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Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning

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Abstract

Current methods in conservation planning for promoting the persistence of biodiversity typically focus on either representing species geographic distributions or maintaining connectivity between reserves, but rarely both, and take a focal species, rather than a multispecies, approach. Here, we link prioritization methods with population models to explore the impact of integrating both representation and connectivity into conservation planning for species persistence. Using data on 288 Mediterranean fish species with varying conservation requirements, we show that: (1) considering both representation and connectivity objectives provides the best strategy for enhanced biodiversity persistence and (2) connectivity objectives were fundamental to enhancing persistence of small-ranged species, which are most in need of conservation, while the representation objective benefited only wide-ranging species. Our approach provides a more comprehensive appraisal of planning applications than approaches focusing on either representation or connectivity, and will hopefully contribute to build more effective reserve networks for the persistence of biodiversity.

KEYWORDS

biodiversity conservation, larval dispersal, marine protected areas, marine reserve design, spatial planning, spatial prioritization

1 | INTRODUCTION

With the rapid loss in global biodiversity, the main challenge faced by conservation planners is to maximize the long-term persistence of biodiversity (Pressey, Cabeza, Watts,

Cowling, & Wilson, 2007). This overarching goal of conservation planning is often articulated by more refined, quantitative conservation objectives, which are based on ecological theory (Game, Kareiva, & Possingham, 2013; Pressey, Visconti, & Ferraro, 2015). The key conservation objectives

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to achieve biodiversity persistence when designing systematic reserves are related to preserving biological features (e.g., ecosystems, species) and the ecological processes that sustain them (e.g., dispersal, migration). Particularly in the marine realm, larval dispersal is a major ecological process influencing the functioning of ecosystems (Cowen & Sponaugle, 2009) and the delivery of services (Kerwath, Winker, Götz, & Attwood, 2013), and hence can serve as a key consideration for objective-setting when designing conservation plans (Magris, Pressey, Weeks, & Ban, 2014).

Conservation planning has focused primarily on representation of biodiversity patterns (Pressey et al., 2007), usually through reserve selection algorithms such as Marxan (Possingham, Ball, & Andelman, 2000) and Zonation (Moilanen et al., 2005) to identify priority areas that protect a proportion of the geographic range of each biological feature (a species for example). The assumption underpinning this approach is that maximizing the representation of species within reserves will ensure their persistence even when reserves are widely spaced or including large portions of habitat discontinuities. However, few studies have explicitly examined the contribution of biologically representative reserve networks to the long-term persistence of biodiversity (but see Nicholson, Westphal, & Frank, 2006; Visconti, Pressey, Segan, & Wintle, 2010). Furthermore, these studies focused on few species across relatively small geographic regions (several to tens of kilometers), limiting insights into the complex relationship between biodiversity representation and persistence across larger planning regions and larger sets of species.

An active debate continues over how connectivity related to larval dispersal should be addressed in conservation planning (Almany, Connolly, & Heath, 2009; Magris, Treml, Pressey, & Weeks, 2016; White, Schroeger, Drake, & Edwards, 2014) and how the connectivity value of individual areas should be quantified (Andrello, Jacobi, Manel, Thuiller, & Mouillot, 2015; Beger, Linke, & Watts, 2010; Jacobi & Jonsson, 2011). To incorporate larval dispersal information in spatial prioritization, current methods typically rely on Marxan's functionality to address spatial dependencies between areas (Beger et al., 2010) or metrics derived from network theory that can serve as surrogates of dispersal potential (Krueck, Ahmadi, & Green, 2016; Magris et al., 2016; White et al., 2014). The former approach is limited because the functionality does not allow species-specific dispersal to be applied. This is a drawback because planning must consider multiple species, each with its own connectivity requirements. The latter approach can overcome this limitation, allowing multispecies spatial prioritization (Magris et al., 2016; White et al., 2014), but the link with more direct estimates of persistence remains untested.

Recent research has attempted to include measures of biodiversity persistence when designing marine reserves

based on mechanisms that influence species distributions and abundances more explicitly (Kaplan, Botsford, O'Farrell, Gaines, & Jorgensen, 2009; Moffitt, White, & Botsford, 2011; White, Botsford, Hastings, & Largier, 2010; White, Botsford, Moffitt, & Fischer, 2010; White et al., 2014). Yet, still missing are efforts to develop spatial prioritization methods integrating both the protection of biodiversity patterns and the maintenance of larval dispersal for species-level conservation. In this study, we propose an approach that links prioritization methods with dynamic population models to determine the performance of such planned reserve networks. We analyze biodiversity persistence from a metapopulation perspective (Hastings & Botsford, 2006) to evaluate whether, for a given reserve network, species are found to have an increase in population size. We apply this approach to predict the effect of protection on population sizes for a wide variety of fish species along a large spectrum of dispersal abilities and geographic range sizes, using the Mediterranean Sea as a regional example.

2 | METHODS

2.1 | Study region and input data

Our analysis included the best and most current publicly available species data on the Mediterranean Sea (Albouy, Lasram, & Velez, 2015) encompassing the geographic distributions of 288 strictly coastal fish species (200 m depth limit; Appendix S1) as surrogates of biodiversity patterns. These fish assemblages play a critical role in ecosystem function and resilience (Guilhaumon, Albouy, & Claudet, 2015), as well as being historically subjected to fisheries exploitation (Bianchi et al., 2012). Their habitats are also being increasingly affected by coastal development and climate change (Coll, Piroddi, & Steenbeek, 2010), and marine reserves have been shown to boost resilience against these stressors (Micheli, Saenz-Arroyo, & Greenley, 2012).

For larval connectivity modeling, we also chose nine different combinations of spawning times and pelagic larvae durations representing key life-history traits (hereafter termed "dispersal strategies") that capture the full range of dispersal potential over the 288 species (see below and Appendix S2). This was done because we were unable to incorporate species-specific information on life-history traits while simulating larval dispersal. Species distributions and connectivity model were summarized at a resolution of 1/10th degree cells called "areas" ($N = 7,703$).

2.2 | Larval dispersal modeling and connectivity analysis

The probability that a larva of a given species dispersed from a source area to neighboring or nonadjacent areas was

quantified using a biophysical model (Appendix S2). Dispersal simulations were performed with Ichthyop 3.1 (Lett, Verley, & Mullan, 2008) and each simulation was carried out by releasing 50,000 virtual larvae per area over 5 years (2004–2008). The yearly connectivity matrices were averaged over years to produce a single connectivity matrix for each dispersal strategy.

Many existing connectivity metrics derived from network theory can be useful in prioritizing conservation. We focused on three—betweenness centrality, outflux, and local retention (Appendix S3)—that have previously assisted to conservation prioritization by identifying stepping-stone, source, and self-persistent areas, respectively (Magris et al., 2016). Stepping-stone, source, and self-persistent areas are valuable because they allow, respectively, for dispersal between larger groups of connected areas, for extensive emigration and postdisturbance recovery, and for self-sustaining ecological refuges (Burgess, Nickols, & Griesemer, 2014; Minor & Urban, 2007; Saura, Bodin, & Fortin, 2014).

Betweenness centrality was quantified as the number of times an area occurs on the shortest path between any other two areas in the network (Minor & Urban, 2007). When calculating this metric, each connection was given a weight = $\ln(1/p)$, where p is the larval dispersal probability associated with that connection (Costa, Petrenko, Guizien, & Doglioli, 2017). The out-flux of an area was calculated by summing all fluxes for all outgoing connections from that area (Magris et al., 2016). We measured local retention for each area as the diagonal elements of connectivity matrices (Treml & Halpin, 2012). We calculated all these metrics using the *igraph* R package (Csardi & Nepusz, 2006). Each metric individually was scaled between 0 and 1 by dividing by the maximum value.

2.3 | Conservation prioritization

We considered two sets of conservation scenarios to evaluate the contribution of reserves to the increase in species demographic sizes (Figure 1). First, we employed Marxan to identify areas that are priorities for an objective of species representation only. Second, we used Marxan to identify priorities that achieved not only species representation but also maximized larval dispersal (Appendix S4).

For scenarios based on species representation only, we used the presence/absence of the 288 species in each area as conservation features. For scenarios including both species representation and connectivity, the contribution of each area for connectivity of each species must be calculated. Each combination of the metrics (betweenness centrality, outflux, and retention) and the nine dispersal strategies ($n = 27$) was assigned separately to each species by considering the metric values only when a given species occurs in that area. This resulted in a total of 7,776 conservation features (3 metrics \times 9

dispersal strategies \times 288 species) to be simultaneously used in the prioritization analysis. Although this might seem unrealistic, this assumption is reasonable in a conservation planning context, where available data are not sufficient and/or many plans will continue to be produced without species-specific models for larval dispersal. We argue that considering hypothetical combinations of species and dispersal strategies provides a better ecological basis than allocating individual, but highly uncertain, dispersal strategies to species (Table 1: Panel A).

In conservation planning, one specifies the minimum amount of each feature that needs to be protected by reserves, i.e., the target levels (Pressey, Cowling, & Rouget, 2003). To allow comparison between the two sets of conservation scenarios, we varied our targets equally for each conservation feature from 10% to 90%, with increments of 10%. The intent was to ensure a minimum level of representation of the 288 conservation features within potential reserves when planning for representation only. For integrating information on connectivity, we followed White et al. (2014) and set representation targets for the 7,776 connectivity-related features.

2.4 | Population dynamic modeling and performance of reserve networks

We developed a population dynamics model following the literature in marine reserve networks (Kaplan et al., 2009) to estimate the potential effects of conservation scenarios on the population size of each species (Appendix S5), as a proxy for biodiversity persistence. Briefly, we modeled population dynamics according to a modified Beverton–Holt model that includes the positive effect of protection on population size and the negative effect of random temporal perturbation events that reduce population sizes to 10% of their original values. We then took the mean population size over the 5 years with the smallest population size. The rationale behind this method is that the effect of protection is assumed to be most important when population size is small (Jacobi & Jonsson, 2011). Then, for each species k we calculated three quantities: (1) $\overline{N}_{k,z}$, the average population size for each Marxan output (lowest cost solutions) at each target level $z = \text{rep10, rep20, ..., rep90, repcon10, repcon20, ..., repcon90}$; (2) $\overline{N}_{k,max}$, the average population size when the entire range of the species is protected; and (3) $\overline{N}_{k,curr}$, the average population size when only areas currently part of a marine reserve are protected. $\overline{N}_{k,z}$, $\overline{N}_{k,max}$, and $\overline{N}_{k,curr}$ were calculated separately for each of the nine dispersal strategies (Table 1: Panel B).

We then compared how the different Marxan scenarios contributed to average population size using a relative measure of population size, defined as

$$\text{relative pop size} = \frac{\overline{N}_{k,z}}{\overline{N}_{k,max}} \cdot 100 \quad (1)$$

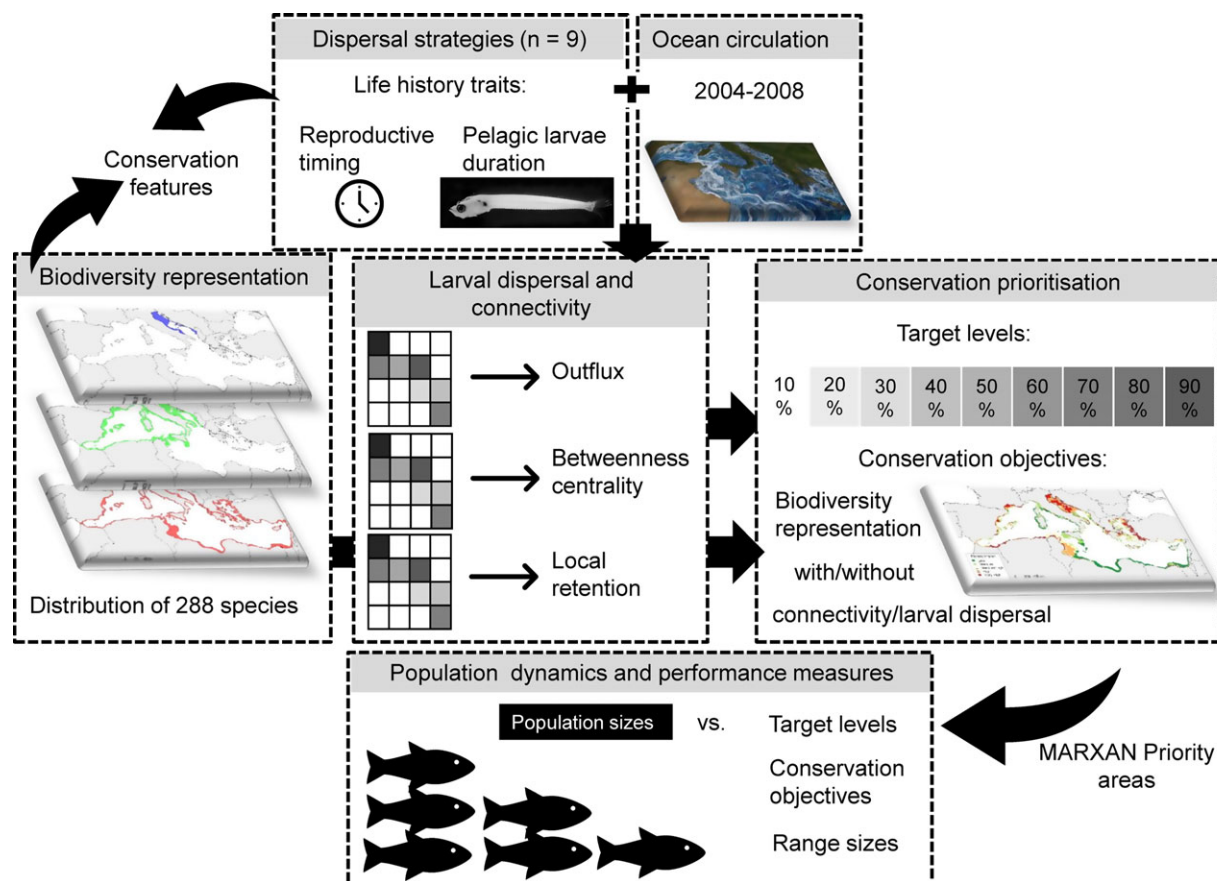


FIGURE 1 Flowchart of the approach to evaluate the achievement of species persistence in conservation planning through representation of biodiversity patterns and connectivity considerations. Data on distributions of fish species ($n = 288$), and on life-history traits related to variable dispersal strategies were used as conservation features. Models of potential larval dispersal were used to derive connectivity metrics (outflux, betweenness centrality, and local retention) based on oceanographic and species life-history data. Species' spatial distributions and combinations of connectivity metrics and dispersal strategies were then used in Marxan to identify priority areas when representation of species were the only objectives included and when maximizing connectivity was also considered, at varying percentage target levels (10–90%). Results from Marxan served as inputs for population dynamic models to obtain estimates of species relative population sizes. We analyzed and compared the percentage of maximum population size provided by marine reserve networks designed under alternative conservation scenarios and target levels. We also evaluated the relationship between gains in population sizes and species geographic range size

TABLE 1 Rationale for conservation features and modeling of population dynamics

Rationale	
Panel A: Conservation features	
288 fish species	For representation of species and modeling connectivity
7,776 connectivity features	9 dispersal strategies \times 3 metrics \times 288 species, to ensure that areas important for each metric and each species were included in planned network of reserves, and assuming that any dispersal strategy could apply to any species, in the absence of better information
Panel B: Population models	
288 \times 9 combinations of species and dispersal strategies	To determine population sizes based on all potential dispersal strategies, with the aim of obtaining values that are well suited to the full range of species, and evaluate all potential demographic responses of species to planning objectives

We assessed the performance of reserve networks in terms of population sizes. First, we compared the relative population sizes when variably increasing the target levels of all conservation features within each set of scenarios. Second, we investigated the influence of species geographic range size on

the population sizes provided by spatial prioritization aiming to represent biodiversity patterns only, and when also aiming to maximize larval dispersal. This comparison was made for reserve networks that had comparable dimensions (i.e., 30% of study region covered by potential reserves following recent

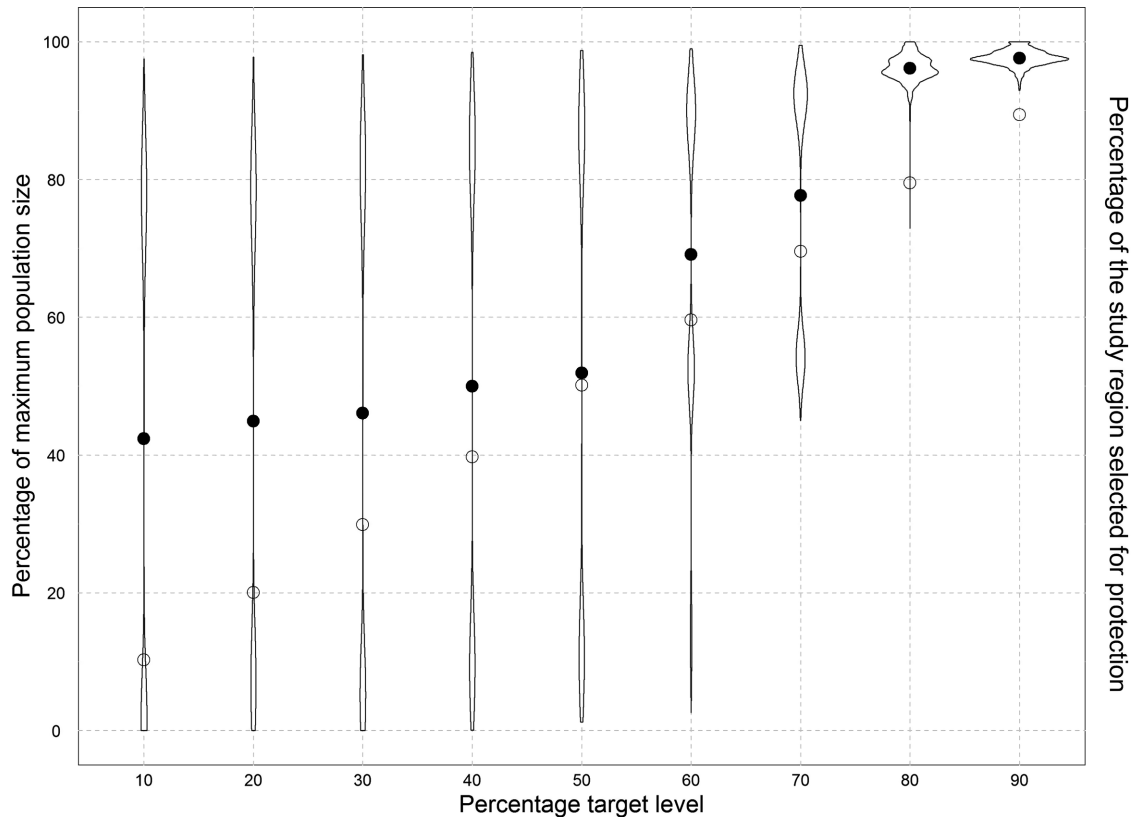


FIGURE 2 Percentages of maximum population size achieved across 288 species \times 9 dispersal strategies when planning for representation of species only. Percentages of maximum population size are expressed as a function of increasing percentage target levels in the prioritization and the resulting percentage of the study region selected for protection. Violin graphs show the variations in density of relative population sizes at each target threshold level. Filled dots display the means across combinations of species and dispersal strategies. Unfilled dots display the percentages of the study region identified by Marxan's best solution as priorities

guidelines; Butchart, Clarke, & Smith, 2015). In this last comparison, we also sought to compare this benefit in terms of population size relative to existing protection. Therefore, we quantified the gain in population size as

$$\text{gain in pop size} = \frac{\overline{N_{k,z}} - \overline{N_{k,curr}}}{\overline{N_{k,max}}} \cdot 100 \quad (2)$$

3 | RESULTS

Potential reserve networks designed with and without connectivity varied strongly in their contribution to population sizes considering the whole set of combinations between species and dispersal strategies. For scenarios considering species representation only, the mean relative population size increased with the target level of conservation features (Figure 2), with pronounced increases when target levels were $>50\%$. Below the 70% target, the mean values of relative population sizes were at least 40%, but there was considerable variation among species and dispersal strategies; above the 70% target, the mean values of relative population sizes

were higher (at least 70%) and the variation among species and dispersal strategies decreased considerably. When targets were set to either 80% or 90%, there was a high density of population sizes $>90\%$.

Overall, adding connectivity to planning offered a strong benefit in terms of enhancing species relative population sizes in comparison to planning in the absence of this information (Figure 3). The relative population size averaged 80% for most combinations of species and dispersal strategies, for any target level used in the prioritization. Notably, we did not observe an increase in the relative population size achieved when increasing percentage target thresholds for conservation features.

Our prioritization analysis showed that species representation only resulted in a scattered distribution of potential reserves throughout our study region (Figure 4a). By including connectivity objectives in the prioritization, potential reserves networks had a much more packed arrangement, and larger individual sizes (Figure 4b). The average size of reserves was 123 km^2 , which contrasts with the average size of reserves designed for species representation which is 81.5 km^2 . The overlap between the two reserve networks was about 60%.

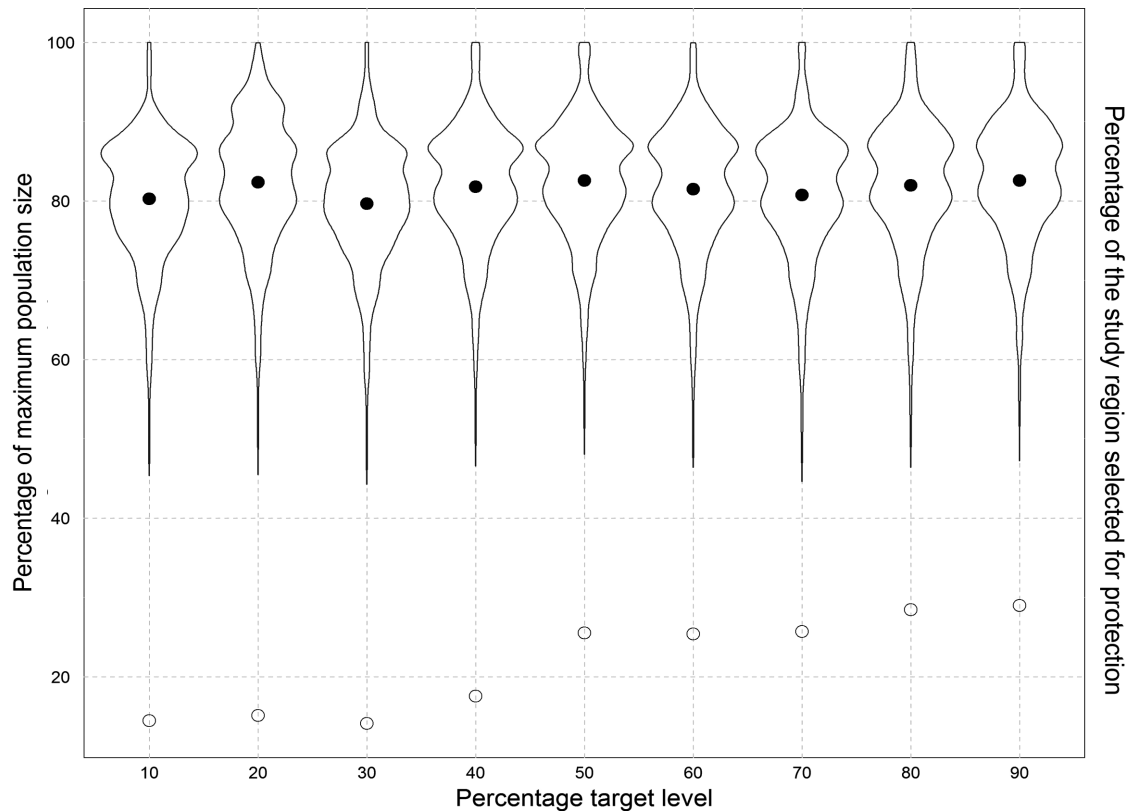


FIGURE 3 Percentages of maximum population size achieved across 288 species \times 9 dispersal strategies when planning for representation of species and maximizing larval dispersal. Percentages of maximum population size are expressed as a function of increasing percentage target levels in the prioritization and the resulting percentage of the study region selected for protection. Violin graphs show the variations in density of relative population sizes at each target threshold level. Filled dots display the means across combinations of species and dispersal strategies. Unfilled dots display the percentages of the study region identified by Marxan's best solution as priorities

Planning only for species representation achieved a mean gain of 49.6% in population size (median: 17.6%) relative to the population sizes provided by the existing reserves (Figure 5). However, this gain was not uniform; higher values were observed for species with ranges $>4,000 \text{ km}^2$, while species with smaller ranges showed lower gains. Conversely, prioritization for both species representation and connectivity achieved a mean gain of 82.4% relative to existing reserves (median 82.9%), and favored a larger number of species range sizes than reserves derived from representation alone (Appendix S6 for additional results).

4 | DISCUSSION

Representing biodiversity patterns and maintaining ecologically connected reserves have long been considered as two major conservation objectives of planning aiming to achieve multispecies persistence (Margules & Pressey, 2000). Our results demonstrate that, for fish species in the Mediterranean Sea, systematic reserves designed to accomplish these paired conservation objectives resulted in larger population sizes, and therefore higher probability of species persistence, than

reserves designed to achieve only biodiversity representation. In addition, our combined scenario yielded better results in terms of maximum population sizes for both small- and large-range species, which vary in their conservation requirements, without requiring additional area coverage for effective protection. To our knowledge, there has been no previous study evaluating the gains in persistence yielded by integrating representation and connectivity into planning in a multiple species context with limited species-specific information on dispersal ability (but see Bode, Williamson, & Weeks, 2016 and White et al., 2014, for applications in data-rich areas dealing with single or few species).

Defining conservation objectives for effective conservation planning (Game et al., 2013) has the potential to significantly alter the configuration and size of reserve networks. The formulation of objectives involves understanding the relationship between conservation value and the amount of each feature within the reserve system (Carwardine, Klein, Wilson, Pressey, & Possingham, 2009), as an attempt to achieve population persistence (Magris et al., 2014). Our findings reinforce the concept that the benefit of a reserve network to a species is an increasing function of its representation (Arponen, Heikkinen, Thomas, & Moilanen, 2005). However,

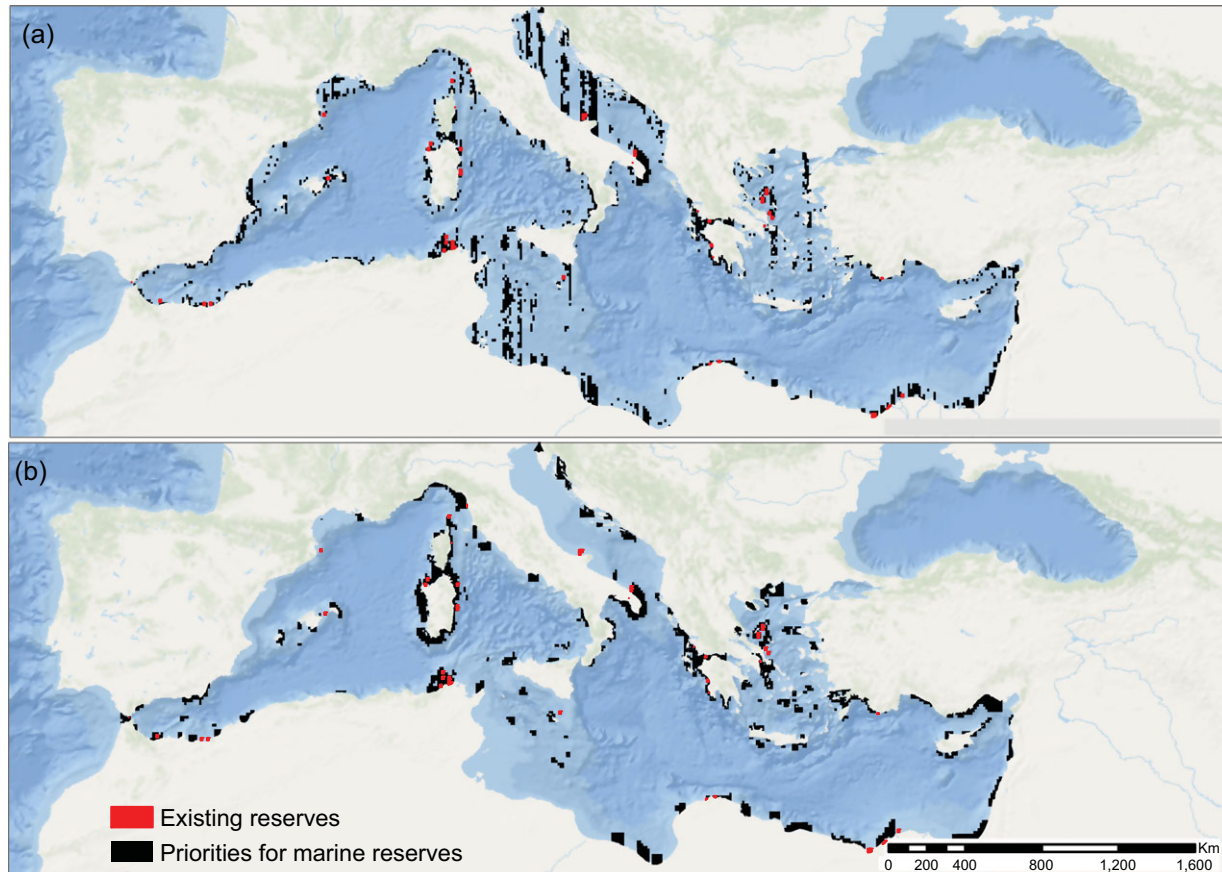


FIGURE 4 Spatial comparison of conservation priorities identified by conservation objectives related to representation of species distribution only (a) and when maximizing larval dispersal was also included (b). Priorities for marine reserves are best solutions (lowest cost) identified in spatial prioritization with Marxan. Areas considered currently protected are shown in red. For both scenarios, the conservation objectives were set to result in about 30% of protection coverage of our study region

a successful reserve plan is often defined by achievement of stated threshold objectives (Pressey et al., 2015), which might not reflect the contribution of reserves to species persistence. Evaluating existing and proposed reserves only by gauging how well they meet conservation objectives (Magris, Pressey, Mills, Vila-Nova, & Floeter, 2017) can miss demographic responses that can be seen with more thorough evaluation using population modeling, as demonstrated in this article.

One implication of our results is that inclusion of small-range species in conservation planning based on representation only must be carefully considered for potential limitations. This poses a dilemma for conservation planners, because small-range species tend to be at higher risk of extinction (Luiz, Woods, Madin, & Madin, 2016), therefore attracting substantial attention in conservation science. Our results indicate that the geographic range of species is a key predictor of species demographic persistence (Lee & Jetz, 2011), reinforcing the idea that representation targets should be higher for species with smaller ranges (Guilhaumon et al., 2015; Magris et al., 2017). Furthermore, species with restricted

ranges are often specialists with low dispersal capacity, characteristics that have made them more heavily dependent upon self-persistence within large reserves (White, Botsford, Hastings et al., 2010).

A major challenge in conservation science is to integrate our understanding of functional connectivity for a broad range of target species at biogeographical scales with ecological certainty needed to inform management decisions. Our study region lacks details of life-history traits for specific taxa (Andreello et al., 2013). Thus, our approach is “inclusive,” including all potential dispersal strategies for any one species. Our formulation of conservation objectives will then need to be adaptively refined as knowledge indicates the relative prevalence of specific dispersal strategies across species and scaled appropriately to reflect differential vulnerability of each dispersal strategy to human threats. For application in future prioritizations, models presented here would benefit from additional data such as life-history evaluations and estimates of multiple human impacts on dispersal patterns.

In future work, our approach can also be expanded to other regions to seek robust generalizations of relationships

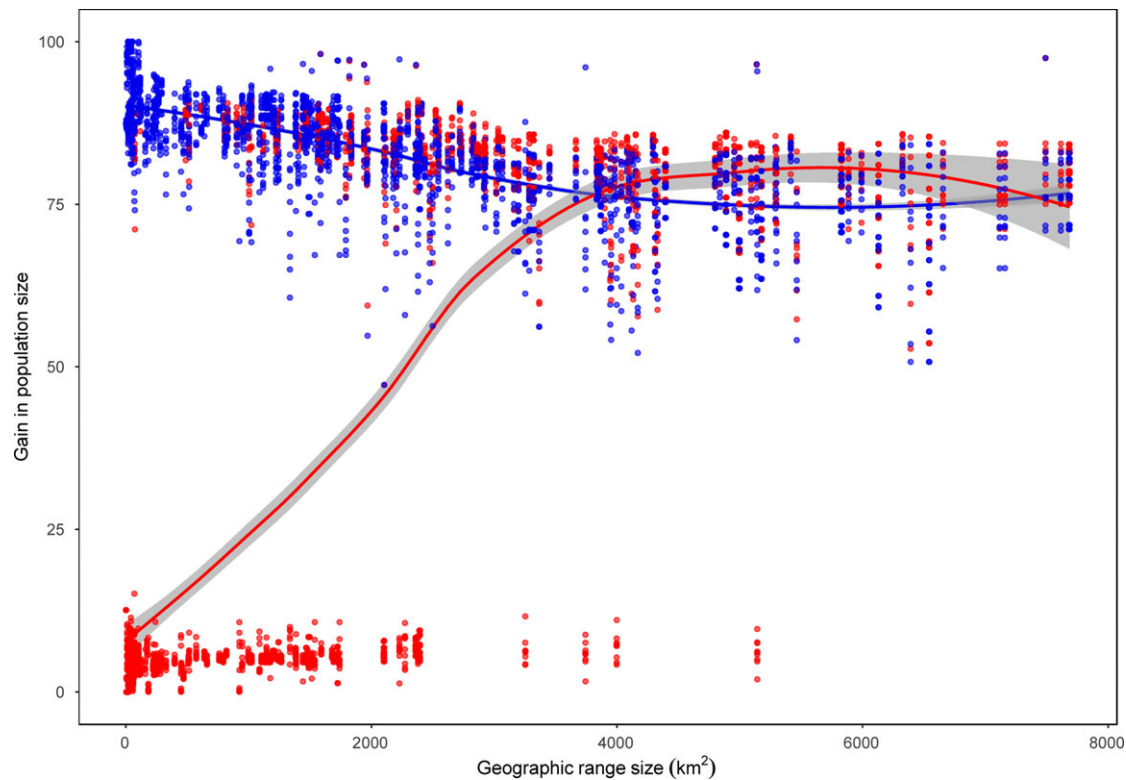


FIGURE 5 Gain in population size (y-axis) provided by reserve priorities identified through representation of species only (red dots) and when also maximizing larval dispersal (blue dots) as a function of geographic range sizes of species (x-axis, in kilometer²) when expanding existing reserves to achieve 30% reserve coverage of the study region. The gains on the y-axis are calculated in terms of proportion (0–100) of the maximum population size provided by protecting the whole distribution of each species and in relation to population sizes provided by existing reserves. Dots represent individual combinations of species and dispersal strategies ($288 \times 9 = 2,592$) while lines indicate mean predictions from the loess regression with the shaded areas representing 95% confidence bands

between conservation objectives and species persistence. Our demographic model can also be easily employed to explore spatial and temporal variation in demographic parameters, such as those affected by fisheries or climate, and for the design of reserve networks whose main purpose is to maximize fishery yields (Kerwath et al., 2013; White, Botsford, Moffitt, et al., 2010). For instance, because the persistence of fish populations depends on exploitation rates outside marine reserves (Moffitt et al., 2011), models should account for spatial variation in fishing intensity across the planning region to investigate its consequences on connectivity between populations and recruitment. Additionally, the model should implement temporal variation in connectivity due to climate change (Andrello, Mouillot, Somot, Thuiller, & Manel, 2015), which could in turn change the conservation priorities over time.

Despite the challenges discussed here, our study supports the idea for decision-making that biodiversity persistence is enhanced through achieving objectives for both representation and connectivity. Furthermore, our results contribute to an understanding of conservation requirements within a multispecies context. Specifically, we show that large-ranged species can increase their persistence when planning is directed at representation, whereas small-ranged species can

be more persistent only if connectivity is included as a specific conservation objective.

4.1 | Recommendations for conservation policy and planning

From this study, we can identify two key recommendations to guide regional conservation planning aiming to achieve long-term conservation goals. First, neglecting connectivity information might severely impair the effectiveness of conservation plans. Identifying areas that are important for facilitating seascape and landscape connectivity is crucial to ensure the effectiveness of reserve networks, especially for small-ranged species. Second, we propose that the original framework of conservation planning should be modified by recognizing the integration of connectivity through well-defined and ecologically informed conservation objectives that address uncertainties associated with species-specific dispersal capabilities and can be operationally implemented within reserve selection algorithms. Particularly for marine systems, conservation prioritization using ecologically informed metrics accounting for species-specific dispersal abilities has the potential to go beyond the current use of automated parameters in reserve

selection algorithms (Beger et al., 2010). We show that using hypothetical traits of modeled species for guiding the optimal siting of reserves within a relatively data-poor context is possible.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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