Marine protected areas are more effective but less reliable in protecting fish biomass than fish diversity

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\textbf{ABSTRACT}

Marine protected areas (MPAs) provide multiple conservation benefits, thus raising the question of how good and consistent they are at their roles. Here, we quantified three components, namely, diversity, biomass, and other relevant variables, in numerous protected and unprotected areas across four marine ecoregions in southwestern Europe. We created a “global conservation status index” (CSI\textsubscript{global}) as the sum of CSI\textsubscript{diversity}, CSI\textsubscript{biomass}, and CSI\textsubscript{relevant}. We then tested whether CSI and its three components varied as a function of protection and marine ecosystem. MPA efficiency, defined as the effect size of protection on CSI\textsubscript{global}, was unreliable and varied with geography. CSI\textsubscript{biomass} and CSI\textsubscript{relevant} contributed to the unreliability of MPA efficiency, while CSI\textsubscript{diversity} was reliable. CSI\textsubscript{biomass} showed the major effect in protected areas (60%). Biomass of threatened species was the single largest variable that contributed to MPA efficiency. Our easy-to-use approach can identify high- and low-efficient MPAs and help to clarify their actual roles.

1. Introduction

Marine protected areas (MPAs) are one of the main management tools for the current human-driven biodiversity crisis. With increasing anthropogenic pressures, MPAs are essential to preserve natural resources, biodiversity, and ecosystem properties (Micheli et al., 2012; Hilborn, 2016; Campbell et al., 2017). MPAs have steadily increased in the last decades to > 5% of coastal areas under national jurisdictions and < 1% of the high seas (Spalding et al., 2013) figures that keep on increasing with the establishment of some large MPAs, particularly in tropical waters (Devillers et al., 2015). MPAs are pivotal tools for fisheries management and biodiversity conservation (Edgar et al., 2014). Yet, only 10% of the MPA surfaces are no-take zones, free of extraction, or habitat alteration activities, while 94% of MPAs allow fishing and other activities (Thomas et al., 2014; Costello and Ballantine, 2015; Campbell et al., 2017). Certainly, MPAs include a high range of areas, designs, uses, and management goals (Al-Abdulrazzak and Trombulak, 2012; Edgar et al., 2014; Pérez-Ruzafa et al., 2017), which could result in many benefits and varying degrees of protection efficiencies.

Besides MPAs, additional protection measures have been taken to contribute to biodiversity conservation, protection of threatened species, and restoration of fish stocks, including national parks, marine sanctuaries, natural parks, or national monuments (Al-Abdulrazzak and Trombulak, 2012). Moreover, areas such as military zones can offer protection because of strong surveillance, highly restrictive access, and ban of extractive activities. All these protection measures can lead to the recovery of natural resources and other positive effects on natural communities (Russ et al., 2005; Weeks et al., 2010; Campbell et al., 2017).

The benefits of protection in marine communities are abundant, mostly focused on traits associated with diversity, biomass, or other relevant aspects related to protection. Protected areas are associated with larger species richness (Wantiez et al., 1997; Ciriaci et al., 1998; Edgar and Barrett, 1999; Barrett et al., 2007), larger trophic diversity (Shears and Babcock, 2003; Harmelin-Vivien et al., 2015), and larger functional diversity (Stelzenmüller et al., 2009; Villamor and Becerro, 2012; Guilhàmon et al., 2015) than unprotected areas. Protection also...
triggers an increase in fish biomass, particularly of commercial fish species (Barrett et al., 2007; Fenberg et al., 2012; Parravicini et al., 2014; Pérez-Ruzaifa et al., 2017), likely as a result of decreased fishing pressures (e.g., larger biomass of fish over 20 cm; Edgar and Barrett, 1999; Barrett et al., 2007; Stuart-Smith et al., 2017). However, the biomass of other groups of species such as fish species in the IUCN Red List (Nieto et al., 2015) has received less attention (Willis et al., 2003; Afonso et al., 2011; Harmelin-Vivien et al., 2015). Other relevant variables unevenly used to assess the effects of marine protection include abundance of higher carnivores (Cole, 1994; Harmelin et al., 1995), vulnerability of fish community (Cheung et al., 2007; Stuart-Smith et al., 2017; Vasconcelos et al., 2017), and fish size (Shears and Babcock, 2003; Sciberras et al., 2013). Overall, most available evidence supports for a positive effect of protection on all these traits, providing ample MPA benefits in terms of fish diversity, fish biomass, and relevant traits of the fish community.

The variability in MPA traits and benefits also points toward the possibility that MPAs may be inconsistent in their multiple roles, leading to varying degrees and contrasting levels of efficiency (Dichmont et al., 2013; White et al., 2014). In fact, the positive effects of protection are unevenly spread across MPAs, and numerous studies fail to provide evidence for the expected beneficial effects of protection. Literature on the so-called paper parks provides ample evidence that MPAs can be inefficient (Bustamante et al., 2014; Gallacher et al., 2016) due to multiple factors (Rífe et al., 2013; Edgar et al., 2014). Often, the protection effects of MPAs, e.g., increase in species richness or abundance, are noticeable after sufficiently long periods together with suitable control sites (Stobart et al., 2009; Chirico et al., 2017). Moreover, many studies that assessed MPA efficiency have focused on one rather than several benefits (McClanahan et al., 1999; Vanderklift et al., 2013), which could account for differences associated with the specifics of each benefit, MPA, or geographic region investigated (Caveen et al., 2015; Fletcher et al., 2015; Hughes et al., 2016).

Studies examining the effects of protection on multiple benefits over large geographic scales can provide opportunities to advance our understanding on how good MPAs are at achieving their multiple benefits and how reliable MPAs are at providing such benefits. In this study, we followed this approach to shed some light on the relationship between protection and their benefits. We used fish communities across south-western Europe to investigate how fish diversity, fish biomass, and other relevant protection-related benefits contributed to the overall differences between fish communities in protected and unprotected areas and tested whether these benefits were consistent or varied as a function of geography. We investigated > 20 protected sites distributed in four marine ecoregions of the world (Spalding et al., 2007) in the Atlantic-Mediterranean confluence area. We used species richness, trophic diversity, and functional diversity to evaluate MPA benefits on fish diversity; biomass of commercial fish, biomass of large fish, and biomass of threatened fish species to evaluate MPA benefits on fish biomass; and fish vulnerability, fish size, and abundance of higher carnivores as other MPA benefits on fish communities. Our results showed evidence for a small but consistent protection effect on fish diversity as opposed to larger and geographically variable protection effects on biomass and other relevant variables that resulted in unreliable MPA efficiency in our study area.

2. Material and methods

2.1. Study area and field survey

We sampled a total of 372 sites that are mostly scattered along, but not limited to, the coast of Spain, Portugal, and North Africa (Fig. 1). The locations included 22 MPAs from four marine ecoregions (Alboran Sea; Azores Canaries Madeira, hereafter Canary Is.; South European Atlantic Shelf, hereafter Atlantic; and Western Mediterranean) defined by Spalding et al. (2007) as “areas of relatively homogeneous species composition, clearly distinct from adjacent systems.” The species composition of each ecoregion is likely to be determined by the predominance of a small number of ecosystems or a distinct suite of oceanographic or topographic features (Spalding et al., 2007, Table 1).

In this paper, we define MPA broadly to accommodate for the multiple protection measures available in our study area, including marine reserves, national parks, natural parks, and no-access military zones with strong enforcement. Specific goals of these 22 MPAs include biodiversity conservation (17 MPAs), fish stock restoration (12 MPAs), national defense (4 MPAs), and protection of endangered species (1 MPA). Our sampling design covered many protected and unprotected sites in each of the four ecoregions investigated, providing a good representation of both factors. All sampling was conducted in the summers of 2014, 2015, and 2016.

We used the Reef Life Survey protocol (Edgar and Stuart-Smith, 2014) to quantify the number, abundance, and size distribution of the fish community at each site. Briefly, in each sampled site, we took at least two underwater visual surveys along 50-m long × 10-m wide transects (Edgar and Stuart-Smith, 2014), with all conspicuous fish (> 25 mm size) identified and their abundances and sizes estimated. We restricted sampling between 6- and 15-m deep to minimize the influence of depth on fish communities.

2.2. Conservation status index (CSI)

Our quantitative data allowed us to calculate multiple variables from which we selected nine mostly unrelated traits to characterize fish communities (Table 2). These selected variables provided quantitative information on the status of each fish community in terms of diversity (species richness, trophic diversity, and functional diversity), biomass (biomass of commercial species, biomass of large specimens, and biomass of threatened species), and relevant traits (vulnerability, size community, and abundance of higher carnivores; Fig. 2). We calculated species richness as the total number of fish species in each transect. To calculate trophic diversity, we categorized every fish specimen into its respective trophic group, i.e., benthic invertivore, browsing herbivore, higher carnivore, planktivore, or scrapin herbivore, and we computed the Shannon-Weaver diversity index as natural logarithm on the abundance of these trophic groups. To calculate functional diversity, we assigned all fish specimens to their corresponding levels of eight functional traits (water column position, preferred substrate, trophic group, dial activity pattern, habitat complexity, gregariousness, trophic breadth, and maximum length) and calculated Rao-Q following Stuart-Smith et al. (2013). Information on the trophic groups and functional traits of every fish species is available in FishBase (www.fishbase.com), (Froese and Pauly, 2000).

We used our observed abundance of fish size groups to estimate biomass of fish species (Ln transformed) based on species-specific length-weight relationships available in FishBase (Froese and Pauly, 2000). We defined large specimens as fish individuals larger than 200 mm length (hereafter biomass > 200 mm). We used Spanish Commercial List of Marine Fishes (http://www.mapama.gob.es/es/pesca/temas/mercados-economia-pesquera/fichas_sp_comerciales.aspx) to assign fish species to the commercially interesting species group and the European Red List of Marine Fishes of the International Union for Conservation of Nature (IUCN) to assign fish species to the threatened species group (Nieto et al., 2015).

We also used FishBase information (Froese and Pauly, 2000) to quantify the abundance of higher carnivores (log transformed) and to assign vulnerability values to every fish specimen in our data set. Then, we used the community-weighted mean as a vulnerability index. We calculated fish size as the community-weighted mean of the total length of the observed fish specimens in each site.

We defined the global conservation status index (CSIglobal) as the sum of the nine variables investigated, which were standardized between 0 and 100 to give equal possible weight to their contribution to
Fig. 1. Location of the 22 marine protected areas (stars) and hundreds of localities (circles) investigated in our study, spanning in four marine ecoregions of the world (A, B, C, and D; Spalding et al., 2007). See Table 1 for details.

Table 1
Marine protected areas investigated in our study, showing the code to find its location in Fig. 1, marine ecoregion, protected area name, protection status, and goals as specified in their official sites.

<table>
<thead>
<tr>
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<th>Marine ecoregion</th>
<th>Protected area</th>
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CSIglobal (Fig. 2). The simple addition of standardized variables also allowed for (i) an easy partitioning of the CSIglobal into its three components of diversity (CSIdiversity), biomass (CSIbiomass), and relevant traits (CSIrelevant) by simply considering their respective variables and (ii) straight ecological interpretation as each variable value contributed directly and proportionally to CSIglobal (Fig. 2).

2.3. Testing MPA efficiency

We defined MPA efficiency as the difference in CSI between protected and unprotected sites, i.e., the effect size of protection. Thus, larger CSI values in protected sites would show evidence for an efficient MPA with further analyses of the threeCSI components (or nine individual variables) pointing to specific benefits over unprotected sites. Equal or larger CSI values in unprotected sites would define inefficient MPAs.

We used general additive mixed models (GAMMs; Wood, 2017) to analyze ecoregion (i.e., Alboran Sea, Canary Is., Atlantic, and Western Mediterranean) and protection (i.e., protected and unprotected) effects on CSIglobal, CSIbiomass, CSIdiversity, and CSIrelevant components. Here, GAMM models were fitted using ecoregion and protection as fixed factors and sampling sites nested with protection as random factors to account for hierarchical pseudoreplication. Moreover, we selected GAMM models because we can correct the spatial autocorrelation including latitude and longitude as tensor product interaction covariable (Wood, 2017). All statistical analyses were conducted in R software environment (R Core Team, 2015) using mgcv package for GAMM (Wood, 2017). We tested three null hypotheses: no interaction between ecoregion and protection, no CSI differences between protected and unprotected sites, and no CSI differences among the four ecoregions. Because we defined MPA efficiency as the difference in CSI between protected and unprotected sites, a significant protection factor indicated efficient (or inefficient) MPAs, while a significant interaction term stressed spatial inconsistencies in MPA efficiency (or inefficiency).

In other words, the model actually tested for the role of geography (ecoregion) in CSI, MPA efficiency (protection), and reliability of MPA efficiency across ecoregions (interaction).

Afterward, we tested the differences in MPA efficiency matrix between the four marine ecoregions by using permutational multivariate analysis of variance with the function “adonis” of vegan package (Oksanen et al., 2016). Here, we applied Euclidean distance to the matrix comprising CSIbiomass, CSIdiversity, and CSIrelevant variables with 999 permutations. The pairwise comparisons between ecoregions were calculated using “adonis.pairwise” function from the EcolUtils package (Salazar, 2015). We also calculated and plotted MPA efficiency as the CSI effect size of protection (protected minus unprotected sites). By examining the effect size of the three CSI components and corresponding standardized variables, we also quantified whether MPAs were more efficient in some specific benefits and whether such benefits remained consistent across the ecoregions. All the results are reported as mean ± standard error for protected and unprotected areas. The supplementary data and the R codes used to compute the CSI index are in the Git repository: https://github.com/Sanabria-Fernandez/Conservation-Status-Index

3. Results

3.1. Global conservation status index (CSIglobal)

MPA efficiency was unreliable and varied significantly with the ecoregions (Table 3, CSIglobal, p interaction < 0.001, Fig. 3a). We found larger CSI values in protected areas than in unprotected areas in the Canary Is. (4.51 ± 0.42 and 2.70 ± 0.11; t = 5.06, p < 0.001) and Western Mediterranean (2.94 ± 0.19 and 1.87 ± 0.07; t = 3.09, p < 0.01) areas.
p = 0.002) ecoregions and no CSIglobal differences in the Atlantic (2.57 ± 0.54 and 1.83 ± 0.06; t = 1.39, p = 0.163) and Alboran Sea (2.56 ± 0.12 and 2.27 ± 0.13; t = 0.84, p = 0.4) ecoregions (Fig. 3a).

The Canary Is. had the largest protection effect size (1.818), followed by the Western Mediterranean (1.069), Atlantic (0.737), and Alboran Sea (0.286) ecoregions (Figs. 3a and 6).

### 3.1.1. Biomass conservation status index (CSIbiomass)

MPA efficiency was unreliable and varied significantly with the ecoregions (Table 3, CSIbiomass, p interaction < 0.001, Fig. 3b). We found larger CSIbiomass values in protected areas than in unprotected areas only in two out of four ecoregions (Fig. 3b): Alboran Sea (1.01 ± 0.09 and 0.66 ± 0.06; t = 2.28, p = 0.022) and the Canary Is. (1.9 ± 0.16 and 0.87 ± 0.07; t = 4.21, p < 0.001). There were no significant differences in the Western Mediterranean (1.12 ± 0.11 and 0.56 ± 0.05; t = -1.73, p = 0.083) and Atlantic (0.74 ± 0.21 and 0.55 ± 0.02; t = -0.14, p = 0.88) ecoregions. Specifically, the biomass > 200 mm was significantly greater with protection (0.33 ± 0.01 and 0.24 ± 0.01; F = 10.31, p = 0.001), and the biomass of commercial species showed significant differences at the ecoregion level, for example, in the Canary Is. (average = 0.28 ± 0.01) and Western Mediterranean (average = 0.25 ± 0.01); (F = 5.07, p = 0.001) ecoregions. The biomass of threatened species varied significantly between protected and unprotected areas irrespective of the ecoregion (F = 8.84, p interaction < 0.001). Alboran Sea (0.45 ± 0.08 and 0.21 ± 0.05) and the Canary Is. (0.40 ± 0.06 and 0.26 ± 0.06) showed the highest values inside the protected areas.

### 3.1.2. Diversity conservation status index (CSIdiversity)

We did not find significant differences in the CSIdiversity among the studied ecoregions nor between ranges of protection (0.85 ± 0.02 and 0.79 ± 0.01; Table 3, Fig. 3c). An independent analysis of CSDiversity components showed that only species richness (F = 12.07, p < 0.001) and trophic diversity (F = 3.73, p = 0.01) exhibited significant differences between the ecoregions. However, there was a significant ecoregion × protection effect over functional diversity (F = 3.3, p interaction = 0.02).

### 3.1.3. Relevant conservation status index (CSIrelevant)

There was a significant interaction between ecoregion and protection for relevant conservation status index (Table 3, CSIrelevant, p interaction < 0.001, Fig. 3d). We found larger CSIrelevant Values in protected areas than in unprotected areas in three out of four ecoregions (Fig. 2d): the Canary Is. (1.51 ± 0.25 and 0.83 ± 0.05; t = 4.41, p < 0.001), the Atlantic (1.22 ± 0.36 and 0.80 ± 0.05; t = 2.03, p = 0.042), and the Western Mediterranean (0.88 ± 0.11 and
Fig. 3. Boxplots representation of the conservation status index (CSIglobal, 3a; CSIbiomass, 3b; CSIdiversity, 3c; and CSGlobalrelevant, 3d) in protected and unprotected areas of the four ecoregions investigated in our study. * indicates significant differences (p < 0.05) between protected and unprotected areas within each ecoregion. See Table 3 for the statistical details.

Fig. 4. (A). Percentage contribution of the three components of diversity, biomass, and other relevant traits to the total MPA efficiency. (B). Percentage contributions as in (A) but disclosed for each ecoregion.

Marine ecoregions
- Alboran Sea
- Canary Is.
- Atlantic
- Western Mediterranean

Efficiency (Protected minus unprotected average)
-0.05 0 0.45

Biomass threatened species
Abundance higher carnivores
Biomass > 200 mm
Trophic diversity
Species richness
Biomass commercial species
Vulnerability
Functional diversity
Large specimens

Fig. 5. MPA efficiency, defined as the effect size between protected and unprotected areas, for each of the nine variables investigated in our study.

3.2. Marine protected areas efficiency

Overall, the three components of biomass, diversity, and relevant contributed 60.01%, 14.41%, and 25.58%, respectively, to MPA efficiency (Fig. 4a). These contributions varied significantly between ecoregions (F = 26.59, p < 0.001, Fig. 4b), with CSIbiomass being the largest contributor in three out of four ecoregions and CSIdiversity in none of them (Fig. 4b). Biomass of threatened species (48.7%) and abundance of higher carnivores (26.9%) were the largest contributors to MPA efficiency (Fig. 5). Biomass of large fish (9.3%), trophic diversity (8%), and species richness (7.4%) were less important contributors to MPA efficiency, while the contribution of the remaining variables was either marginal or negative, i.e., biomass of commercial fish (2.1%), vulnerability (0.1%), functional diversity (−1.1%), and fish size (−1.4%) (Fig. 5). Biomass of threatened species was consistently a major contributor to MPA efficiency, although the magnitude of the contribution varied largely among ecoregions (from 81.1% in Alboran Sea to 19.3% in the Atlantic, Fig. 6). Vulnerability was consistently a minor contributor, with positive or negative effect sizes close to zero in all ecoregions (Fig. 6). The contribution of the remaining variables to MPA efficiency was highly unreliable among the ecoregions (Fig. 6).

4. Discussion

MPAs are becoming one of the most prevalent tools to promote biodiversity conservation and sustainable use of marine resources (Gaines et al., 2010; Spalding et al., 2013). Available evidence supports for multiple benefits of protection and points to ineffective MPA management when benefits are missing (Rife et al., 2013). These arguments may lead to believe that MPAs would excel at all their multiple roles under good management practices. Although good management is imperative for effective protection, MPAs differ in many aspects that could contribute to differences in their degree of efficiency at one or multiple roles regardless of their management practices (Villamor and Becerro, 2012). Here, we analyzed nine protection benefits in numerous MPAs of four marine ecoregions of the world and tested whether MPA efficiency was reliable or varied as a function of ecoregion. Our results showed the existence of large differences in MPA efficiency across ecoregions, with varying degree of efficiency at protecting multiple roles. Our results warned against the belief that implementation of an MPA may lead to the achievement of every protection-related benefit as we still lack predictive knowledge on how protection benefits apply into specific protected areas. Our approach may help quantify the degree of achievement of MPA objectives and the circumstances under which MPAs accomplish certain benefits more efficiently.

MPA efficiency varied significantly between ecoregions. We found effective MPAs with larger CSI values in protected areas than in unprotected areas in the Canary Is., Western Mediterranean, and Atlantic ecoregions and ineffective MPAs in the Alboran Sea ecoregion. MPAs in the Canary Is. were the most efficient in our study area, driven by high CSI values in protected areas as compared to those in the remaining geographic regions. Although the causes underlying the good conservation status of MPAs in the Canary Is. are diverse, the high fishing pressure throughout unprotected areas in the archipelago (Garcia-
Mederos et al., (2015) and the decrease in density of the voracious sea urchin *Diadema africanum* and associated regime shifts in protected areas (Sangil et al., 2012) are likely contributors. Difficulties in surveillance, enforcement, and monitoring may underlie the inefficiency of MPAs in the Alboran Sea ecoregion, as it occurs in other vast offshore MPAs in the ocean (Wilhelm et al., 2014). In addition, the major unprotected sampled points in this ecoregion have been conducted in the Spanish coastal zone; hence, a gap exists in the unprotected Moroccan coastal area. An extensive sampling survey in the northern African coast is needed to shed light on the effects of protection in the Alboran Sea ecoregion.

Biomass-related traits were the largest contributors to MPA efficiency in our study, which was mostly explained by the contribution of the biomass of threatened species within the studied MPAs. The strong positive effect of protection on the biomass of threatened species (49% efficiency) was in contrast with the weak effect of protection on the biomass of commercial species (2% efficiency). Further, the biomass of threatened species was consistently a major contributor to MPA efficiency, while the contribution of the biomass of commercial species to MPA efficiency varied substantially between ecoregions. In the Atlantic ecoregion, the biomass of threatened species was the second major contributor to MPA efficiency. Although the Atlantic is a hotspot of threatened fish species (Nieto et al., 2015), biomass was minor because threatened species were accidental in our sampling stations. These results contrasted with the specific goals of the 22 MPAs investigated in this study. Twelve out of 22 MPAs included commercial fish stock restoration as a specific goal, while only 1 MPA (Cabo de Creus, Western Mediterranean) was designed to protect endangered species. It seems, therefore, that the sought-after goal of fish stock restoration is at risk in the MPAs investigated herein, making these MPAs an unreliable tool to protect coastal fisheries in our study area. Increased biomass of commercial fish species is a common benefit of protection (Barrett et al., 2007; Fenberg et al., 2012; Parravicini et al., 2014; Campbell et al., 2017; Pérez-Ruzafa et al., 2017) and failure to achieve this goal may rely on the small-size of no-take zones, as suggested by other studies (Claudet et al., 2008). The biomass of large fish (> 200 mm) was similar within the studied MPAs from the Canary Is. and Western Mediterranean. However, this biomass was surprisingly lower in the Alboran Sea and Atlantic ecoregions, though these ecoregions are characterized by a high productivity. Hence, the efficiency of MPAs regarding biomass is reliable but showed a high spatial variability among ecoregions, perhaps due to suboptimal MPA surveillance to control illegal fishing.

The effect of protection on fish diversity was reliable but small in the studied MPAs. MPAs were not only a successful conservation tool to preserve biodiversity but, they also seemed to promote an increase in biodiversity within the studied protected areas. Our results suggest that MPAs may function as both biodiversity conservation and restoration areas. European MPAs have demonstrated evidence of preserving biodiversity of local ecosystems (Fenberg et al., 2012) through the re-establishment of biological variables, e.g., trophic interactions that characterized unfished ecosystems. The importance of functional diversity has recently increased in the marine realm because of the advantages of using functional traits as surrogates of the status of coastal environments (Stuart-Smith et al., 2013); further, it has been demonstrated that functional diversity greatly contributes to the stability of marine communities (Bates et al., 2013). In our study, functional diversity showed the highest values in the Canary Is. ecoregion though we found no differences associated with protection in the studied ecoregions.

MPA efficiency on other traits associated with the fish community was highly variable among the ecoregions. We found higher CSIvalues in protected areas than in unprotected areas of the Canary Is., Western Mediterranean, and Atlantic. These differences were mostly driven by the abundance of higher carnivores, which was the second largest contributor to MPA efficiency in our study. Our results showed large abundances of higher carnivores within MPAs, which is likely a consequence of the impact of fishing on the density and structure of fish assemblages (Clemente et al., 2009; Guidetti et al., 2014). Yet, the Alboran Sea showed higher abundances of higher carnivores in unprotected areas. Illegal fishing associated with suboptimal surveillance could lead to these unexpected results in the Alboran Sea. Vulnerability was a minor contributor to MPA efficiency regardless of the ecoregion, probably because of the dominance of species with low vulnerability and high to medium resilience in the studied ecoregions, as it has been shown in other coastal environments (Vasconcelos et al., 2017). Vulnerability showed slightly higher values in protected areas than in unprotected areas of the Canary Is. (1.7%), which is likely to be associated with larger fish size (5.6%). The effect of protection on fish vulnerability was virtually nonexistent in the remaining ecoregions.

The lack of a consistent trend regarding MPA efficiency in the studied ecoregions may be explained by the high spatial unreliability of most of the variables investigated in our study. Except for the biomass of threatened species and vulnerability, the remaining seven variables showed high spatial variability that prevented reliable protection effects. This spatial variability is multifaceted because it is dependent upon fish characteristics, such as fish mobility and spill-over effect (Pérez-Ruzafa et al., 2008; Le Quesne and Codling, 2009) and features regarding protection measures (Edgar et al., 2014) such as size of no-take zones (Claudet et al., 2006), time of creation (Babcock et al., 2009), and associated regime shifts in protected areas.
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