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Mapping Mediterranean bentho-demersal communities to better inform marine conservation

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Abstract

Marine conservation and spatial planning are seeing increasing interest by stakeholders at the local, regional and international levels to balance biodiversity protection, sustaining fisheries and accommodating new uses of the marine environment. Marine protected areas (MPAs) are one of the most common conservation tools being implemented worldwide to reach conservation targets. However, their implementation does not usually take the heterogeneous distribution of bentho-demersal communities into account. This has led to uneven conservation of existing communities, resulting in the misinterpretation of current protection coverage levels. Here, we mapped the distribution of the bentho-demersal community of the Balearic Sea, in the northwestern Mediterranean Sea, using a joint species distribution model of 129 species of fish, crustaceans and cephalopods. We identified three distinct bioregions, and found that only 3.13% of the Shelf, 2.96% of the Upper slope and 0.89% of the Middle slope bioregions are covered by the 1089 km^2 of demersal no-take MPAs included in our analyses. Bentho-demersal communities were distributed mostly as a factor of bathymetry, but were also clearly delimited by bottom temperature, and had lower species-rich communities in deeper bioregions. Furthermore, we found a negative effect of bottom trawl fishing on species richness in more heavily fished locations. Our results allow for the evaluation of an already implemented MPA network in the Balearic Sea, and suggest that more coverage is needed to fulfill current conservation set at the European and international levels. In order to achieve meaningful biodiversity conservation and help future marine conservation efforts, increases in MPA coverage will need to be supported by studies such as this one to ensure even representation of all marine bioregions and their communities.

KEYWORDS

benthic habitat, biodiversity, bioregionalisation, bottom trawling, fisheries, marine reserves

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1 | INTRODUCTION

Mediterranean bentho-demersal communities—groups of interacting species that occur together in space (Stroud et al., 2015) and that live on the seafloor or in direct interaction with it—have been under human exploitation by trawling fisheries for over 200 years (Osio, 2012). In the Mediterranean and Black Seas, bottom trawling and other forms of fishing have significantly impacted bentho-demersal habitats and their communities to their current impoverished state, where 58% of the stocks are fished at unsustainable levels (FAO, 2023). This fishing pressure, with time, has led to a shift in our perception of what constitutes healthy marine communities in terms of abundance and biomass (Pauly, 1995). Moreover, it has also shifted how marine communities are distributed and assembled. Marine ecosystems also face extended threats, including climate change (Doney et al., 2012), pollution (Balcells et al., 2023; Irizuki et al., 2018), and new uses of the marine environment such as wind farms (Galparsoro et al., 2022), all of which may synergistically affect bentho-demersal communities and overall marine ecosystem functioning. Balancing conservation targets and extractive activities such as fishing is a challenge being addressed through a diverse range of local, regional and international measures and solutions. Some of these include improving selectivity and implementing semi-pelagic trawling doors to lower ecosystem impact locally (Bahamon et al., 2024), aiming for maximum sustainable yield (MSY) to achieve sustainable and economically viable fishery activities at the regional level (Maynou, 2014), and international agreements and regulations such as the EU Biodiversity Strategy for 2030 (European Commission, 2020) or the Kunming-Montreal Global Biodiversity Framework (CBD, 2022).

However, one of the most commonly available and widely used management measures to carry out conservation for marine ecosystems presently are marine protected areas (MPAs), which have seen an increase in implementation in recent years (CBD, 2022). MPAs have been shown to improve ecosystem resilience, protect biodiversity, increase local biomasses, and enhance the socio-economic fabric of neighboring human communities (Jacquemont et al., 2022). These benefits are mostly seen in MPAs that are fully protected and permanently closed to fishery activity, such as no-take MPAs (Sala & Giakoumi, 2018), which are further enhanced if the closures are part of a well-connected network of MPAs (Berkström et al., 2022). However, even when MPAs are properly implemented and their restrictions enforced, not all marine communities are equally protected. This is reflected at the global scale, and currently implemented MPAs do not cover an even representation of all marine ecoregions (Pike et al., 2024).

Achieving efficient implementation and enforcement of management regulations targeted at protecting biodiversity and reducing the impact of fisheries on marine ecosystems requires knowing where and how biodiversity is distributed, as well as how it responds to the diverse driving forces that shape it (Richardson & Whittaker, 2010). Mediterranean bentho-demersal communities include hundreds of macrofaunal species which, in turn, support diverse multispecific bottom trawl fisheries (FAO, 2023). Understanding how co-existing species that compose bentho-demersal communities are distributed poses a challenge that is not easily solved by studying the distribution of single species with relation to their environment alone. However, bioregionalisation, or the process of classifying biodiversity into geographically defined communities, is a valuable tool that can help our understanding of current protection measures (e.g., MPAs), fill the gaps of under-protected marine communities, and improve management decisions (Hill et al., 2017; Woolley et al., 2020). Its strength relies on leveraging statistical analyses of multi-species biological datasets and environmental data over areas where the species included are relatively constant to simplify and structure biodiversity data in an informative and applicable way (Woolley et al., 2020).

Here we use data from the bentho-demersal community of the northwestern Mediterranean Sea, including species of commercial and non-commercial value, to fit a JSDM of 129 species of fishes, cephalopods and crustaceans. Our main objectives are to: (1) model the Mediterranean bentho-demersal community distribution in the Balearic Sea using a joint species approach; (2) evaluate environmental and human (i.e., fishing impact) drivers in distributing community richness; (3) classify the bentho-demersal community into spatially delineated bioregions, and characterize their associated environment; (4) assess the protection offered by an existing no-take MPA network in the northwestern Mediterranean using the mapped distributions as a case-study to inform and improve marine conservation in the area.

2 | MATERIALS AND METHODS

2.1 | Community data and study area

The study was conducted over the Balearic Sea, located in the northwestern Mediterranean Sea (Figure 1). Bentho-demersal community data were obtained from the ICATMAR database, supported by an ongoing fishery monitoring program in the area (ICATMAR, 2023). This included bottom trawling samples collected on board 13 fishing vessels from nine ports over the 2019–2023

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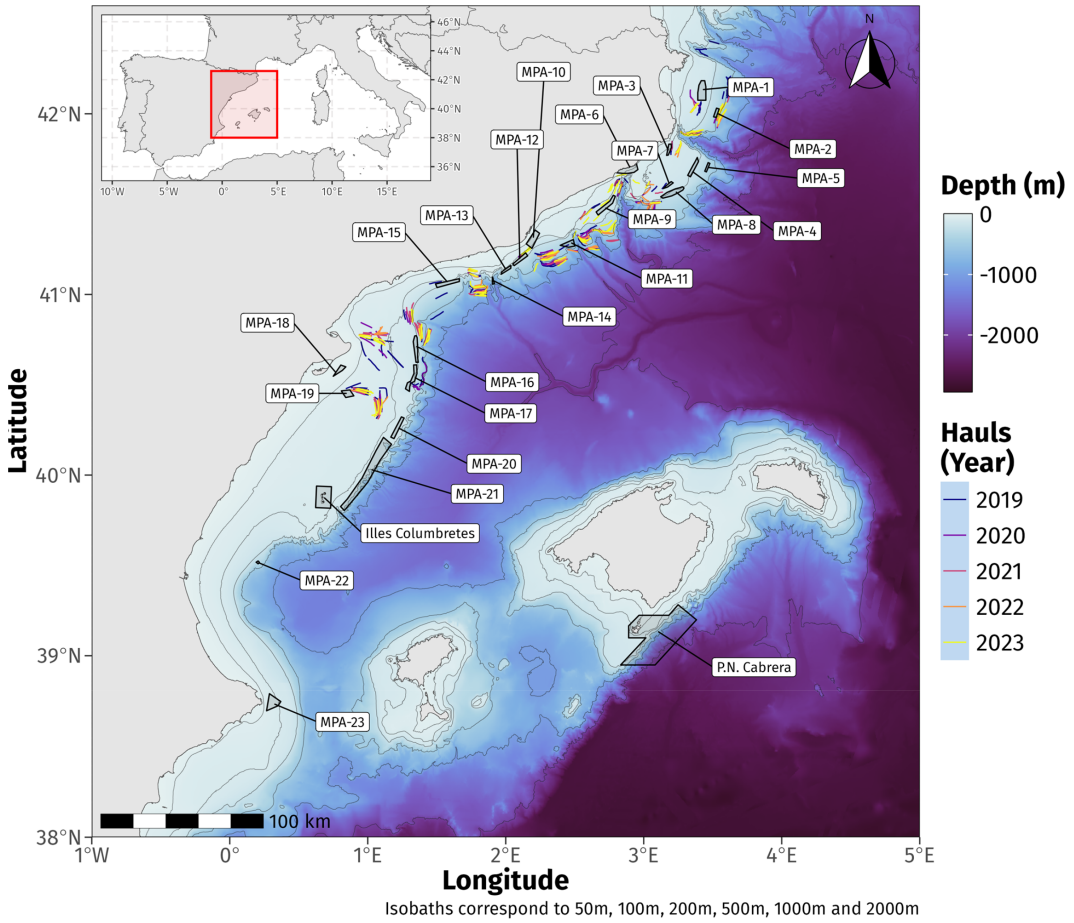


FIGURE 1 Study area (Balearic Sea, northwestern Mediterranean Sea). Colored lines show transects of the fishing hauls during the period 2019–2023. Black polygons show the 25 no-take MPAs currently established in the area and considered in the analyses.

period (Figure 1). GPS trackpoints during fishing maneuvers, along with the net mouth opening, allowed for the standardization of the capture as detailed in Carreton et al. (2025). While monitoring is done onboard commercial fishing vessels, the sampling stations follow a semi-directed structure and all of the captured community is collected and classified (including commercial and non-commercial species, as well as other organic and inorganic materials present on the seabed). Data for the analyses were restricted to hauls performed below 50 m depth (minimum allowable bottom trawling depth; EU Reg. 1967/2006), while the maximum depth included in the sampling was 733 m, close to the maximum depth most commonly fished by trawlers in the area (ICATMAR, 2024). Most of the captured individuals were thoroughly classified to the species level, and unclassified individuals were removed from downstream analyses (usually belonging to rare and difficult to classify species). Species with a total of less than 30 individuals for the whole period, or appearing in less than 5% of the hauls, were also removed to avoid including very rare species with few data points in the analysis. In total, 472 hauls with 129 species of 3 phyla, 5 classes, 32 orders, 77 families and 105 genera were included in the final model (Supplementary Table 1).

The Balearic Sea has multiple spatial management areas that widely differ in the level of protection they offer and their target taxa. However, no real fully no-take MPA exists in the Balearic Sea to date (Aminian-Biquet et al., 2024). For that reason we refer to no-take MPAs as the existing network of demersal no-take MPAs (Figure 1), composed of: (a) 23 permanent areas (MPA-1 to MPA-23) established in 2020 by Spanish government decree (Ministerio de Agricultura, Pesca y Alimentación, 2020) aimed at protecting bentho-demersal communities; (b) a permanent marine reserve (Illes Columbretes), initially established in 1990 but further regulated to its current form in 2008 (Ministerio de Medio Ambiente, y Medio Rural y Marino, 2008); and (c) the Cabrera Archipelago National Park, established in 1991 but extended to its current size in 2019 (Ministerio para la Transición Ecológica, 2019). Regulation for these areas is complex, but bottom trawling is permanently forbidden in all 25 areas. Illes Columbretes only allows troll fishing (a surface-only type of fishing aimed at pelagic and

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migratory fish) with restrictions. The Cabrera Archipelago National Park allows for various artisanal fishing techniques, including a range of gears that target bentho-demersal species, with their own set of restrictions and fleet limitations. Lastly, MPA-6, MPA-18, MPA-21 and MPA-23 do allow bottom longlines and gillnets for certain periods of the year. Since the capture of bentho-demersal resources is permitted, at least partially, these four areas and the Cabrera Archipelago National Park are not technically fully demersal no-take MPAs. However, as their main high impact activity is banned (i.e., bottom trawling), for practical reasons, they are hereafter included and referred to as being in the same group as the rest of the areas.

2.2 | Environmental variables and fishing effort

In total, six variables were selected for the analyses (see Supplementary Table 2 for details). Environmental variables were chosen for their known ecological significance in influencing the distribution and composition of bentho-demersal communities, and included (1) bottom depth (GEBCO Compilation Group, 2023), (2) bottom slope (calculated from GEBCO's bathymetry using *terra* v.1.7–78 (Hijmans, 2024)), (3) sea bottom temperature (SBT; Copernicus Marine Service Data), and (4) seabed type (European Marine Observation and Data Network). The two anthropogenic variables included were (5) fishing effort (fishing hours) and (6) sampling effort (surface trawled). Sampling haul trackpoints were used to extract variable data over the transects covered by each haul. A single variable value per haul was obtained by averaging the extracted values for each trackpoint for continuous variables and by obtaining the mode for seabed type (categorical). Continuous variables underwent scrutiny for strong correlations, and all pairs of covariates exhibited correlation coefficients below 0.7 (Supplementary Figure 2).

We included bottom trawl fishing effort (hereon fishing effort) as a potential anthropogenic driver of bentho-demersal communities, given its known impact on their composition and structure (Foster et al., 2015), as well as on the morphology of the seabed (Puig et al., 2012). Fishing effort corresponded to the accumulated fishing hours/km^2 over the Balearic Sea by the Spanish bottom-trawling fleet obtained from Vessel Monitoring System (VMS) data (see Sala-Coromina et al. (2021) for detailed methodology). Following Montanyès et al. (2023), bottom-trawling impact on the bentho-demersal communities was assumed to be better represented by the accumulated trawled hours of the previous year. The same one-year lag approach was used to capture the effect of bottom trawling on the seafloor and the community. As the effort of the sampling hauls differed between samples, we accounted for this by including the sampling effort in the model as the logarithm of the surface trawled per haul (in km^2).

2.3 | Species traits and phylogeny

In addition to the aforementioned environmental and fishing pressure variables, the model also included traits and the taxonomic structure of the community as a proxy for phylogenetic data. Due to the diversity of the taxonomic groups included in the dataset (bony fishes, elasmobranchs, one species of chimera, cephalopods, decapod arthropods and one stomatopod), only 4 traits common to all groups were selected: (1) trophic level (continuous, from diet studies or based on the occurrence of prey); (2) habitat within the water column (categorical, including "bathydemersal," "bathypelagic," "benthic," "benthopelagic," "demersal," and "pelagic"); (3) reproductive guild (categorical, including "bearers," "guarders" and "nonguarders"); and (4) maximum length dependent on their phylum (continuous, log transformed), as not all phyla are measured the same way (total length is measured for fishes, cephalothorax length for crustaceans and mantle length for cephalopods). Data were obtained from FishBase and SeaLifeBase both directly from the website and with the R *rfishbase* package v5.0 (Boettiger et al., 2012).

The phylogenetic relationship of the species included in the model was defined through a taxonomic tree, using taxonomic data (Class, Order, Family, Genus, and Species) updated to the 02/2024 version of World Register of Marine Species (WoRMS; https://www.marinespecies.org) to construct a taxonomic tree. The parameter *rho* measures potential phylogenetic signal in the structure of the species responses to the variables that were used to fit the model (species niches) (Ovaskainen & Abrego, 2020). This parameter ranges from 0 to 1, where 0 means the community responses to their environment (or species niches) are completely unrelated to their phylogenetic structure, while a *rho* value of 1 means the species' niches are fully related to their phylogeny. As not all traits are known or measured, these missing traits can also leave a signal in the *rho* parameter. We used the "as.phylo" function from the *ape* package v.5.7 (Paradis & Schliep, 2019), with a branch length of one between nodes as a proxy of phylogenetic information, following the approach of Weigel et al. (2023). While this can potentially overestimate phylogenetic distances between species that are closer while underestimating the differences with more distant species (Ovaskainen & Abrego, 2020), it was deemed a reasonable approach to

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real evolutionary hierarchy due to the lack of phylogenetic trees for the studied community.

2.4 | Modeling approach

A JSDM was fitted to presence-absence bentho-demersal community data using the R package *Hmsc* version 3.0-13 (Tikhonov et al., 2020) and a "probit" link function. We used the Hierarchical Modeling of Species Communities (HMSC) framework, which allows fitting community data to environmental predictors, species traits and phylogenetic relationships, as well as the spatio-temporal structure of the sampling where the community data originate from. The fitted model took into account the spatial structure of the data by assigning all of the fishing hauls' centroids to their corresponding grid cell centroid. This resulted in 287 locations, which were included in the spatially explicit random effect using the full spatial method implemented in the *Hmsc* package. Briefly, spatially explicit models extract information of species presences and the species that either co-occur in the same sampling locations or in nearby sampling locations and are thus expected to improve model predictions (Ovaskainen & Abrego, 2020).

We assumed the default prior distribution of Hmsc (see Chapter 8 of Ovaskainen and Abrego (2020) for more details) and sampled the posterior distribution with four Markov chain Monte Carlo (MCMC) chains, with a thinning of 250 and 250 retained samples per chain (1000 samples total), resulting in 62,500 iterations (the initial 31,250 discarded as burn-in). The model achieved satisfactory MCMC convergence, as indicated by the maximum value of the Gelman-Rubin Potential Scale Reduction Factor (Gelman & Rubin, 1992) being <1.03 for all parameters. The effective sample size of the MCMC chains was also close to the number of posterior samples, meaning that samples are not autocorrelated (Supplementary Figure 2). The mean explanatory power of the model had an AUC of 0.89, while the predictive power from a five-fold cross validation resulted in an AUC of 0.86.

2.5 | Species richness and bioregionalization

We used the fitted JSDM model to project species richness (summed probability of the occurrence of all 129 species in the model) over the Balearic Sea for the mean environmental conditions of the sampling period using a 4 km^2 grid. To do this, variables linked to seabed structure such as bottom depth, bottom slope, and seabed type were assumed to remain constant. SBT extracted from Copernicus data were averaged for the period 2019–2023 for each 4 km^2 grid cell, while mean fishing effort was extracted and averaged from VMS data with the same year lag approach followed to fit the model—that is, for the period 2018–2022.

For each grid cell, the function "zonal" of the R package *terra* version 1.7-78 (Hijmans, 2024) was used to extract the mean values of every environmental predictor, with the exception of seabed type, for which the function "extract" of the *terra* package was used to obtain the modal value. The projections were constrained to the 50–750 m depth range present in the original sampling, and all cells where the categorical variable of seabed type included levels that were not included in the final model (i.e., "rock and boulders" and "coarse-grained sediment") were removed from the prediction matrix.

Following Weigel et al. (2023), we used the clustering approach implemented in the *NbClust* R package v.3.0.1 (Charrad et al., 2014) (method = "kmeans", distance = "Euclidean") to obtain the optimal number of clusters based on the projected species' occurrence probability matrix and a maximum consensus of 30 indices, resulting in three differentiated bioregions. This allowed assigning each projected 4 km^2 grid cell to one of these three bioregions to understand their spatial distribution and environmental characteristics. Lastly, the species composition of each cluster was extracted using the function "cluster_analysis" from the package *parameters* v0.22.1 (Lüdecke et al., 2020) to obtain the species' center values (i.e., how close/far they are to the three cluster centers). These center values were used to extract the 10 species closest to the center of the bioregion cluster as a way to obtain the most "representative" species of each bioregion (Supplementary Figure 3).

We assessed the area coverage of the no-take MPA network in the northwestern Balearic Sea over the identified bioregions' predicted area and richness using the *sf* v.1.0-17 (Pebesma, 2018) and *terra* v.1.7-78 (Hijmans, 2024) R packages. We cropped the projected distributions using the MPA boundaries and calculated the areas in km^2 included within them. Lastly, we plotted the maps using the *ggplot2* v.3.5 (Wickham, 2016) and *ggspatial* v.1.1.9 (Dunnington, 2023) R packages.

3 | RESULTS

3.1 | Bentho-demersal community bioregionalisation

Prediction of the bentho-demersal community ($n = 129$ species) over the study area resulted in three differentiated bioregions, in both composition and spatial

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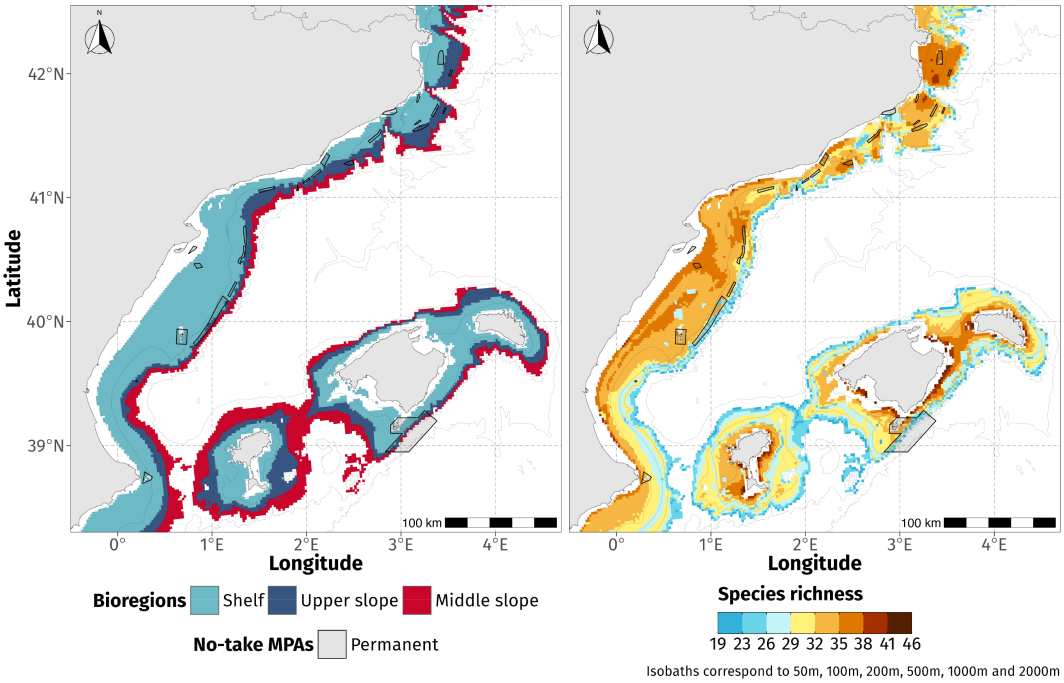


FIGURE 2 Distribution of the bentho-demersal bioregions (left) and species richness (right) in the Balearic Sea. Bioregions were named based on an approximation of the geomorphological division of the continental margin where they are located. The species richness shown here is relative to $n = 129$ species included in the model. Predictions were constrained to a bathymetric range of 50–750 m and excluded areas of "rock and boulders" and "coarse-grained sediment."

distribution, which show a strong bathymetric gradient (Figure 2a). Each bioregion has been named after its approximate distribution over the continental margin, namely and hereafter "Shelf," "Upper slope," and "Middle slope." In terms of spatial coverage over the study area, the Shelf bioregion (light blue area in Figure 2a) covers around 23,629 km^2 of the Balearic Sea, while the Upper slope and Middle slope bioregions cover 9020 and 9052 km^2, respectively. These area numbers strictly refer to the total area modeled as seen in Figure 2, and not to the total area encompassed by the Balearic Sea.

Bottom depth, sea bottom temperature and species richness are markedly bioregion-specific, having clear differences between the three identified bioregions (Table 1, Figure 3). All three bioregions are characterized by clear bathymetric ranges with little overlap between them (Figure 3d): 50–208 m depth (Shelf bioregion); 176–554 m (Upper slope bioregion); 459–751 m (Middle slope bioregion). The Shelf bioregion (i.e., the shallowest) is distributed over a warmer and much wider SBT range (13.48–17.48°C) than the other two (Figure 3e), with the Upper slope bioregion being distributed over slightly warmer bottoms (13.24–14.11°C) than the Middle slope bioregion (i.e., the deepest), which is distributed over the coldest habitat in the studied area (13.13–13.74°C). In terms of species richness (Figure 3a), all three bioregions have relatively wide but clearly distinct biodiversity ranges, with the Shelf bioregion having the highest number of species (median richness of 33.6), followed by the Upper slope (median species richness of 29.9) and the Middle slope (median species richness of 26.1) bioregions. The differences between the three bioregions are less marked for the seafloor slope and fishing effort variables. The Shelf bioregion has the most distinct seafloor slope values of the three, with a median value of 0.26° compared to the Upper and Middle slope bioregions (median values of 2.74 and 2.61, respectively) (Figure 3c). The three bioregions are also under different fishing pressure by bottom trawlers, with the Shelf bioregion having the highest fishing pressure out of the three (median of 6.8 annual hours/km^2), followed by the Upper slope bioregion (median of 4.8 annual hours/km^2) and the Middle slope bioregion (median of 2.8 annual hours/km^2).

In parallel to being the most defining variable of the bioregions in the area, depth is overall the best environmental predictor of the species included in the model, explaining an average of 63.5% of the variance in the species' occurrence. This is followed by the spatial random effect with a 14.1%, seafloor slope with a 6.4%, fishing effort with a 4%, the random effect of year with a 3.8%, the seabed type with a 3.6%, and the bottom temperature and sampling effort with a 2.6% and 1.8% respectively (Figure 4a). However, these vary species-to-species and even between different bioregions, as shown by the

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TABLE 1 Bioregion characterization and demersal no-take MPA (DNTK MPA) coverage in the Balearic Sea.

Bioregion	Predicted area (km²)	DNTK MPA coverage (km²)	Median depth (meters)	Median slope (degrees)	Yearly median bottom temp. (°C)	Median fishing effort (hours trawled/year)	Median species richness
Shelf	23,629	740 (3.13%)	92 (50–208)	0.26 (0–8.06)	14.38 (13.48–17.48)	6.8 (0–78.8)	33.6 (21.3–45.9)
Upper slope	9020	268 (2.97%)	340 (176–554)	2.74 (0.09–16.37)	13.59 (13.24–14.11)	4.8 (0–111.6)	29.9 (19.6–38.3)
Middle slope	9052	81 (0.89%)	632 (459–751)	2.61 (0.27–21.80)	13.34 (13.13–13.74)	2.8 (0–123.7)	26.1 (18.9–35.0)

Note: Minimum and maximum values are shown between parentheses. Values were rounded to their respective upper and lower units and decimals.

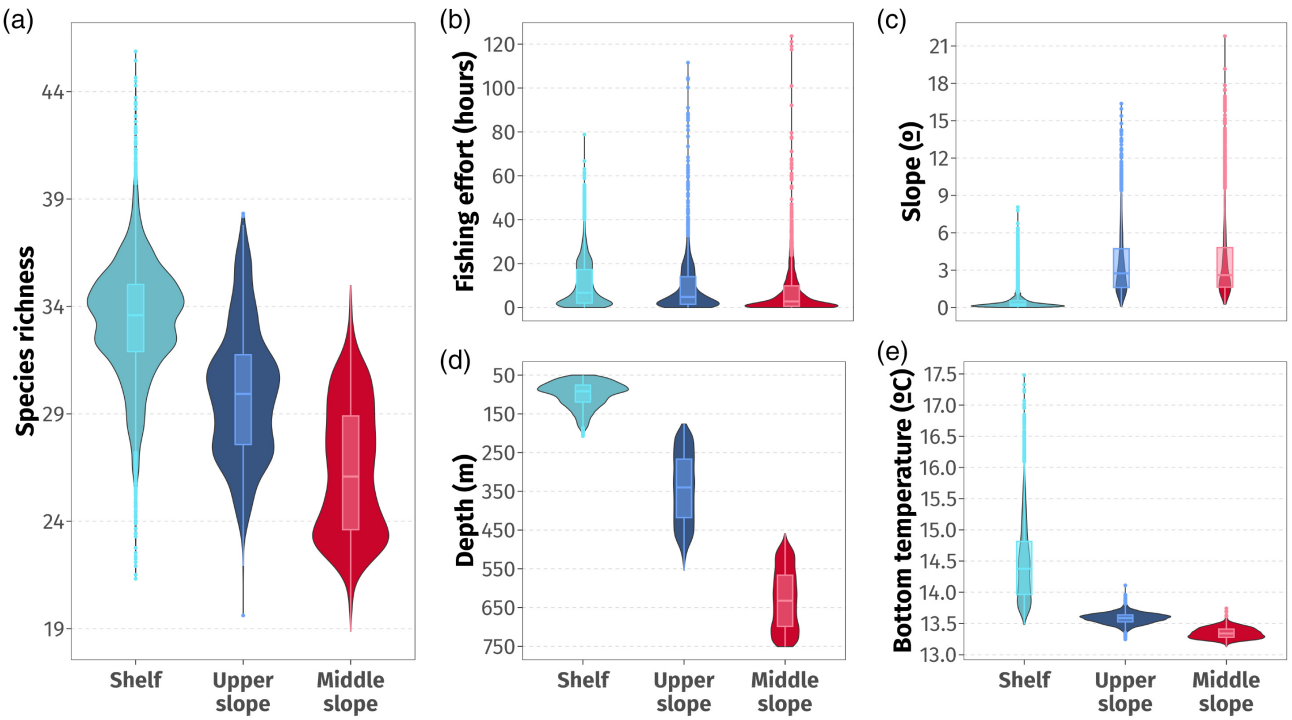


FIGURE 3 Characterization of the three bentho-demersal bioregions (Shelf, Upper slope, Middle slope) in the Balearic Sea. Panel (a) shows the species richness associated with each bioregion, while panels (b)–(e) show their anthropogenic (i.e., fishing effort) and environmental (i.e., slope, depth, and bottom temperature) characteristics. Environmental and anthropogenic values are averages over the 2019–2023 and 2018–2022 periods respectively.

higher variability in environmental responses and the spatial random effect shown by the 10 most representative species of the Upper slope bioregion when compared to their Shelf and Middle slope counterparts (Figure 4b).

3.2 | Bentho-demersal richness distribution

The spatial distribution of predicted species richness ($n = 129$) over the Balearic Sea shows a clear bathymetric distribution of biodiversity, with shallower depths showing a higher community richness than deeper areas (Figure 2b). Bentho-demersal richness is also predicted to be higher in the 50–100 m depths (the shallowest fraction of the modeled depths) around the Balearic Islands, located at the eastern part of the Balearic Sea basin, than in the same depths of continental Spanish waters at the western side of the basin. We generally found negative relationships between most of the continuous variables (bottom slope, depth, fishing effort) and the species richness of the bentho-demersal community in the Balearic Sea, with the exception of sea bottom temperature, which shows a positive relationship (Figure 5).

3.3 | Traits, phylogeny and species associations

The species' traits included in the model explain 17.45% of the variation in the species occurrences. Regarding the environmental variables selected in the model, traits

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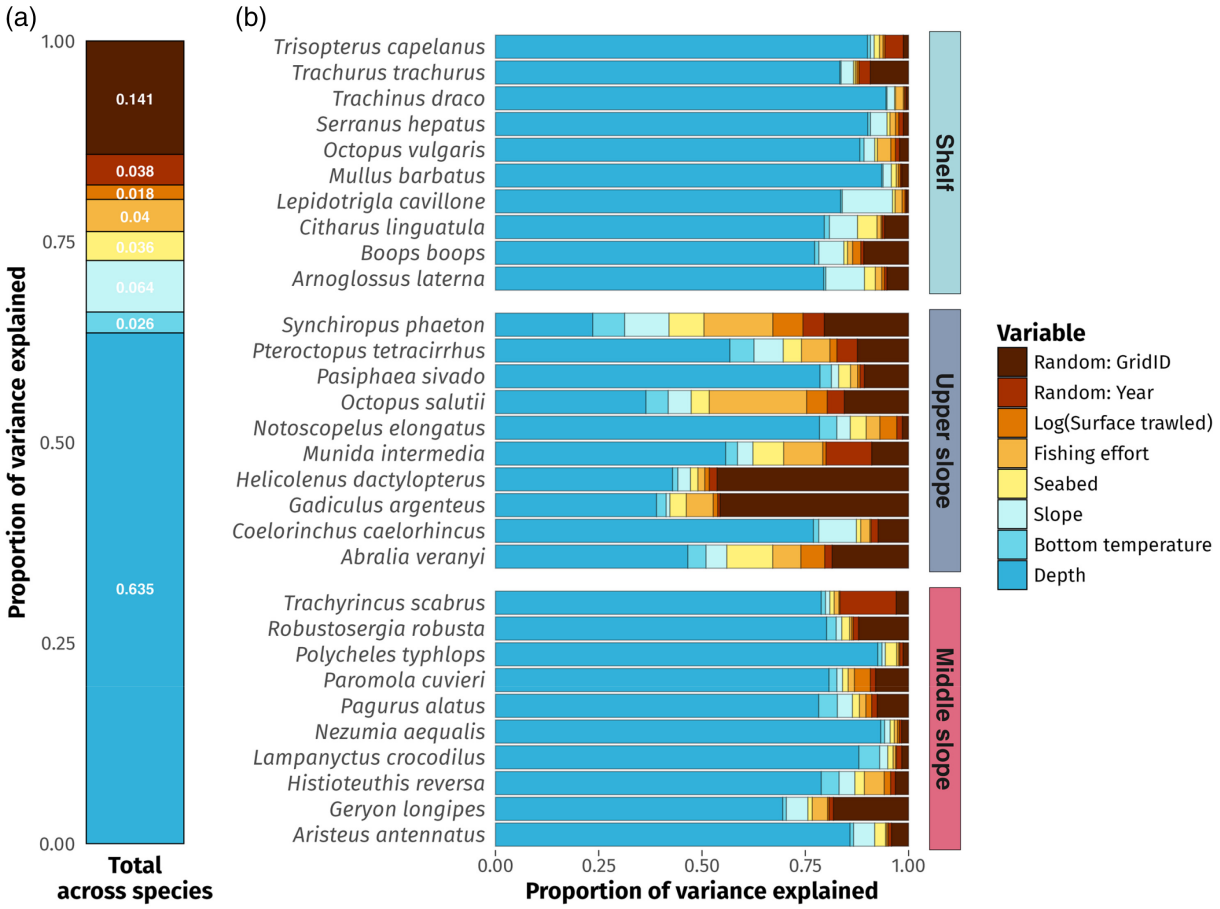


FIGURE 4 Variance partitioning of the included variables. Panel (a) shows the summarized variance for all the species included in the model ($n = 129$), while panel (b) shows the variance for the 10 most representative species of each bioregion (Shelf, Upper slope, and Middle slope).

explain between 6.6% (for the response to depth) and 67.9% (for the response to SBT). We found a strong phylogenetic signal (*rho* parameter) of 0.78 (95% C.I. = 0.62–0.91), indicating a high phylogenetically structured response to the environmental variables or species niches that are not explained by the included traits.

3.4 | MPA network and conservation of the bentho-demersal community

The identified bentho-demersal bioregions (Figure 2a) and species richness distribution (Figure 2b) were mapped over the existing no-take MPAs boundaries to assess what bioregions these spatial management measures are protecting, as well as what their predicted within-boundary diversity is. From the 1769 km^2 of no-take MPAs in the area, 1089 km^2 were included in the spatial predictions. Of those, 68% cover the shallowest Shelf bioregion, while 24.59% and 7.43% cover the Upper slope bioregion and Middle slope bioregions, respectively, (Figures 6 and 7; Table 1). The area not covered by the model answers to the seabed being either coarse-grained sediment or rocks and boulders, as they were not present in the data used to train the model, or because the depth is shallower than 50 m or deeper than 751 m.

Our results show uneven conservation benefits from the existing no-take MPAs in depths where trawl fishing is allowed in the Balearic Sea. No-take MPAs are currently covering only 3.13%, 2.97%, and 0.89% of the Shelf, Upper slope, and Middle slope bioregions, respectively. No-take MPAs in the Balearic Sea are currently mostly located where they cover either one single bioregion or, at most, two different bioregions (Figure 6; Figure 7; Supplementary Table 3). Only MPA-21 (Figure 6e,f) and the Cabrera Archipelago National Park (Figure 7a,b), the two biggest no-take MPAs currently in place in the Balearic Sea, cover parts of all three identified bentho-demersal bioregions within their boundaries (Supplementary Table 3). In terms of species richness, there are almost no no-take MPAs currently located over the areas of maximum modeled species richness identified in the Balearic

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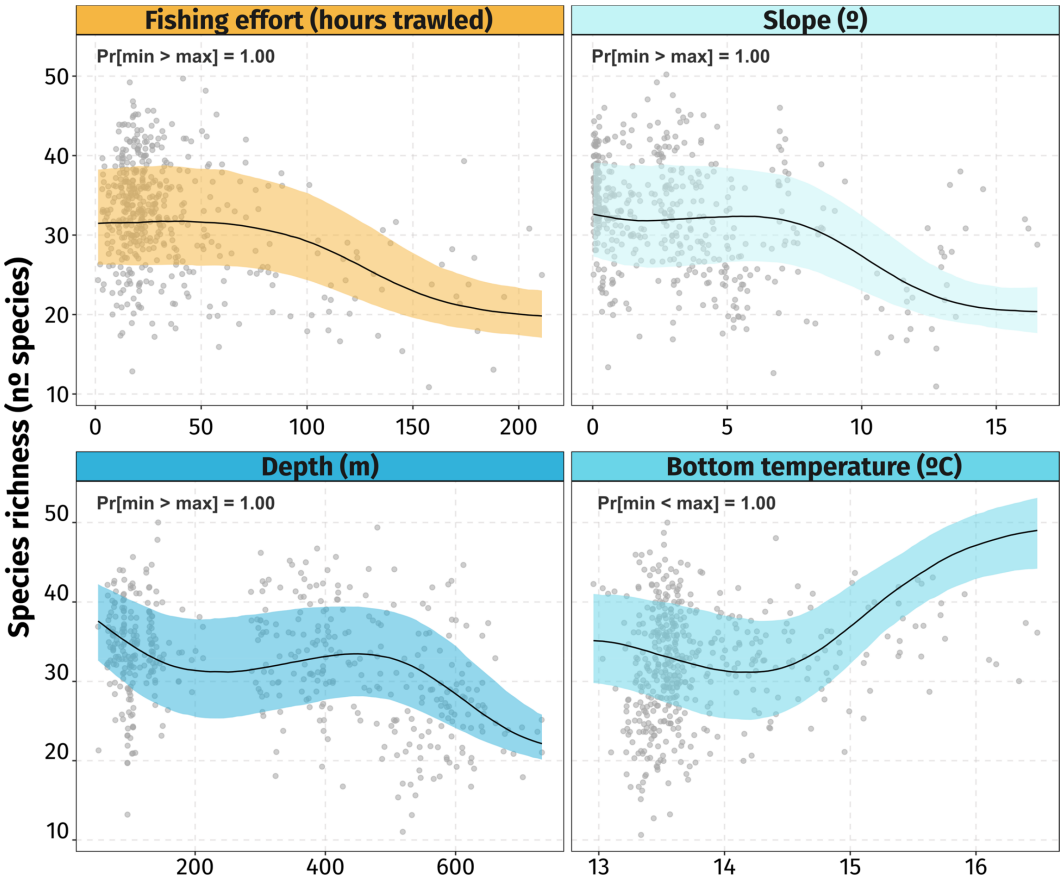


FIGURE 5 Effects of the continuous environmental variables and fishing effort on the species richness of the bentho-demersal community. Colored areas represent the 95% credible intervals of the model predictions. Gray points show the raw species richness of the sampling hauls at the given value. The probability of species richness being either higher or lower at maximum values of the environmental variable compared to the lower values is shown on the top-left corner of each plot.

Sea, which are mostly present surrounding the Balearic Islands where there is only one permanent no-take MPA (Figure 2b).

4 | DISCUSSION

There is a pressing need to increase and improve biodiversity conservation at both the European (EU Biodiversity Strategy for 2030; European Commission (2020)) and global (Kunming-Montreal Global Biodiversity Framework; CBD (2022)) levels. For the marine environment in particular, it is reasonable to suggest that the following actions are necessary to achieve this goal: (1) expand the current MPA networks—that is, the total marine surface area covered by the boundaries of a figure of protection; (2) improve (and map) our best-available knowledge on the existing spatial management measures—that is, identifying the communities that are under their protection in a way that is informative and useful for the different stakeholders involved in the marine environment and its conservation; and (3) implement a certain degree of flexibility in the MPA design process, where the initial implementation does not set their original boundaries permanently and where boundary modifications (e.g., MPA expansions) are allowed based on new information or environmental changes. In practice, knowledge-based expansions of current MPA networks need to prioritize identified hotspots of species richness and seek an even representation of known bioregions.

Community level analyses are particularly important when studying and managing marine activities such as fisheries, which in the Mediterranean Sea are highly multi-specific. The western Mediterranean Sea, currently the most heavily fished region of the entire Mediterranean Sea after the Black Sea, represents 18.5% of all landings (FAO, 2023) and has highly diverse fisheries with around 44 species composing 90% of the catch (FAO, 2023). This makes community data, and a multi-specific approach that considers environmental and anthropogenic stressors on species distribution and community assemblages, essential for advancing our understanding and management of Mediterranean

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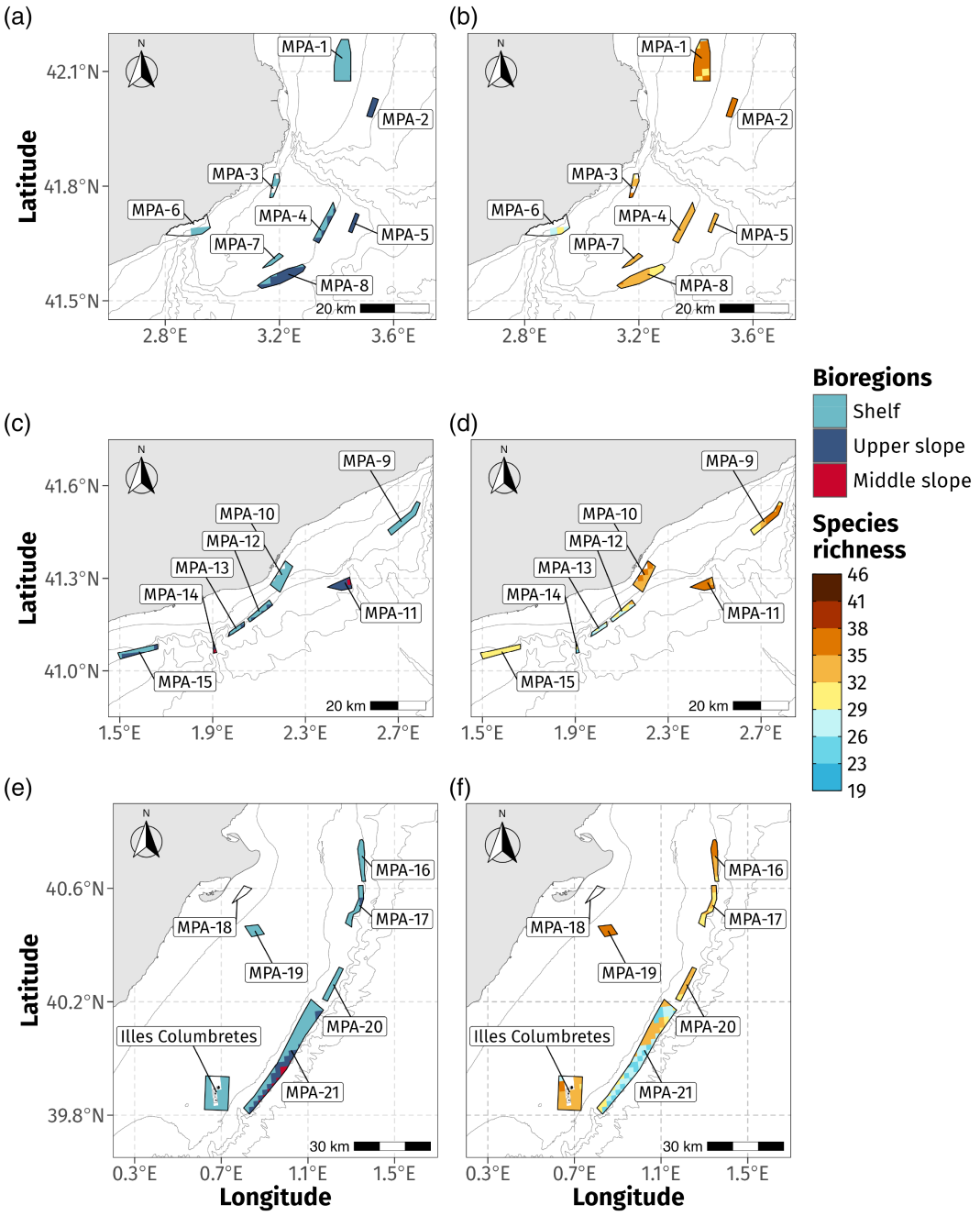


FIGURE 6 Northern section of the demersal no-take MPA network in the Balearic Sea and the projected bentho-demersal bioregions (a, c, e panels) and species richness (b, d, f panels) within the MPA boundaries. See Figure 1 for the locations within the study area.

bentho-demersal biodiversity. Here, we used a "Jointly predict, then group" approach for our bioregionalisation analysis of the Balearic Sea (Woolley et al., 2020), which resulted in the delimitation of three differentiated bioregions. These, although represented on the map as spatially clear-cut areas, are rather a part of a continuum where species with wider niches can appear in more than one bioregion. The three identified bioregions are mostly differentiated by their bathymetric ranges and sea bottom temperatures, with species richness being lower in deeper communities. Our bioregionalisation results share some similarities with previous non-spatial community clustering analyses done in the Balearic Sea from trawling data for fish (Moranta et al., 1998), crustaceans (Abelló et al., 1988; Cartes et al., 2011) and cephalopods (Quetglas et al., 2020). These works also found the studied communities or assemblages bathymetrically distributed, to an extent, into relatively similar depths as the bioregions we present here. However, past analyses in the area were not spatially distributed and differed in

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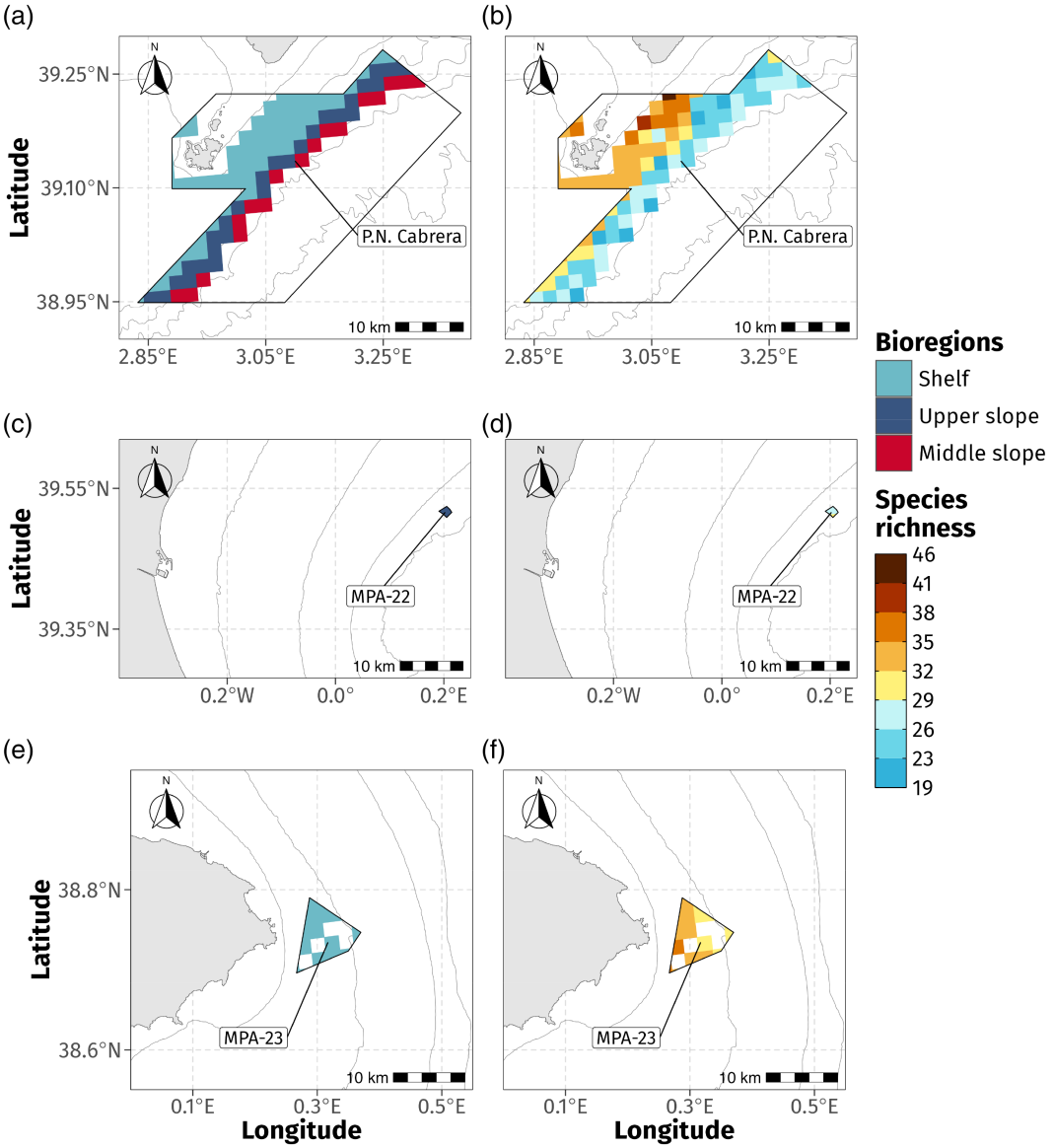


FIGURE 7 Southern section of the demersal no-take MPA network in the Balearic Sea and the projected bentho-demersal bioregions (a, c, e panels) and species richness (b, d, f panels) within the MPA boundaries. See Figure 1 for the locations within the study area.

both the species considered, and in the way these were studied as isolated taxonomic groups instead of as a community with varied taxa.

Current international protection targets highlight even representation of different habitats or communities as a necessary consideration, such as Target 3 of the Kunming-Montreal GBF, and when bioregionalisation studies are available at least 20%–40% of each bioregion should be covered by no-take MPAs (Ceccarelli et al., 2021). Our results, however, suggest that protection in the Balearic Sea is lacking, particularly when the representation of the three identified bioregions under protection is considered: only 3.13% of the Shelf bioregion, 2.96% of the Upper slope bioregion, and 0.89% of the Middle slope bioregion are currently located within no-take MPA boundaries. Some individual no-take MPAs within the network, such as Columbretes Islands (entirely located over a single bioregion), show varying species richness spatially. However, for the most part their small size means a relative uniformity within their boundaries in terms of species richness. We believe that comprehensive and regionally informed bioregionalization efforts at the basin level, using year-round data like the one we present here, should be made throughout the Mediterranean Sea in order to properly evaluate the surface area and the marine communities currently under protection.

Variance partitioning helps discern the relative importance of the different environmental and spatial explanatory variables that structure communities and their diversity (Chase & Myers, 2011). Apart from the

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clear bathymetrical distribution of the identified bioregions, we observed differences in the other physical and anthropogenic variables included in the analysis. Regarding sea bottom temperature, the Shelf bioregion is not only significantly warmer than the other two bioregions, but also has a much wider temperature range. This is expected as it is also the shallowest and is directly influenced by variations of the seasonal thermocline (Bahamon et al., 2020). The identified Upper slope and Middle slope bioregions have colder, more stable, and narrower bottom temperature ranges, with their median temperatures being less than 1°C apart. Narrower temperature ranges may make these two bioregions and their communities particularly sensitive to temperature changes in the context of climate change, as species with wide thermal ranges could be less impacted or even favored by the eventual greenhouse gas-mediated warming of the marine ecosystem (Pörtner & Farrell, 2008), particularly so for species with relative motility and the capacity to migrate. Already reported consequences of induced warming of SBT are the deepening of demersal fish assemblages (Dulvy et al., 2008) and the northward displacement or "meridionalization" of some species (Mingote et al., 2024). The monitoring of these particular bioregions (Upper slope and Middle slope) should be of interest not only for biodiversity conservation but also for fishery management, as the same process appears to be happening for commercially important species in the NW Mediterranean Sea (e.g., the deep-water rose shrimp, Mingote et al., 2024). The deepening of some species that are part of these bioregions would in practice mean a distancing of valuable fishery resources farther away from the coast, potentially resulting in higher associated costs for the fishing sector. On the other hand, the meridionalization of species could also alter bentho-demersal community structure and redistribute fishery stocks, potentially posing further stress in the fishery sector. Besides fisheries, for marine conservation planning these shifts could mean potential movement outside of protected areas and other spatial conservation measures. Adjusting current management measures to these distribution changes will require an adaptive approach towards both MPA implementation and fisheries regulation. As bentho-demersal communities, and with them fishery resources, shift their current distributions, periodic evaluation of the effectivity of these measures through time will be needed (Holsman et al., 2019).

The variability of fishing pressure over the three identified bioregions may respond to a wide range of interactions between the commercial value of the species that compose the different bioregions and the socioeconomic dynamics of bottom-trawl fisheries in the northwestern Mediterranean Sea. For example, higher average hours trawled over the Shelf bioregion might be due to assured profits from fishing capture with a relatively low associated cost, as it includes the communities closest to the harbors. At the same time, the Balearic Sea, particularly in its northern sector or north of 41° N, has a well-developed fishery targeting highly valuable commercial species such as the blue-and-red shrimp *Aristeus antennatus* (Company et al., 2008), which is a representative species of the defined Middle slope bioregion. This fishery is facilitated by the existence of submarine canyons very close to the coast, allowing local bottom-trawlers to capture the valuable species also for a fraction of the cost, as fewer working hours and less fuel are needed compared to other blue-and-red shrimp fisheries. This is a possible reason for the higher upper limit of the fishing effort over the Middle slope bioregion compared to the other two, being otherwise the least fished bentho-demersal community on average out of the three identified.

Fishing effort explained a low proportion of the variation in our model, similarly to previous HMSC studies carried out with bottom trawling data (e.g., Montanyès et al., 2023). However, it was a more relevant driver for the community inhabiting the Upper slope bioregion than for the other two, at least when considering its 10 most representative species. Nevertheless, our results show strong evidence of lower species richness with increasing accumulated impact from bottom trawl fishing in hours trawled. This was expected considering bottom trawling affects the structural complexity and heterogeneity of the seabed and is known to generally reduce species richness (and abundance) in heavily fished areas (Thrush & Dayton, 2002). Predicted reduction of richness in highly fished areas might have been more pronounced and visible if sessile taxa such as anthozoans (e.g., soft corals, sea pens), sea sponges (Phylum Porifera), and similar species were included in the model. These species are particularly at risk, as bottom trawling harms sessile taxa in a much more long-lasting way than motile species (Althaus et al., 2009). Loss in bentho-demersal species richness from fishery impacts, apart from the direct removal of the individuals, may be a result of the habitat loss that fragile biogenic species create as well as the loss or homogenization of seabed complexity and structure caused by the fishing gears (Althaus et al., 2009; Thrush & Dayton, 2002).

One of the caveats, or rather a precaution, when interpreting the results we present here is that they are all relative to the taxa and number of species included in the final model. The Balearic Sea is home to many species not included in the current analyses such as sessile octocorals, sponges, or ascidians, as well as many other motile species. The original dataset used for this study included well over 400 species, trimmed down to 129. This allowed us to keep reasonable computational times while ensuring a reasonable proportion of the community with over 100 genera. Longer time-series and updates in the computational methods will allow for rare

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species to be incorporated in future iterations of the JSDM. Most of the studies applying HMSC to marine community data have focused on one taxonomically formal or informal group of varying diversity, mainly fishes (Gomes et al., 2023; Gordó-Vilaseca et al., 2024; Montanyès et al., 2023). This allows for a common set of straightforward traits relevant to that taxonomic group (formal or informal) to be defined, such as fin shape when working with fish. We had a diverse taxonomical community that included morphologically and behaviorally very distinct species, without many apparent or publicly available clear-cut definable traits common for all of them. However, HMSC allows overcoming this to some extent by accounting for the phylogenetic relationships of the species (Ovaskainen & Abrego, 2020). Moreover, model-based bioregionalisations can easily be updated and redefined to allow for continuous adaptation and improvement of the classifications (Woolley et al., 2020) whenever new data becomes available. Being able to update bioregionalisation classifications over time will help monitor changes in the distribution of not only single species, but entire ecological communities due to stressors such as climate change, which affect species differently (Antão et al., 2022).

The identification and mapping of biodiversity and bioregionalisation patterns in the Balearic Sea are key to achieving a more efficient no-take MPA network design and future marine spatial planning efforts in the area. Having spatially identified bioregions could also help move toward a more precise management of human impacts in the marine environment. While different bioregions may be spatially close to each other, particularly where bathymetry has more pronounced increases close to land masses, they are compositionally different and this should be reflected in the way they are managed. Once taken into account that including representation of the different existing bioregions is needed for adequate design conservation measures (Ceccarelli et al., 2021; Stephenson et al., 2023), knowing the distribution of species richness within an area, and more specifically within a bioregion, also opens the way for a more directed and data-based approach to assess current MPAs and to guide potential new locations for future MPAs. Our findings help to better understand current protection measures, even when sampling is unfeasible due to already implemented restrictions and/or costs. Furthermore, they give valuable information for future conservation efforts and marine spatial planning design using already available data.

AUTHOR CONTRIBUTIONS

Miguel López: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing—original draft. **Morane Clavel-Henry:** Conceptualization, Methodology, Supervision, Writing—review and editing. **Nixon Bahamón:** Conceptualization, Supervision, Writing—review and editing. **Joan B. Company:** Conceptualization, Supervision, Writing—review and editing, Funding acquisition. **Otso Ovaskainen:** Methodology, Software, Supervision, Writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data will be made available upon request to ICATMAR.

ETHICS STATEMENT

The surveys and sampling that led to this work are routinely conducted under both national (Spanish Government) and regional (Catalan Government) permits.

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