribution. The relationship between our response variable is positive, i.e. the most coastal impact the higher value of the fish richness index. A similar result was also found for the fishing effort which presents a positive relationship, meaning than areas where the fishing effort is higher are also the ones with higher fish richness value (Table 2).

Finally the exploitation of marine resources and the maritime activities presented a negative relationship with the fish richness index, i.e. higher values of these anthropogenic factors correspond to lower fish richness index values (Table 2).

The map of the posterior mean of the spatial effect (Fig. 4) confirms the longitudinal pattern with higher fish richness values from the Western to the Eastern areas of the Mediterranean Sea. From Fig. 4 it is also possible to see a latitudinal trend with higher fish richness values in the Northern areas of the Mediterranean with respect to the Southern ones.

As fish richness hot-spots it is possible to identify from the Western to the Eastern: 1) waters off the Ebro Delta and Balearic islands in the Iberian waters; 2) the Gulf of Lion in France; 3) waters around the Sardinia and Corsica islands, as well as the Tuscan archipelago between the Ligurian Sea and Tyrrhenian Sea; and 4) waters off the Po Delta in the Adriatic Sea (Fig. 4).

The map of the spatial standard deviation clearly shows that the Adriatic and the Aegean Sea are the areas where there is the larger amount of variability (Fig. 5).

4. Discussion

Understanding the spatial patterns of fish species richness is key for marine conservation and management planning. Although both environmental processes and human activities influence the richness variability, it is only the anthropogenic component that is generally manageable. In this context, the novelty of the proposed approach is the possibility of identifying which are the drivers (environmental or anthropogenic) that explain the Mediterranean distribution of fish richness using a spatially explicit framework.

Bathymetry, together with distance from the coast, were the most relevant environmental variables, which is not surprising since they have often been related to the distribution of fish species and, more generally, to the structure of fish assemblages (Kendall and Haedrich, 2006; Pittman et al., 2009; Vilas et al., 2020; Lloret-Lloret et al., 2021). Several studies have shown that fish richness decreases with depth, since deep seas are more homogeneous than coastal systems in terms of temperature, light, salinity, and nutrients (Fonseca et al., 2017; Worm and Tittensor, 2018).

Fish richness was sensitive to sea surface temperature (SST), showing that with higher temperature, lower fish richness values are expected. This result is in line with recent studies, as for example Chaudhary et al. (2021), which shows that climate change is impacting the marine richness at a global scale, making waters in tropical and subtropical areas too warm to survive for many species. However, it is also possible that the negative relationship of the fish richness with the SST is reflecting the longitudinal trend of this index in the Mediterranean Sea as warmer waters are present in the Eastern Mediterranean were the richness index is lower. Similarly the negative relationship with the sea surface concentration of chlorophyll-a and phosphate is possibly due to the fact that the areas where these two variables have highest values are also areas with lower fish richness values as for example the Aegean Sea.

Both the coastal-based impact and the fishing effort showed a positive relationship with the fish species richness as both threats are concentrated in coastal areas and specifically where the richness hot-spots are. Relevant threats that occur in the open sea are marine activities and exploited marine resources and were also selected relevant by the model but showed a negative relationship with the richness index. This is probably due to the fact that these factors affect areas with lower richness and influence specific groups as for example large predatory fish (Coll et al., 2012).

The differential gradient of species richness has been already described in the Mediterranean Sea to be linked with the gradient of environmental factors, and it is known to be decreasing from the NW to the SE Mediterranean Sea (Coll et al., 2010). However, some parts of the Mediterranean Sea are better studied than others and the low values of the Southern part of the basin, especially, are partially due to a lower sampling effort (Coll et al., 2010)). In fact, there is only few areas of the Mediterranean Sea and European Seas that show enough sampling effort to have a good species richness description (Ramírez et al., 2022). This highlights the need to intensify the study of marine biodiversity.

By describing the spatial patterns of the fish richness and which drivers explain these patterns we can also identify which anthropogenic

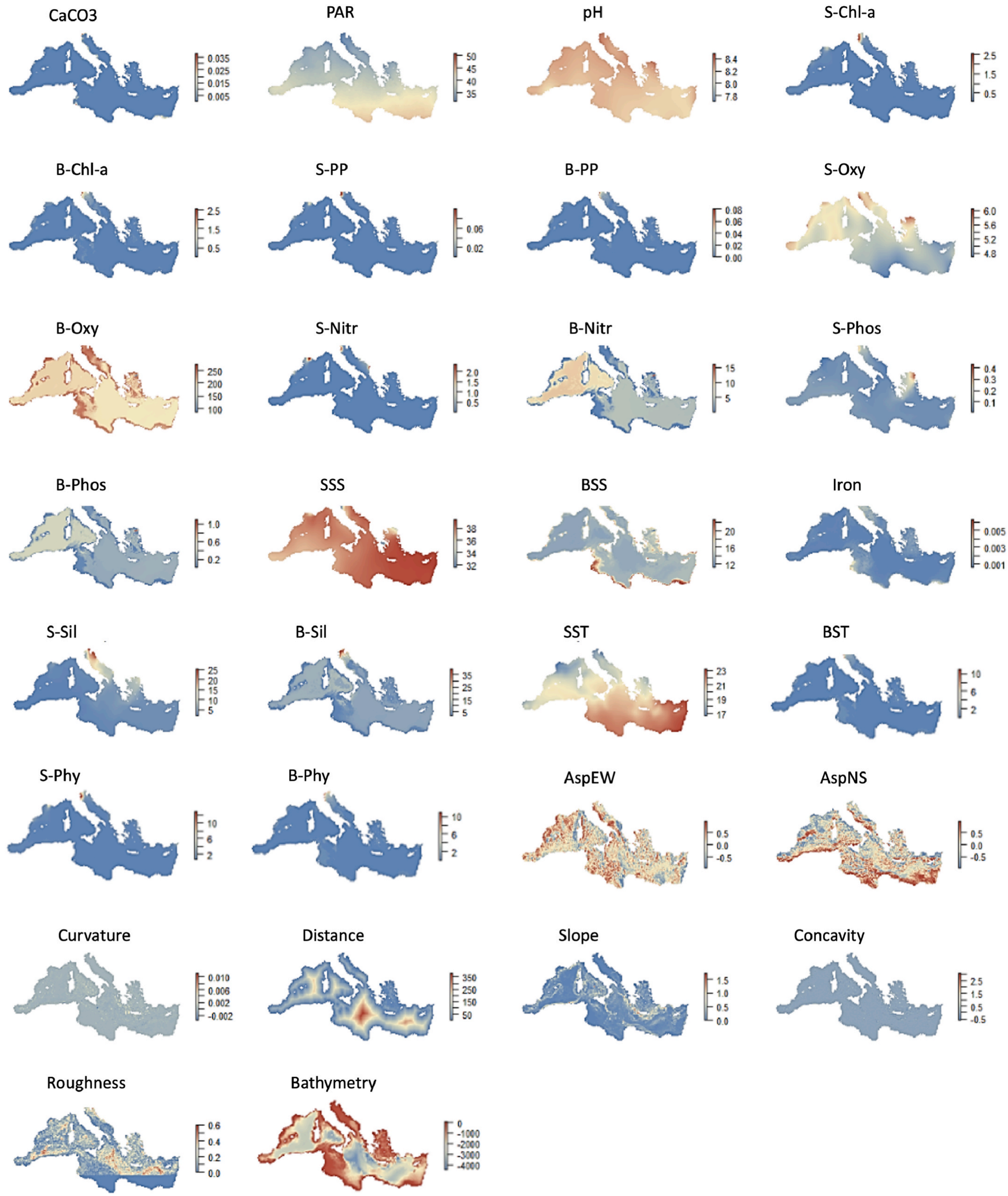

Fig. 2. Maps of the environmental variables used in the study.

activities can be managed more effectively to conserve it. Patterns of fish species richness are an essential piece of ecological information that forms the basis for conservation decisions (Levin et al., 2014). However, distilling useful ecological information from species distribution patterns can be methodologically complex and challenging. In this regard, it is mandatory that analyses of spatial distribution patterns have a clear focus that is based on sound ecological principles. The present work used Bayesian hierarchical models, with a spatially structured

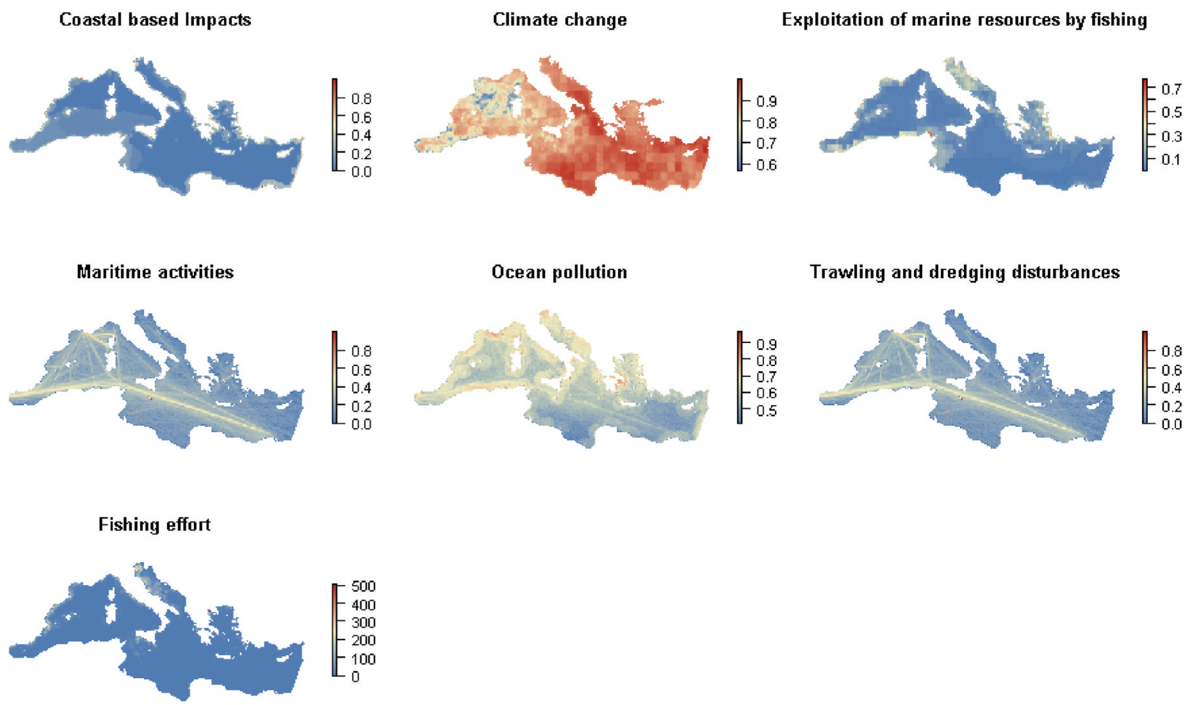

Fig. 3. Maps of the cumulative anthropogenic threats used in the study.

Table 2
Posterior mean, standard deviation (Sd) and 95% symmetric credible intervals corresponding to the parameters regarding the fixed effects.

Variable	Mean	Sd	95% CI
Intercept	5.00	< 0.001	[4.99, 5.00]
S-Chl-a	−0.05	> 0.001	[-0.07, −0.02]
S-Phos	−0.01	> 0.001	[-0.01, 0.01]
SSS	0.02	< 0.001	[0.02, 0.03]
SST	−0.06	> 0.001	[-0.10, −0.00]
Distance	−0.07	< 0.001	[-0.08, −0.05]
Bathy-cod-1	0.16	> 0.001	[0.14, 0.18]
Coastal impact	0.33	< 0.001	[0.32, 0.33]
Exploitation-resources	−0.03	< 0.001	[-0.03,-0.01]
Maritime activities	−0.02	< 0.001	[-0.03,-0.01]
Fishing effort	0.02	< 0.001	[0.01,0.03]

random effect, to estimate fish species richness as a function of environmental, topographic and anthropogenic covariates based on data collected from various sources. Results generated by the models present a very intuitive graphical interpretation. From the maps obtained from the final model, it is possible to spatially identify the regions of highest and lowest fish species richness in the Mediterranean Sea. Interesting, our results highlight different areas of maximum richness at the end of the continental shelf that maybe are easier to be protected with respect to the coastal waters where human activities are concentrated. In addition these transitional areas from the coast to the deep sea are important for cold coral reefs, seamounts and submarine canyons (de Juan and Lleonart, 2010).

It is important to bear in mind that this study does not consider the temporality of the data, but aims to make a mesoscale spatial approximation of the fish richness in the Mediterranean sea. Further analysis are needed exploring complementary databases to investigated the possible

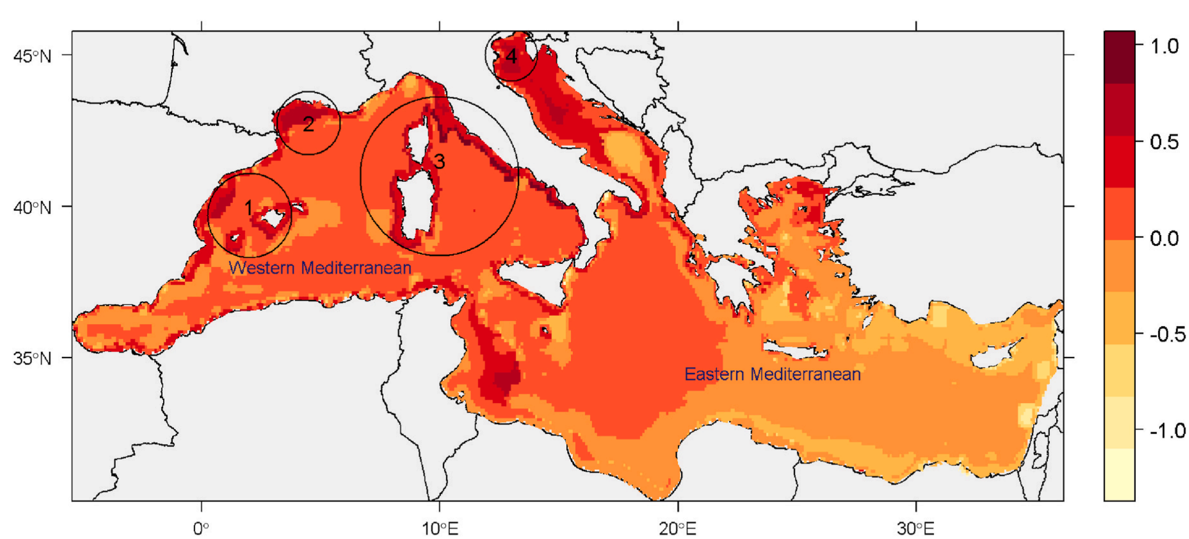

Fig. 4. Posterior mean of the spatial effect in the model for the fish richness index.

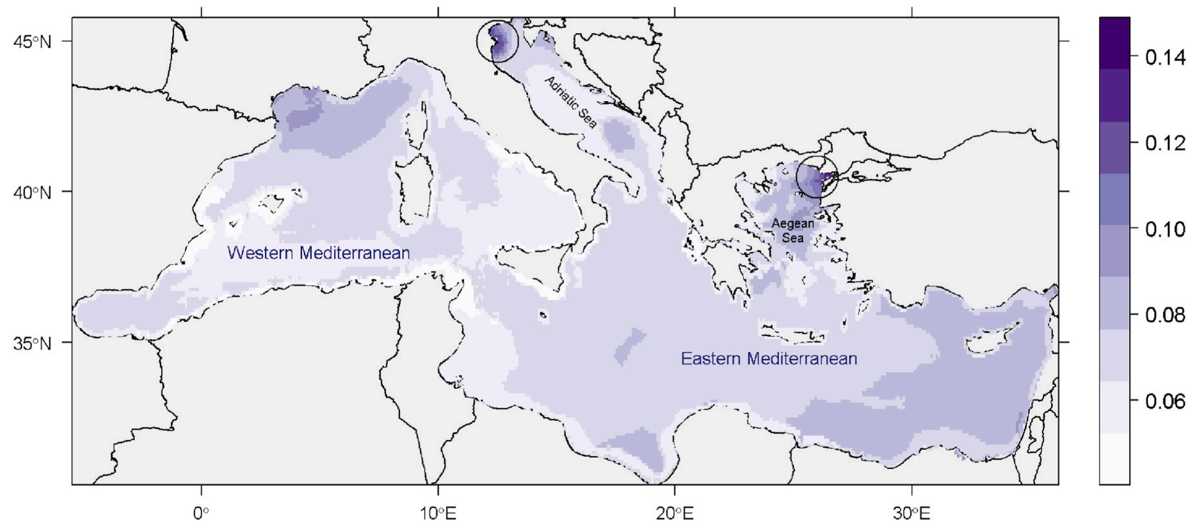

Fig. 5. Standard deviation of the posterior distribution of the spatial effect in the model for the fish richness index.

seasonal and annual trends related with the species and habitat dynamic. Also, due to the nature of the variables and the large scale of the analysis, our study may be missing the identification of important finer scale patters that are involved in describing the heterogeneity of diversity distribution (Veloy et al., 2022).

This work highlights the importance of the coastal and offshore region of the Mediterranean Sea as a relevant area for conservation due to its high fish species richness and stresses the need to implement marine spatial planning approaches to identify priority areas of conservation.

Author statement

Conceptualization: MGP and MC; Methodology: JC, DC, JM, MGP; Formal analysis: JC, JM; Writing - Original Draft: JC, DC, MGP; Writing-Reviewing and Editing: JC, MGP, DC, MC, JM.

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.

Acknowledgments

MGP to the project IMPRESS (RTI2018-099868-B-I00), ERDF, Ministry of Science, Innovation and Universities - State Research Agency. MC acknowledges partial funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869300 (FutureMares project) and the Spanish project ProOceans (Ministerio de Ciencia e Innovación, Proyectos de I + D + I (RETOS-PID2020-118097RB-I00). MC acknowledges the institutional support of the 'Severo Ochoa Centre of Excellence' accreditation (CEX2019-000928-S). D.C. would like to thank the Spanish Ministerio de Ciencia e Innovación - Agencia Estatal de Investigación for grant PID2019-106341 GB-I00 (jointly financed by the European Regional Development Fund, FEDER). J.M.-M. would like to thank the Ministry of Science, Innovation and Universities for PID2020-115882RB-I00 research project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105702.

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