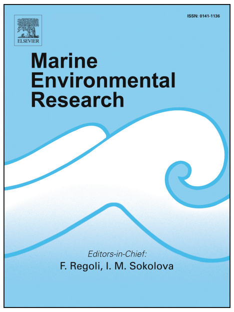

Spatial patterns of β-diversity under cumulative pressures in the Western Mediterranean Sea

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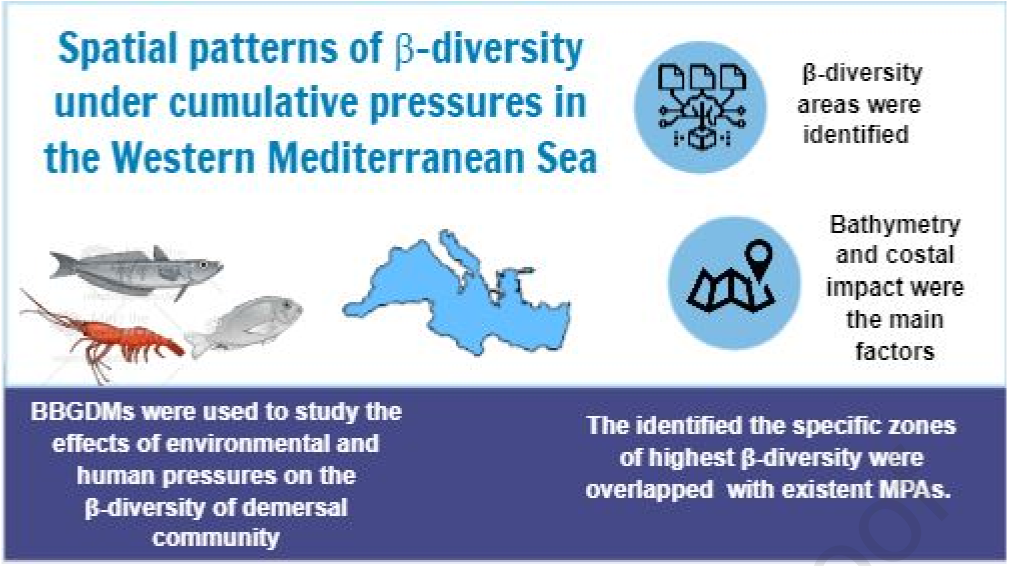

Spatial patterns of β-diversity under cumulative pressures in the Western Mediterranean Sea

β-diversity areas were identified

Bathymetry and costal impact were the main factors

BBGDMs were used to study the effects of environmental and human pressures on the β-diversity of demersal community

The identified the specific zones of highest β-diversity were overlapped with existent MPAs.

Spatial patterns of β-diversity under cumulative pressures in the Western Mediterranean Sea

Running Head: β-diversity in the Western Mediterranean

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Abstract

Understanding the spatial dynamics of biodiversity is an essential issue in marine ecology and requires combining information at local and regional scales. β-diversity is an important measure of biodiversity that informs on the differences in community composition between sites and, thus, in the species turnover in the community structure. In this study, we analysed and predicted the spatial patterns of β-diversity for fishes, invertebrates and the demersal assemblage along the Iberian Mediterranean coast. We used Bayesian Bootstrap Generalized Dissimilarity Models (BBGDMs) to study the effects of environment and human pressures on the β-diversity of invertebrate, fishes and the entire demersal assemblage from 1994 to 2015 using different time windows to account for temporal variability. Then, we used these relationships to predict the spatial patterns of β-diversity in the whole Iberian Mediterranean coast. Our results highlighted that the regional spatial patterns of β-diversity were best described by bathymetry and a cumulative index of coastal impacts. We identified specific regions with the highest β-diversity in the study area, which were complementary to hotspots of species richness and presented different degree of overlapping with existent marine protected areas. Overall, our study illustrates that by modelling spatial turnover using β-diversity we can better understand and predict spatial variation of biodiversity and the effects of particular variables, providing relevant information to end-users and policy makers for designing specific spatial conservation and management strategies.

Keywords: β-diversity, environmental change, anthropogenic pressures, Bayesian Bootstrap Generalized Dissimilarity Models

INTRODUCTION

Assessing the role of spatial dynamics of ecological and environmental processes in determining the biodiversity variation is an essential issue in marine ecology (Fitzpatrick et al., 2013). Indeed, one of the fundamental paradigms of the Ecosystem Based Management (EBM) approach is to understand the complex spatial patterns and processes in the ecosystem in order to protect the largest number of species possible instead of a single species under a single threat at a time (Palumbi et al., 2008). A better understanding of this complexity and the multidimensionality of diversity, which operates at different spatial and temporal scales (González et al., 2020), is a first step towards an integrative ecosystem assessment.

Many studies have considered why some places have more species than others, using both alpha (α) and gamma (γ) diversity measures. The α-diversity is measured with species richness or diversity indices (e.g., the Shannon- Wiener index or the Simpson index) to determine spatial variations at a local scale (Lasram et al., 2015). The γ-diversity is estimated at regional scales to assess total species diversity across a group of local habitats (Ellison et al., 2010). However, the biggest challenge is to develop conservation and management strategies and tools considering the beta-diversity (β), which reflects the community composition variation between sites within the same geographic area (Whittaker, 1972). The β-diversity represents the species turnover (*i.e.,* the rate with which species replace each other from site to site) or the effective number of distinct compositional units in a region, which makes this biodiversity measure a paramount information for an effective spatial planning. To understand the spatial variation of biodiversity, it is crucial to reveal the structural and external drivers of variation of β-diversity given its important role to community stability (Shackell et al., 2012; Mellin et al., 2014).

Many approaches have been proposed and can be generally grouped according to two components and applications of β-diversity (Anderson et al., 2011): directional turnover along a gradient vs. non-directional variation. These two components answer two complementary different questions. The non-directional β-diversity answers to the question: do we see the same species over and over again among different units? This component is measured among all possible pairs of units, without reference to any particular gradient or direction, and it has a direct correspondence with variance in community structure (Anderson et al., 2011). β-diversity based on directional turnover framework answers to the question: how many new species are found along a gradient? And how many of those initially present are now lost? This component is more frequently used and it is usually estimated comparing the rates at which similarity in species composition decreases as a function of geographical and/or environmental gradients, with greater rates of decreases in similarity indicating more turnover of species in space, or higher β-diversity. These decreases could be due to different causes such as (i) the reduction in environmental similarity with distance (niche-based processes) (Fitzpatrick et al., 2013), (ii) spatial processes benefiting or jeopardizing organisms to find more favourable environments, notably through dispersal ability and its interplay with habitat configuration and history (e.g. environmental filtering and climate stability) (Soininen et al., 2007), and (iii) anthropogenic threats that could affect the biological processes of the species at the spatial scale deconstructing and eroding the community structure (Shackell et al., 2012; Lasram et al., 2015). Among these possible causes, the anthropogenic threats are the least explored ones because the difficulty to quantify their effects within a spatially explicitly modelling approach.

Understanding how anthropogenic, environmental and geographical factors may influence the β-diversity can provide insights into marine conservation and management planning and, particularly, can contribute to the implementation of a Marine Spatial Planning (MSP hereafter) process. The MSP considers those ecological processes as well as the anthropogenic activities that occur in a certain location that need to be managed. However, it is only the anthropogenic component (human activities and resource use) that can be spatially managed (Ehler and Douvere, 2009; Bellido et al., 2019; Pennino et al., 2021). Therefore, identifying whether and where anthropogenic impacts affect the β-diversity, as well as the strength of this impact, is essential for an ecosystem-based management approach and to inform more efficient conservation planning. For example, this can allow identifying high β-diversity areas that need to be prioritized in management procedures, given the important role in supporting the structure of communities and the pathways of functional connectivity.

In this study, we used Generalized Dissimilarity Models (GDMs hereafter) (Ferrier et al., 2007) to analyse and predict spatial patterns of β-diversity in marine exploited demersal species assemblages along the Iberian Mediterranean coast. Differently to previous studies modelling β-diversity in Mediterranean marine ecosystems (Lasram et al., 2015; Farriols et al. 2019; Veloy et al., 2022), we included in the modelling approach spatially-explicit information of anthropogenic variables in order to assess the role of these threats on β-diversity. 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 marine biodiversity in the area (Navarro et al., 2015, 2016; Veloy et al., 2022) and neighbouring regions (Farriols et al., 2017).

In addition, since different taxonomic groups can display different community dynamics and sensitivity to environmental and anthropogenic impacts, we performed the GDM analysis not only on the entire demersal assemblage but also on two aggregated taxonomic groups (fishes and invertebrates). We hypothesized that groups with higher vagility (i.e., the degree that an organism does move or spreads within an environment), as fishes, could be less sensitive to anthropogenic factors with respect to more resident species groups, as sessile invertebrates, that have lower dispersal capacity during the adult phase. We performed GDM analysis for the entire time series (1994-2015) and also for three different time windows (i.e., T1: 1994-2000; T2: 2001-2007; T3: 2008-2015), selected to contrast homogeneous time periods between them and consider possible temporal differences. Moreover, we quantified the degree of overlap of areas with high β-diversity with Marine Protected Areas (MPAs hereafter) to explore how current approaches are protecting this important biodiversity component. Our hypothesis is that the β-diversity hotspots only partially overlap with the current MPAs due to this ecological metric has not been considered to define current protected areas. Finally, in order to quantify uncertainty in the analysis we applied a Bayesian Bootstrap to the classical GDMs as suggested by Woolley et al., (2017). This modelling approach (BBGDMs hereafter) 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 (Pennino et al., 2019a; Carmezim et al., 2022). This is a fundamental issue in marine ecology, where identification of priority habitats is one of the most common conservation and management tools used to ensure the long-term sustainability of species, populations and communities.

MATERIALS AND METHODS

Study area and species data

The present study concerns the area which borders the Iberian Mediterranean coast in the Balearic Sea, from Cape of Palos to Cape of Creus (*Figure 1a*). This study area covers the continental shelf and upper slope of the Spanish Mediterranean Iberian Peninsula including depths from 25 m to 800 m. This area is characterized by large-scale environmental gradients, including the temperature of surface and intermediate water masses, and primary productivity regimes resulting from the influx of deep water from the Gulf of Lion, fluvial contributions of nutrients from the Ebro River, and submesoscale and frontal processes (Ramirez-Romero et al., 2020). According to the division of the Mediterranean Sea stated by the General Fisheries Commission of the Mediterranean (GFCM), this area is formally named Northern Spain and it corresponds to the Geographical Sub-Area 06 (GSA-06).

Species data were collected from 1994 to 2015 during the EU-funded MEDIterranean Trawl Survey (MEDITS) project (Bertrand et al., 2002). The MEDITS survey program was designed to produce basic information on demersal species in terms of abundance and demographic structure as well as spatial distribution. The MEDITS project has been carried out annually in spring or early summer (from April to June) since 1994. Sampling is based on stratified random sampling (Bertrand et al., 2002), in which similar sampling stations (in terms of depth and composition of the seabed) are carried out each year.

Species richness (number of species) obtained from the sampling was divided for the analyses in different groups: fishes, invertebrates (*i.e.*, molluscs and crustaceans) and the whole demersal assemblage (*i.e*., demersal fishes and invertebrates) (see Table S1 for details of the list of species).

Environmental data

Three environmental variables were considered as potential predictors of β-diversity. These included an oceanographic variable, Sea Surface Salinity (SSS), and two bathymetric features, depth and slope of the seabed (Figures S1). These variables were chosen because previous analyses highlighted them as potentially important to describe biodiversity patterns (Sarzo et al., 2023; Carmezim et al., 2022; Veloy et al., 2022; Navarro et al., 2015). As no exhaustive and validated time series of SSS (expressed in Practical Salinity Units) were available, the climatology of SSS for the entire year was downloaded from the World Ocean Database 2013 (WOA13).

Bathymetric features were derived from the MARSPEC database, (http://www.marspec.org), also with a spatial resolution of 0.1 x 0.1 grid cell resolution. Depth was considered as it is one of the main factors controlling species distributions and has been identified as key predictor to determine spatial patterns of many species and fish assemblages (Albouy, et al., 2012; Vilas et al., 2020). In addition, the slope accounts for the seabed steepness. In general, low values of slope correspond to flat ocean bottom (usually areas of sediment deposition), while higher values indicate potential rocky ledges (Fonseca et al., 2017).

Cumulative anthropogenic pressures

Anthropogenic pressure data were represented at a spatial resolution of 0.1° x 0.1° grid cell. Three different direct and indirect anthropogenic threats occurring in the Mediterranean Sea were considered for this study based on previous data compilations (Coll et al., 2010; 2012; 2015) and previous biodiversity studies (Navarro et al., 2015; Carmezim et al., 2022;Sarzo et al., 2023) (Figure S2). 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. Specifically, the threats used were:

(1) Coastal-based impacts: cumulative effects from inorganic and organic coastal pollution, litter, nutrient runoff and hypoxia as well as the presence of alien species and aquaculture activities.

(2) Ocean-based pollution: cumulative effects from shipments of toxic substances, such as toxic waste, radioactive waste or fertilizers, and other pollution deposition of heavy metals and inorganic nitrogen.

(3) Climate change: cumulative effects from changes in sea water temperature, in the intensity of ultraviolet radiation and in water acidification.

In addition, the Automatic Identification System (AIS) fishery footprint extracted from the European Commission BlueHub project (https://maritime-spatial-planning.ec.europa.eu/practices/mapping-fishing-activities) was used as a fourth anthropogenic stressor (Figure S2). This footprint was obtained using the AIS data of the number of trawlers (bottom otter, beam and midwater trawls) of over 15 m in length operating in the area at 5 min intervals at a spatial resolution of 0.1° x 0.1° grid cell (Vespe et al., 2016; Pennino et al., 2019a) for the last 5 years of the time series. Higher value of this index represents higher fishing pressure.

All variables were upscaled at 0.5° x 0.5° grid cell to have the same spatial resolution of species data and to have one sample per each grid cell. Following Zuur et al. (2010), environmental and anthropogenic variables were explored for collinearity, correlation (Pearson's index), outliers, and missing data before their use in the modelling analyses. Slope and bathymetry were highly correlated (r >= 0.60) and thus, after running alternative models (i.e., only with slope or bathymetry), slope was excluded from the analysis as it was less informative (Table S2).

The Generalized Dissimilarity Modelling Approach

Bayesian Bootstrap Generalized Dissimilarity Models (BBGDMs) (Woolley et al., 2017) were implemented to analyse and predict spatial patterns of β-diversity. BBGDMs are a nonlinear matrix regression technique for analysing spatial patterns in the species compositional dissimilarity (quantified with the Jaccard measure as it is one of the most used dissimilarity measure) between pairs of locations as a function of environmental dissimilarity, geographical distance, and in our case of anthropogenic pressures dissimilarity.

This approach can be considered as a reformulation of the Mantel method into a generalized linear model in which a single response matrix can be modelled as a function of distance matrices of a number of non-correlated explanatory variables. By doing this, we can overcome two major problems that usually arise in this context: non-linearity in community dissimilarity between sites and geographical distance and uneven rates of species turnover along environmental and anthropogenic pressures gradients. Here, the strength of this method is that, instead of parametric transformations of the variables, it uses flexible splines (Ferrier et al., 2007).

In particular, the three I-spline basis functions were implemented for the analysis (Ferrier et al., 2007). When I-splines are plotted the maximum height of each I-spline indicates the total amount of compositional turnover associated with that variable, holding all other variables constant in their mean value. In other words, the I-splines are indicators of the importance of each variable in determining patterns of β- diversity. In addition, the slope of the I-spline represents the rate of species turnover and how this rate varies at any point along the gradient studied (holding all other variables constant in their mean). Finally, the difference height between any two sites along the I-spline corresponds to the modelled contribution of that predictor variable to the total ecological distance between those sites.

To fit the BBGDM models, we constructed presence/absence site-by-species and site-by predictors' matrices for each groups of species and for all the demersal assemblage, where sites are 0.5° x 0.5° degree resolution. This analysis was performed for the three different temporal windows (*i.e.*, T1: 1994-2000; T2: 2001-2007; T3: 2008-2015). These temporal windows were selected to compare homogeneous periods of time and to account for possible temporal variabilities. Since no substantial change was detected, an overall analysis on the whole dataset (1994-2015) was also performed. In addition to environmental and anthropogenic variables, the predictors' matrices included geographical coordinates of cell centroids based on equidistant conic projections to account for the effect of spatial separation of observed dissimilarities (Mokany et al., 2022). From these predictors, the BBGDM model derives sets of I-splines and calculates distances between all possible pairs of sites. We tested variable relevance using Bayesian bootstrap (BB), instead of the classical permutations (Woolley et al., 2017), which allowed us to also estimate credible intervals for each selected variable included in the final models. According Woolley et al., (2017), when the I-spline are created, all covariates are scaled to the same units within a given data set. Parameter estimates are those provided by the BB since GDM is a single realization of BB resampling (with all equal weights). Therefore, the important regression coefficients will be those with larger magnitudes (absolute values) and smaller credible intervals around these coefficients. Model selection was performed using the `Wald-like' test, which assesses the relevance of the variables in relation to its posterior variance (obtained from the BB). BB differs from standard bootstrapping in that a site's data is never completely removed from the bootstrap sample. This acts as a cross-validation for predictions, ensuring that all dissimilarities are observed in each of the bootstrap samples and that no pairwise dissimilarity between the bootstrap samples is identically zero.

Results included for each analysed group: (i) I-spline for each relevant predictor variable, with a 95% credible interval, describing the relationship between β-diversity and that gradient, (ii) BBGDM predicted species turnover map, which represents the prediction of the final model considering the effect of the predictor variables on diversity change, and (iii) β-diversity hotspots, defined as those areas above the quantile 95th of β-diversity values (for fishes, invertebrates or the whole demersal assemblage).

BBGDMs were performed using the “*bbgdm*” package (Woolley et al., 2017) in the R software version 4.1.1 (R Core Development, 2022).

β-Diversity hotspots

In order to assess if the identified β-diversity areas overlap with high richness values, we first interpolated the observed richness data (number of species in each sample site) of each group using the *interpolation TIN* function of the Quantum GIS (available in: http:// www.qgis.org/en/site/) to obtain a spatial raster with a 0.5° x 0.5° degree spatial resolution. Richness hotspots were defined as those areas above the quantile 95th of the richness values. Afterwards, we compared the BBGDM spatial outputs of each group with richness map using the Spearman's spatial correlation and the "layerStats" function of the raster package (Hijmans et al., 2016) in R software. Values of Spearman's correlations range from -1 to 1, being 1 equal to a perfect positive correlation between the two datasets.

Finally, we computed the degree of overlap of the identified β-diversity hotspots with existing MPAs. The shapefile of MPA areas was obtained from the World Database on Protected Areas (WDPA, https://www.protectedplanet.net/c/world-database-on-protected-areas). The shapefile contained national and regional parks, World Heritage sites (WHS) and Specially Protected Area of Mediterranean Importance (Barcelona Convention) (SPAMI) (*Figure 1b*). In order to assess the overlap between the existent MPAs and the hotspots of β-diversity, we measured the percentage of each identified hot-spot included within the boundaries of MPAs. All these analyses were performed using the final model of the entire time series as results were consistent over the temporal periods explored.

RESULTS

During the MEDITS surveys (1994-2015) 248 different species of fishes and 256 invertebrates were collected in 376 different sites. In particular, in the first period (1994-2000) 204 fishes and 191 invertebrates were collected in 210 different sites; in the second one (2001-2007) 210 fishes and 188 invertebrates were sampled in 259 different sites;

and in the third period (2008-2015) 196 fishes and 206 invertebrates were sampled in 202 different sites.

Overall results were very similar along the entire time series and groups analysed. Indeed, for the all groups and temporal periods, the most important environmental variable that affected the species turnover was the bathymetry, which showed a positive relationship (*i.e.,* faster turnover rates occurred in deeper waters) (*Figure 2* and *Figure S3*). In all models the slope and the SSS were not significant.

Among the anthropogenic variables, the coastal-based impact was the only relevant predictor in all the analysed groups and temporal periods (*Figures 2, S3 and Tables 1 and S3*). This predictor presented a positive relationship (*i.e*., turnover increased with increasing impact) with species β-diversity, although the effect seemed smaller with respect to the bathymetry variable, and in particular in the fishes' group, which also displayed higher uncertainty compared to the invertebrates (*Tables 1 and S3*). Among the three groups analysed, the coastal-based impact was more relevant for the invertebrates' group in the T1 and the model with all the years together, while for T2 and T3 was more relevant for the demersal assemblage (*Table 1*). The model intercept is also informative, as it indicates the average dissimilarity between pairs of sites when they have identical predictive values (i.e., the environmental distance between sites equals zero). As shown in Table 1, invertebrates showed the greatest dissimilarity, as indicated by the relatively large intercept value. The maximum height of the spline function (hence the maximum value of the transformed predictor), indicated the importance of the predictor in explaining dissimilarities (*Figure 2*), that in all cases was the bathymetry. Finally, the geographical distance was not significant in any resulting model.

Models diagnostics were performed as usual, testing all the theoretical assumptions of normality and homogeneity of the variance (*Figures S4-S7*).

As there was a persistent pattern along the temporal periods analysed, maps were generated for the model with all the years together to reflect the cumulate effects of the variables evaluated. Regarding the geographic space, the patterns of β-diversity were more pronounced along the gradients of bathymetry (*Figure 3*). For the fish and invertebrate groups, four main high β-diversity areas were identified: a large hot-spot in the north in the waters between the Tarragona and Girona; another one located in the south close to Cartagena; and the third and fourth hotspots in waters around Baleares islands (*Figures 3a and 3b*). In the turnover map of the entire demersal assemblage, the β-diversity hotspots were similar to the ones identified in the two species groups' maps, although patterns were more pronounced (*Figure 3c*).

The richness map of the fish group highlighted different hotspots from those of correspondent turnover ones (*Figure 4a and Figure 3a,* respectively). In particular, the three main richness hotspots were located, from the north to the south, in the vicinity of Blanes and the Canyon of Palamos, at the south of the Ebro Delta and in waters off the Valencia city (*Figure 4a*). The spatial correlation between richness and β-diversity invertebrate's hotspots was non-informative (Pearson rho = 0.03, p-value < 0.05).

The main richness hotspots of the invertebrate group corresponded to those of the fish species, although the size of the hotspots was different (*Figure 4b and Figure 3b,* respectively). The overall correlation between richness and β-diversity fish's hotspots was 0.14 (p-value < 0.05). Finally, in the richness map of the demersal assemblage the identified hotspots coincided with the fish group (*Figure 4c*). In this case, the spatial correlation with the β-diversity areas was non-informative (Pearson rho = 0.03, p-value < 0.05).

When the high β-diversity areas were overlapped to the existing MPAs we found an overlap of 50.10% between these areas and the MPAs, for invertebrates the overlap increased to 50.23%, while for the demersal assemblage it was of 50.49%. In addition, the identified hotspots of richness of the demersal assemblage showed an overlap of the 84% with the existing MPAs.

DISCUSSION

Understanding the spatial patterns of marine biodiversity is key to establish effective marine conservation and measures for the application of a Marine Spatial Planning (MSP). Although goals and objectives of MSP are usually set for both natural processes and human activities, it is only the anthropogenic component that can be usually managed. Here, the use of broad groups for categorizing anthropogenic impact precludes specific attempt to manage these impacts but it is a first approximation of the possible cumulative assessment effects. Within this context, the novelty of the proposed approach is the possibility of identifying which are the key elements (environmental, anthropogenic or shared) that explain the distribution of marine β-diversity (and thus the species turnover) using a spatially explicit framework.

Conserving the β-diversity is essential as it can ensure both conservation and ecological functionality of unique natural communities and assemblages by promoting species replenishment after disturbances, maintaining demographic and functional connectivity (Lasram et al., 2015). However, it is worth noticing that preserving biological similarity over large- spatial scales (*i.e.*, low β-diversity) contributes to the ‘rescue’ of neighbouring communities after long-term depletion effects (Shackell et al., 2012), which is likely the current scenario in the Mediterranean Sea (Fernandes et al., 2017) resulting in a more heterogeneous spatial distribution of communities due to anthropogenic disturbance (Hidalgo et al., 2017).

Our findings show that the β-diversity of the demersal assemblage in the Spanish Mediterranean waters is mainly influenced by the bathymetry and the coastal impacts, highlighting accentuated dissimilarities in the invertebrate community. In particular, fishes was the group most affected by bathymetry. This is not really surprising as bathymetry has often been related to demersal species distributions and assemblages structure (Katsanevakis et al., 2009; Navarro et al., 2015; Pennino et al., 2013; Bellido et al., 2019; Vilas et al., 2020), and has been shown to be a main structural driver shaping β-diversity (e.g. Zintzen et al., 2011, Anderson et al., 2013). Until recently, deep continental margins (200-4000 m) were perceived to be environmentally homogeneous compared to continental and coastal systems in terms of temperature, light, salinity and nutrients, which would explain greater biotic homogeneity (Levin and Sibuet, 2012). Advances in seafloor mapping and direct observation now reveal unexpected heterogeneity, with a mosaic of habitats and ecosystems linked to geomorphological, geochemical and hydrographic characteristics that influence biotic diversity (Levin and Sibuet, 2012). Our results show an increasing β-diversity with depth, which is generally observed at large spatial scales (*i.e.*, ocean-wide) with orographic and oceanographic barriers to dispersal, contributing to regional segregations and endemism (Van Dover et al., 2002). This pattern can be related to the increase of the contribution of species with lower mobility (*i.e.*, invertebrates) as depth increases, and to a greater dissimilarity as spatial heterogeneity of communities increases in greater depth, a structural pattern already suggested for the impacted Mediterranean communities (Hidalgo et al., 2017). All the other environmental variables (i.e., SSS and slope), as well as the geographic distance, were not relevant for explain the β-diversity of these demersal communities. Specifically, although geographic distance was included in the model as a variable, it failed to capture the more complex role of biogeographic history in influencing the spatial separation of compositional dissimilarity. Other more complex distance metrics (e.g., least cost paths or circuit theory) should be tested in future analyses to explore possible neutral processes (Hubbell, 2001) and biogeographic history (Lu et al., 2019). However, so far, there are no computationally efficient solutions in both the adjustment and prediction phases (Mokany et al., 2022).

Among the anthropogenic variables, coastal-based impacts were the most important predictors that influenced the β-diversity in all groups and in particular for invertebrates, specially the sessile invertebrates that have lower dispersal capacity to move and avoid highly impacted areas (Shackell et al., 2012). Our results suggest higher β-diversity in more impacted areas. These results highlight that higher anthropogenic pressures may have a key role in spatially deconstructing marine ecosystems and, as such, increasing their heterogeneity and β-diversity. In consequence, this suggests that a generalized increase of β-diversity and the associated dissimilarity at short spatial scales is not a signal of healthy demersal ecosystems (Shackell et al., 2012), as preserving similarity over larger spatial scales (*i.e.*, low β-diversity) ensures higher capacities of ecosystems to overcome spatially-structured anthropogenic impacts. In this sense, our results support the notion that Mediterranean ecosystems have largely suffered from long-term changes of β-diversity through the erosion of similarity at relatively small spatial scales (Hidalgo et al., 2017), probably larger in coastal areas due to cumulative effects and decreasing as bathymetry increases (Coll et al. 2012). It is worth mentioning that our indicator of coastal impacts includes several activities that may be impacting β-diversity and represents an anthropogenic indicator of 'mesoscale', between local and regional scales. However, it is also possible that the effects of coastal anthropogenic impacts are confounded with natural environmental heterogeneity (e.g., variability in substrate type) that was not included in the model due to the lack of available data. Future studies should analyse in depth which individual coastal human impacts are driving these mesoscale patterns.

Waters surroundings the Blanes and Palamós Canyons in Catalonian waters were identified as important β-diversity areas for both species' groups and the entire demersal assemblage. Commonly, waters around canyons are high-productivity and dynamic areas which attract aggregation of demersal species (Pennino et al., 2017). On the contrary, richness maps identified some areas that were not highlighted by the species turnover patterns. Waters located south of the Ebro delta, an area with a high river run-off and known for boosting primary production, was important in terms of number of species but not for the β-diversity. Our results showed a positive but not meaningful correlation between the areas of β-diversity and the hotspots of richness. This mismatch between richness and β-diversity hotspots could be due for the spatial scale implemented in the study as spatial scale changes the relationship between richness and β-diversity (pooled species richness) (Sreekar et al., 2018). However, these finding highlights that both diversity measures are somehow complementary and should be considered in conservation and management plans. In the study area, current MPAs cover larger areas of these hotspots, despite they represent better the important areas for fish rather than for invertebrates. It is also worth mentioning that the MPA areas included in this study are highly heterogeneous and diverge largely on their protection and conservation measures, and thus in their efficiency (e Costa et al. 2016). Deeper analysis should be done to corroborate these results that are the first approximation in the study area.

Finally, the data used in this study were provided by the MEDITS surveys that covers only a short season from late spring to early summer. Consequently, our results only reflect a seasonal snapshot view of the diversity and richness of the demersal species, while an effective MSP should incorporate a more complete spatial-temporal dynamics. Unfortunately, the only complementary source of information available in the study area during the rest of the year is fishery-dependent data, which have a bias sampling design (Pennino et al., 2019b), and it is also limited because of the spatial-temporally patchy resolution of the data and the lack of information on smaller and non-commercial specimens. When fisheries-independent data representing other periods of the year become available, this study can be complemented to better understand the overall annual ecological dynamics and explore if β-diversity patterns follow a seasonal change as other spatial patterns of biodiversity indicators in the study region (De La Hoz et al., 2018, Vilas et al., 2020; Lloret-Lloret et al., 2021). A possible solution could be to deploy a winter survey to complement the identification of key areas for conservation in the Mediterranean Sea.

CONCLUSIONS

The β-diversity of the demersal assemblage in Spanish Mediterranean waters is mainly influenced by bathymetry and coastal impacts, highlighting, above all, accentuated dissimilarities in the invertebrate community. Several β-diversity hotspots were identified and they only partially match with current MPAs and richness hotspots. These results highlight that a complementary use of biodiversity measures (i.e. β-diversity, richness, etc.) should be adopted in order to identify the most important areas for demersal species and communities in Spanish Mediterranean waters.

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Tables

Table 1: BBGDM `Wald-like' tests on the intercept and sum of I-splines for the fishes, invertebrates and demersal assemblage in the Iberian Mediterranean Sea. W = `Wald-like' statistic; DF = degrees of freedom (number of I-spline bases); P= p-values.

	DF	**W BBGDN**	**P-BBGDM**
FISH			
Intercept	1	0.33	0.56
Bathymetry	3	690.23	***
Coastal impact	3	35.15	***
INVERTEBRATE			
Intercept	1	46.24	***
Bathymetry	3	354.73	***
Coastal impact	3	50.31	***
DEMERSAL ASSEMBLAGE			
Intercept	1	13.45	***
Bathymetry	3	606.46	***
Coastal impact	3	46.26	***

Figures

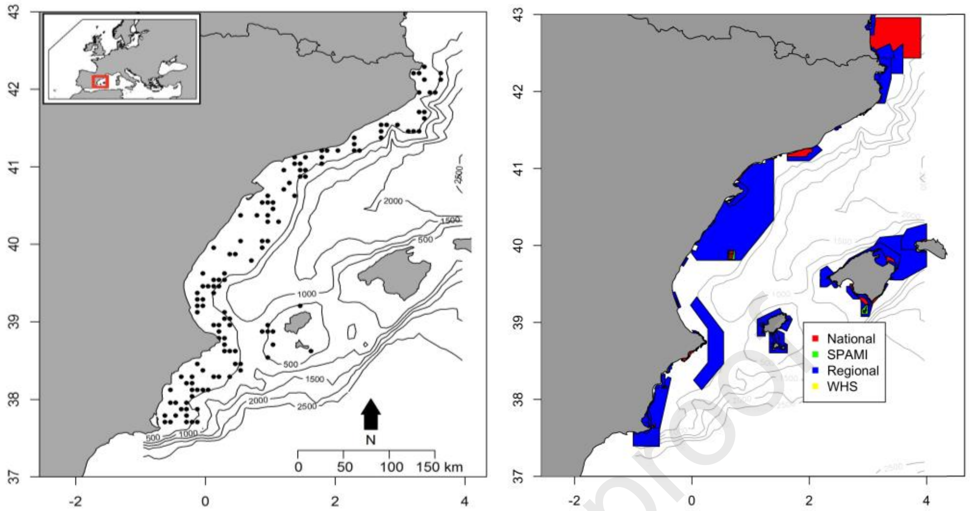

Figure 1: (A) Maps of the sampling locations of the MEDITS surveys from 1994 to 2015 along the Iberian Mediterranean coast. (B) Marine Protected Areas (d) acronyms are: National parks, Regional parks, World Heritage sites (WHS) and Specially Protected Area of Mediterranean Importance (Barcelona Convention) (SPAMI).

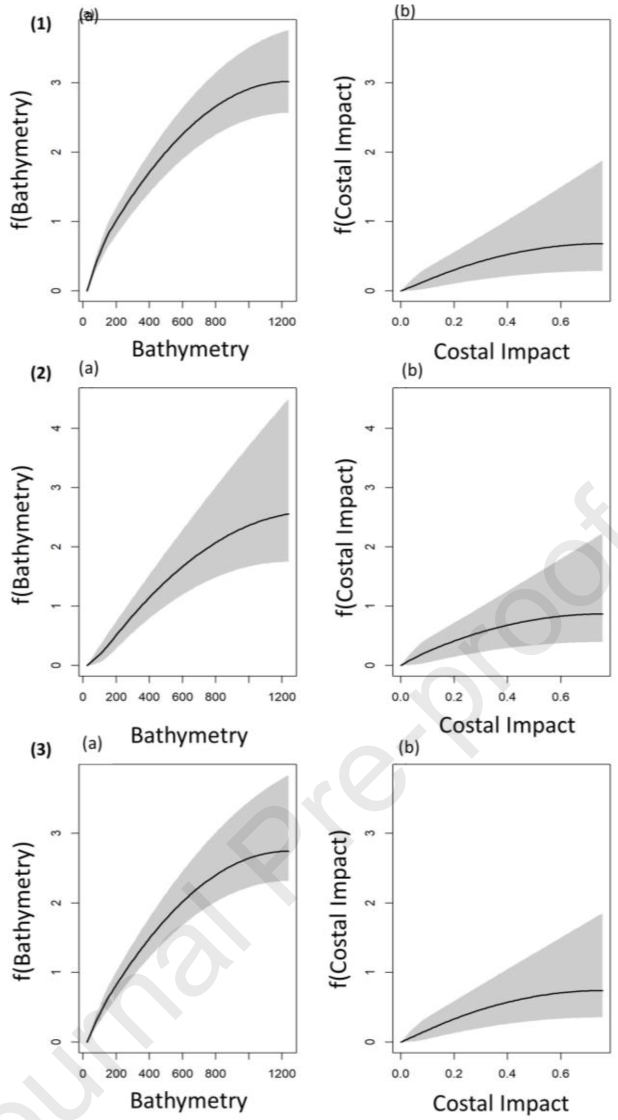

Figure 2: Partial response plots of BBGDMs for fishes (1), invertebrates (2) and demersal assemblage (3) data. The black line is the BBGDM mean estimate while shading indicates the 95% credible interval.

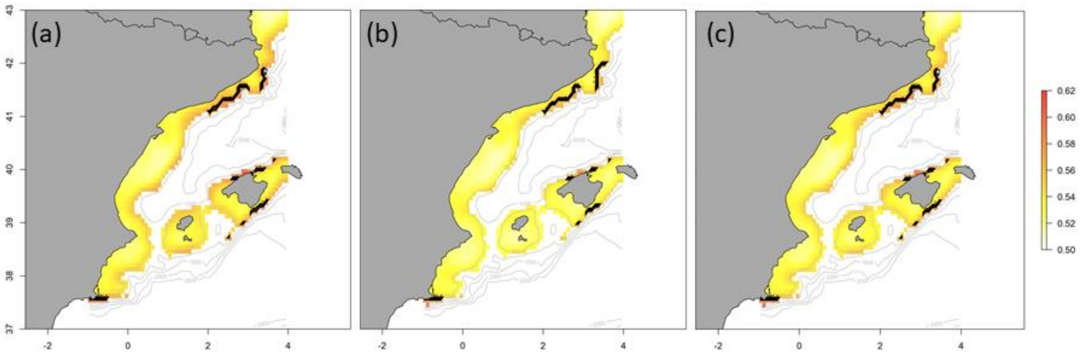

Figure 3: Predicted species turnover in the geographic space for (a) fishes, (b) invertebrate and (c) the demersal assemblage. Colors represent gradients in species turnover. β-diversity hotspots are highlighted in black.

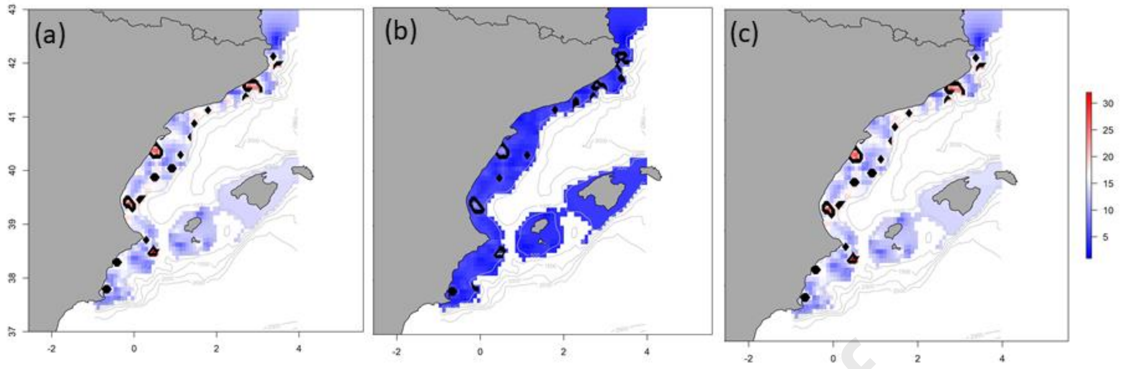

Figure 4: Richness map in the geographic space for (a) fishes, (b) invertebrate and (c) the demersal assemblage. Richness hotspots are highlighted in black.

BBGDMs were used to study the Iberian Mediterranean β-diversity demersal community.

Regional spatial patterns of β-diversity were best described by bathymetry and coastal impact.

The identified highest β-diversity areas presented different degree of overlapping with existent MPAs.

Declaration of interests

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

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