

Protected and Threatened Components of Fish Biodiversity in the Mediterranean Sea

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Abstract:

The Mediterranean Sea (0.82% of the global oceanic surface) holds 4%–18% of all known marine species (~17,000), with a high proportion of endemism [[1] and [2]]. This exceptional biodiversity is under severe threats [1] but benefits from a system of 100 marine protected areas (MPAs). Surprisingly, the spatial congruence of fish biodiversity hot spots with this MPA system and the areas of high fishing pressure has not been assessed. Moreover, evolutionary and functional breadth of species assemblages [3] has been largely overlooked in marine systems. Here we adopted a multifaceted approach to biodiversity by considering the species richness of total, endemic, and threatened coastal fish assemblages as well as their functional and phylogenetic diversity. We show that these fish biodiversity components are spatially mismatched. The MPA system covers a small surface of the Mediterranean (0.4%) and is spatially congruent with the hot spots of all taxonomic components of fish diversity. However, it misses hot spots of functional and phylogenetic diversity. In addition, hot spots of endemic species richness and phylogenetic diversity are spatially congruent with hot spots of fishery impact. Our results highlight that future conservation strategies and assessment efficiency of current reserve systems will need to be revisited after deconstructing the different components of biodiversity.

Highlights : ► The Mediterranean Sea is a marine biodiversity hot spot under severe threats ► The system of marine protected areas covers 0.4% of the Mediterranean Sea surface ► This system is spatially congruent with hot spots of fish taxonomic diversity ► This system misses hot spots of fish functional and phylogenetic diversity

Results

The geographic location of the Mediterranean Basin, at the margins of Africa, Europe, and West Asia (Figure 1A), provides a unique diversity of habitats, within which a succession of colonization events has shaped a remarkable diversity of species [4]. Indeed, the Mediterranean Sea may be seen as a marine biodiversity hot spot, exhibiting a singular mixture of endemics, species from the Atlantic, and others of tropical origins [1, 2]. Although it represents only 0.32% of the global oceanic volume and 0.82% of its surface area, the Mediterranean Sea holds 4%–18% of all known marine species (w17,000) and has a high level of endemism [1, 2].

Like most marine ecosystems worldwide, the Mediterranean Sea is highly impacted by several human-mediated threats [1], including intensification in the exploitation of resources from industrial, artisanal, and recreational fisheries, aquaculture, ever-increasing density of coastal populations, and pesticides and fertilizer runoff from agriculture. To counteract these increasing threats, about 100 marine protected areas (MPAs) have been established and reinforced in the Mediterranean Sea to conserve both species and habitats [5, 6]. However, these MPAs cover jointly 9910 km², i.e., only 0.4% of the surface area of the Mediterranean Sea [7]. Moreover, they have thus far been created as a result of national or even subnational initiatives, without regional consideration or management plans [8]. Hence, the spatial design of the realized MPA system in the Mediterranean Sea is mainly contingent on local socioeconomic and historical factors, rather than being based on large-scale scientific information, e.g., macroecological considerations [6]. For example, 73% of Mediterranean MPAs are located along its northern shores [7]. Surprisingly, the perceived efficiency of this existing MPA system, i.e., whether and how this system spatially matches with critical areas for conservation, has never been assessed.

In 2010, during the tenth meeting of the Conference of the Parties to the Convention on Biological Diversity (COP10), several headline targets were proposed toward a Strategic Plan for Biodiversity. Following target 11, at least 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, would be conserved by 2020 through systems of protected areas and other effective area-based conservation measures. However, despite this decision, and the existence of approximately 100 MPAs, little attention has been devoted to the spatial overlap— if any—between the present system of Mediterranean MPAs, the hot spots of fish biodiversity (top sites ranked according to biodiversity level), and the hot spots of anthropogenic stresses (top sites ranked according to threat level). This oversight is particularly striking in comparison with the situation prevailing with terrestrial ecosystems [9]. Though delayed because of the lack of detailed and spatially explicit regional-scale data sets, such assessment is urgently needed if we are to achieve the targets of the COP10. Here, we present a fine-resolution mapping of spatial layers containing

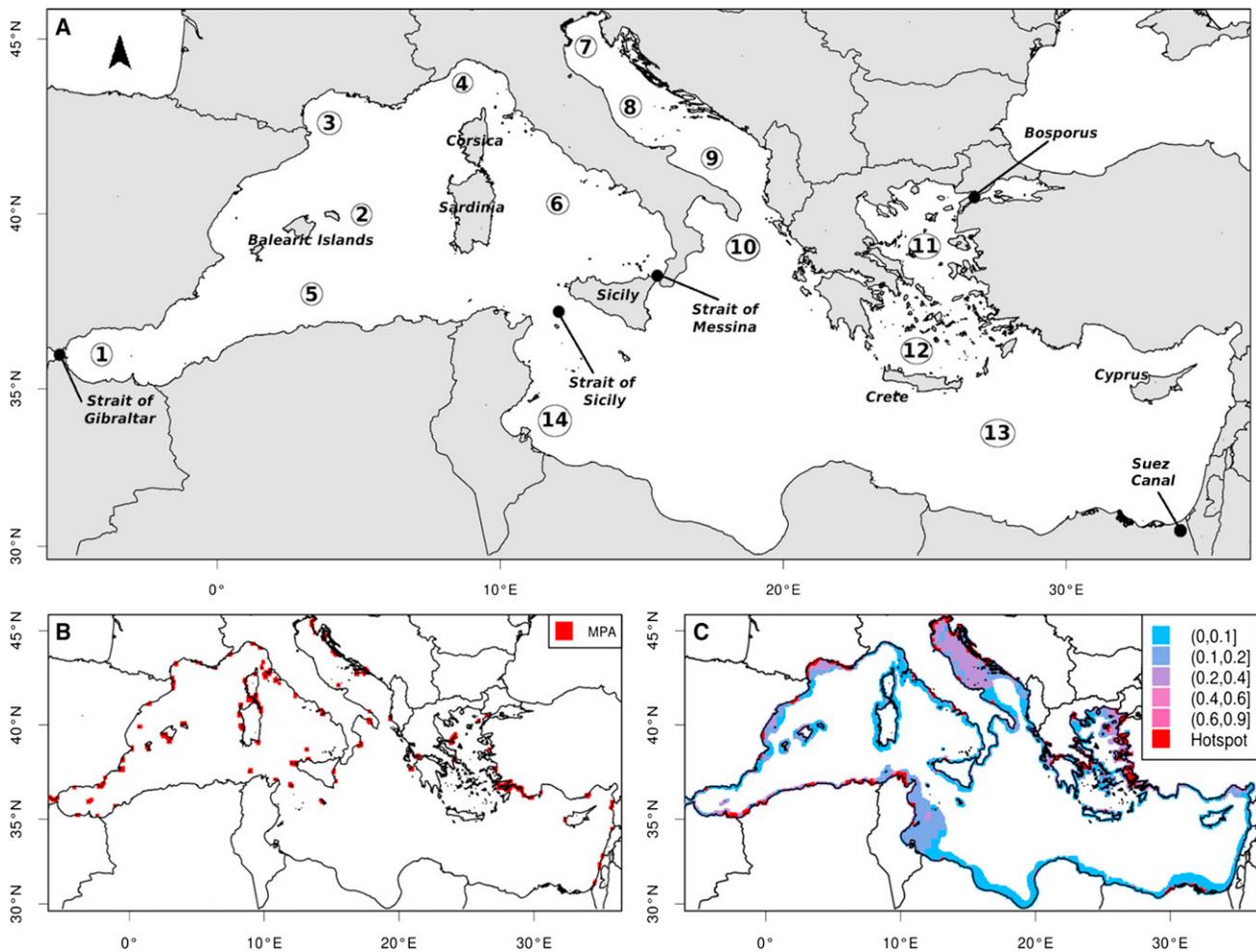


Figure 1. Regions, Basins, Marine Protected Areas, and Fishing Pressure in the Mediterranean Sea

(A) Main regions and basins in the Mediterranean: 1, Alboran Sea; 2, Balearic Sea; 3, Gulf of Lions; 4, Ligurian Sea; 5, Algerian and Tunisian waters; 6, Tyrrhenian Sea; 7, North Adriatic Sea; 8, Central Adriatic Sea; 9, South Adriatic Sea; 10, Ionian Sea; 11, North Aegean Sea; 12, South Aegean Sea; 13, Levant Sea; 14, Gulf of Gabès.

(B and C) Locations of the 100 marine protected areas (MPAs) (B) and gradient of fishing pressure (C). See [Supplemental Experimental Procedures](#).

extensive information on fish species distributions, fishing pressure, and MPA location. We use this data set to evaluate how Mediterranean coastal fish biodiversity is protected by the extant MPA system and threatened by coastal fisheries.

The IUCN Red List rankings are largely based on criteria of rarity and range size, especially when population size and temporal trends are not available. However, the recent literature has highlighted the need to rely on other attributes that make species unique in terms of biological traits [10, 11] or genes [12, 13] for biodiversity conservation. More generally, the concept of biodiversity encompasses many components [3, 14], and total species richness, the most commonly used component of diversity in conservation, may remain silent on the number of threatened or endemic species [15] or on functional and phylogenetic differences among species [3]. We adopted a multifaceted view of Mediterranean fish biodiversity by considering, probably for the first time in aquatic systems, the species richness of total, endemic, and threatened (IUCN) fishes as well as the functional (traits) and phylogenetic (lineages) diversity of assemblages. The two last components have been largely ignored in conservation

planning and reserve network assessment (but see [3, 16]), yet they both are key to the diversity of life on Earth [10, 12] and ecosystem functioning [17, 18].

We created a database gathering the geographical distribution of the 282 coastal and continental shelf teleost species using a grid cell at a resolution of $0.1^\circ \times 0.1^\circ$ [19]. For those species, we built a dated phylogeny based on molecular data and a functional dendrogram based on 15 traits to estimate phylogenetic and functional diversity, respectively. We then mapped all the components of fish biodiversity that we overlaid with the geographic occurrence of MPAs and the spatial distribution of fishing intensity. We also identified hot spots of total, IUCN, and endemic species richness; hot spots of phylogenetic and functional diversity; and hot spots of threats corresponding to the cells with the highest 5% values (roughly the percentage of cells contained in the MPA system). Our study provides the first comprehensive assessment of the extent to which fish biodiversity components spatially match the current distribution of MPAs and fishing pressure.

We recorded a total of 100 MPAs in the Mediterranean Sea (Figure 1B). Among the 8186 spatial cells used in this analysis,

Fish Conservation in the Mediterranean Sea

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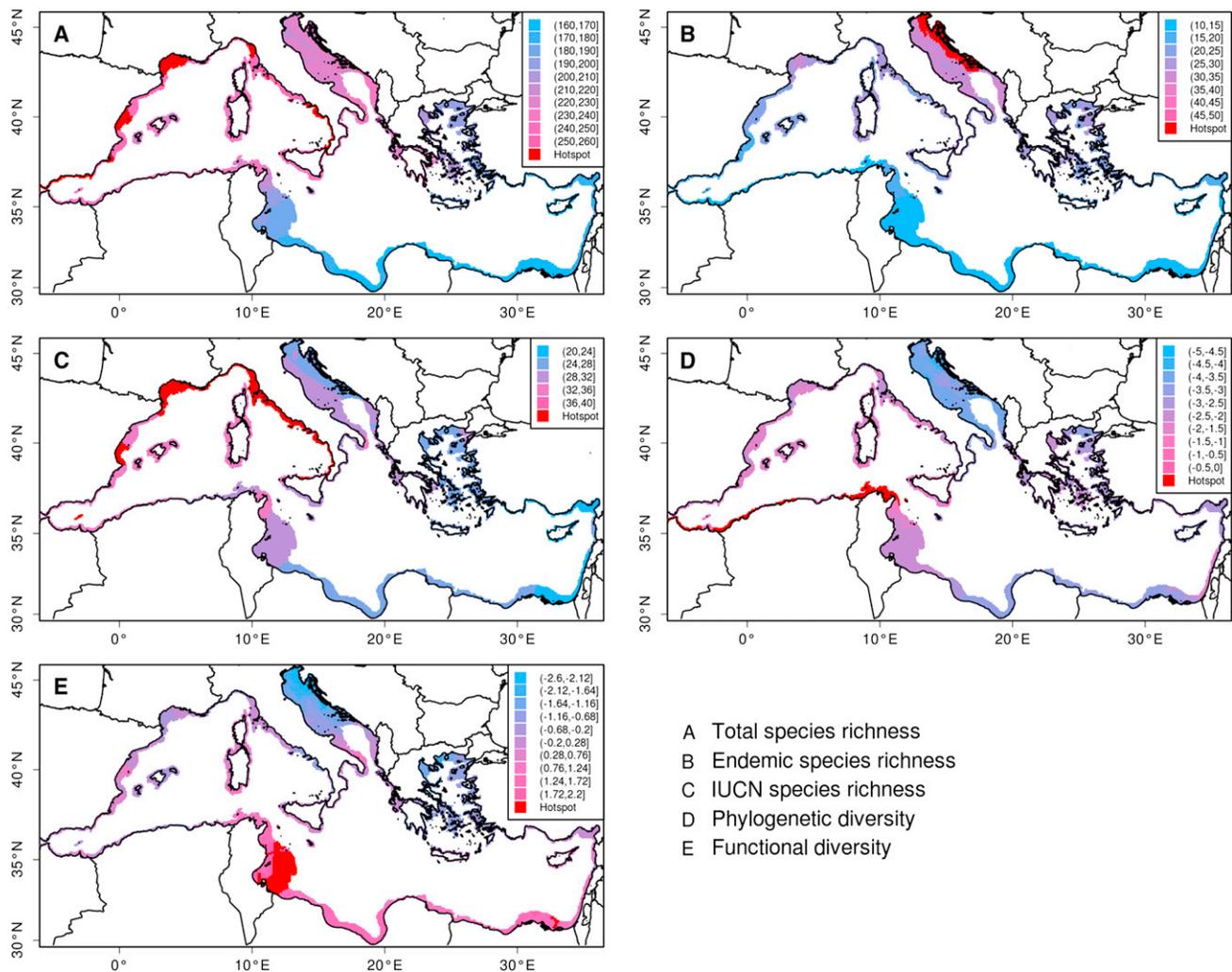


Figure 2. Observed Gradients for All Fish Biodiversity Components

Range maps for 282 coastal species, among which 81 are endemic and 45 are on the IUCN Red List, were digitalized on a regular grid (8186 cells) of 0.1° latitude \times 0.1° longitude covering the continental shelf [19]. Nonnative, migratory large pelagic species as well as those mainly occurring beyond the continental shelf (60% or more of their total range) were also excluded because they do not benefit from MPAs situated on the continental shelf. From a dated phylogeny and a functional dendrogram built using 15 functional traits, phylogenetic and functional diversity of fish assemblages contained in each grid cell were respectively computed using a standardized effect size estimation to provide a diversity value independent of species richness (see Supplemental Experimental Procedures).

390 overlapped with an MPA, and about three-fourths of those were along the north coast of the Mediterranean. The coasts least impacted by fisheries were located in the southeast; hot spots of fishery impact were widespread in the rest of the Mediterranean (Figure 1C).

There was a decreasing gradient from west to east in total fish richness (Figure 2A). Sicily was the hot spot of richness, with up to 257 species per cell. The endemic richness gradient was more pronounced from north to south: the northern side exhibited a greater richness, and the Adriatic appeared as a hot spot of endemism, with 42 species per cell (Figure 2B), i.e., 18% of endemic fishes. Similar to the total fish richness gradient, the IUCN species richness gradient decreased from west to east, with up to 37 endangered species per cell, i.e., 15% of total fish richness in these cells, on the western Italian coast and along the French and Spanish coasts (Figure 2C). Similarly, phylogenetic diversity of fish assemblages showed a decreasing gradient from west to east, with hot spots mainly

located along the western North African coast (Figure 2D). Finally, there was an increasing gradient of functional diversity from north to south, and almost all hot spots were in the Gulf of Gabès, Tunisia (Figure 2E).

Endemic and IUCN species richness were significantly and positively correlated with total species richness, functional diversity was negatively correlated with endemic species richness, and phylogenetic diversity was positively related with IUCN species richness (Table 1, top). Fishing pressure was positively correlated with total and endemic richness but negatively correlated with functional diversity ($r = -0.423$, $p < 0.05$).

Phylogenetic and functional diversity hot spots spatially mismatched with all other components of fish diversity, whereas total and IUCN richness hot spots were spatially congruent (Table 1, bottom). The system of MPAs was highly congruent with hot spots of total, endemic, and IUCN species richness components of fish diversity but missed the hot spots

Table 1. Spatial Congruence between Biodiversity Components, Fishing Pressure, and Marine Reserves

	End	IUCN	SES.FD	SES.PD	Press	Res
Rich	0.616*	0.839*	-0.413	0.290	0.268*	0.101
End		0.202	-0.800*	-0.413	0.330*	0.079
IUCN			0.010	0.557*	0.128	0.068
SES.FD				0.334	-0.423*	-0.078
SES.PD					-0.003	0.040
Press						0.028

	End	IUCN	SES.FD	SES.PD	Press	Res
Rich	0 (26.1) ***	372 (52.6)***	0 (30.1)***	0 (26.0)***	33 (26.0)	44 (24.7) ***
End		0 (41.8)***	0 (23.9)***	0 (20.6)***	64 (20.6) ***	32 (19.6) **
IUCN			0 (48.2)***	0 (41.6)***	17 (41.6)**	60 (39.6)***
SES.FD				0 (23.7)***	1 (23.8)***	0 (22.6)***
SES.PD					81 (20.5)***	16 (19.5)
Press						20 (19.5)

Top: pairwise correlations between variables (Rich, fish richness; End, endemic fish richness; IUCN, IUCN threatened fish richness; SES.FD, standardized functional diversity [see [Supplemental Experimental Procedures](#)]; SES.PD, standardized phylogenetic diversity [see [Supplemental Experimental Procedures](#)]; Press, demersal fishing pressure; Res, presence of reserve) and their significance level after correction for autocorrelation (see [Supplemental Experimental Procedures](#)) (* $p < 0.05$).

Bottom: pairwise observed spatial overlaps between hot spots of variables (and expected value under independence: null hypothesis) and their significance level after permutation test (** $p < 0.01$, *** $p < 0.01$).

of functional diversity (Table 1, bottom). Endemic richness and phylogenetic diversity hot spots significantly matched hot spots of fishing pressure, whereas IUCN richness and functional diversity hot spots mismatched this pressure.

Because the above approach relies on an arbitrary hot-spot threshold criterion (5%), we also used an alternative tool that quantifies the percentage of protected sites (or alternatively, the percentage of hot spots of high fishery pressure) for any level of diversity. This approach provides a synthetic and continuous assessment of whether sites including a given diversity value are also protected or, on the contrary, exposed to high fishing pressure. This analysis revealed that, beyond only considering hot spots, cells with high functional diversity values and high numbers of endemic species (except the very first ranks) were not congruent with MPAs, whereas those including high species and IUCN richness values mostly belonged to the existing system of MPAs (Figure 3A). Also, cells with a high number of endemic species and a high phylogenetic diversity value spatially matched hot spots of fishery impact, whereas cells with a high number of IUCN-listed species and a high functional diversity value tended to have low congruence with the highest fishery impact (Figure 3B).

Discussion

Protected areas are indisputably the primary tool for in situ biodiversity conservation across the world, and 0.65% of the world's oceans were protected by the mid-2000s [20]—a low percentage, but one that has recently doubled through the creation of very large MPAs in the Pacific and Indian oceans. Currently, about 4% of global continental shelf areas are incorporated within MPAs, and protection is greater in tropical than in temperate realms [21]. For coastal ecosystems, MPAs have been shown, consistently over the world, to enhance the abundance, size, and diversity of sedentary species, with benefits for local fisheries [22, 23]; this also applies to the Mediterranean Sea [5].

Beyond these local benefits and to reach the COP10 target 11 of protecting at least 10% of coastal and marine areas by 2020, there is an urgent need to identify biodiversity hot spots and human-mediated threats at the fine spatial scale

corresponding to MPA size. This is particularly critical in regions with low MPA coverage such as the Mediterranean Sea. Moreover, these MPAs have different status, with various impacts on fish recovery [5, 6]. Here we considered all MPAs as having the same impact on fish populations; thus, our study can be considered as a conservative “best-case scenario.” This being said, we have addressed two largely overlooked issues in marine environments. First, we have studied the spatial congruence between the system of MPAs and biodiversity hot spots. Second, we have identified the components of biodiversity that are protected and those that are under threat.

These two goals have been achieved only recently for terrestrial networks of protected areas, and results generally indicate a failure of reserve networks to be representative of the entire biodiversity of a region [3, 24, 25]. Yet, no comparable integrative assessment has been carried for marine environments because, until now, they have relied only on species richness [26, 27]. Here we show that despite its relatively small size, the Mediterranean MPA system is spatially congruent with the hot spots of taxonomic fish diversity (total, endemic, and IUCN) even if cells with medium to high levels of endemism are underrepresented in the system (Figure 3A). However, this system completely misses hot spots of functional diversity and partly those of phylogenetic diversity.

Phylogenetically informed conservation research is not new [28]. Protecting phylogenetic diversity [3, 16, 29] would imply, for instance, prioritizing conservation efforts toward species that have a singular evolutionary history [28, 30]. The rationale of this approach is that the loss of the most phylogenetically distinct species would remove a greater proportion of the Tree of Life [31]. As a consequence, it would be likely to decrease the ability of nature to cope with environmental changes. Indeed, losing phylogenetic diversity at any scale can lead to a reduced potential for communities to respond to changing conditions [29] because climate tolerances are not randomly distributed across phylogenies [32, 33]. Phylogenetic diversity has also recently been proposed as a good proxy for ecosystem functioning [17]. Based on the assumption that fishes from different lineages are more likely to perform different functions [34], we may expect an impact of

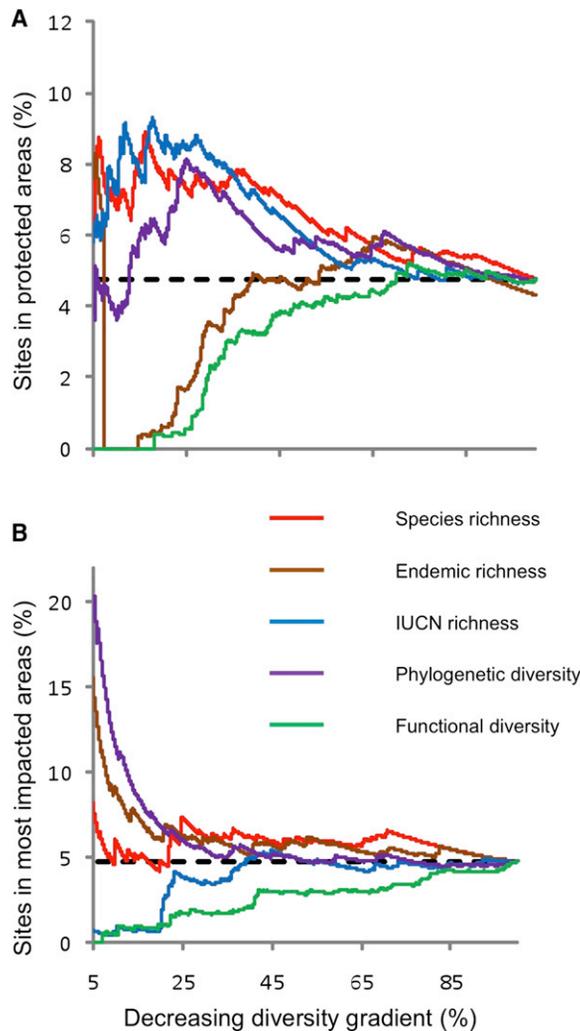


Figure 3. Proportion of Biodiversity Components Included in Marine Protected Areas and Hot Spots of Fishing Pressure

Cumulative proportion of total species richness, endemic richness, IUCN richness, phylogenetic diversity, and functional diversity included in marine protected areas (A) and hot spots of fishing pressure (B). For each diversity component, we ranked the 8186 cells from the most to the least diverse. Along this decreasing diversity gradient (x axis, expressed as a percentage), we calculated the cumulative percentage of protected cells (y axis). For any given value of the diversity gradient, if the MPA system is unbiased, one expects the proportion of protected cells to match the overall proportion of protected cells among all cells (i.e., 4.7%, dashed horizontal line). Therefore, proportions of protected cells located over and under the dashed line reveal the over- and underrepresentation, respectively, of cells located in protected areas or hot spots of fishing pressure.

the breath of evolutionary diversification on ecosystem functioning [35]. Our study has shown that the present Mediterranean MPA system does not protect fish phylogenetic diversity hot spots present along the southwestern coast. We also show that fishing pressure is highest in these ecosystems. These areas should thus be of primary conservation focus when establishing new MPAs, in order to protect the large amount of fish evolutionary history that they represent.

We highlighted that the hot spots of Mediterranean fish functional diversity are located in the Gulf of Gabès (Figure 2E) and, more generally, along the eastern North African coast, where few MPAs have been established (Figure 1B) but also where

fishing pressure is low (Figure 1C). Experiments [36] and empirical studies carried out on the Mediterranean coast [18] have shown that fish functional diversity has a major influence on ecosystem functioning, and thus the conservation of this overlooked biodiversity component should be of main concern in aquatic systems. Recent studies suggest that human-mediated pressures decrease fish functional diversity [37], whereas MPAs successfully restore or maintain this critical component [11, 38]. However, the incorporation of functional diversity into conservation strategies is very recent and only limited to terrestrial cases [3, 39]. In the Mediterranean, hot spots of fish functional diversity are overlooked by the current Mediterranean system of MPAs. A new MPA establishment strategy would need to pay more attention to such areas, given their potential to be representative of overall coastal ecosystem functioning.

Conservation targets for systematic conservation planning, i.e., optimizing the combination of sites that either achieves conservation targets at minimum cost (the minimum set coverage problem) or satisfies the largest number of conservation targets given a budget constraint (the maximum coverage problem), are usually set at the level of individual species [9]. Previous studies attempting to incorporate phylogenetic diversity into the systematic conservation planning process have shown that considering the optimization of phylogenetic diversity would not fundamentally change the results of the planning effort except in very limited cases [16]. Our results suggest that phylogenetic and functional diversity do not always overlap with taxonomic diversity; this implies that conservation planning integrating all biodiversity components would be more useful than previously thought. Current strategies to incorporate phylogenetic (or functional) diversity into conservation planning involve the ranking of species according to their phylogenetic (or functional) originality, a combination of threat and originality [31], or the representation of phylogenetic (or functional) diversity without a minimum area requirement [16]. These strategies are not fully appropriate to represent these two crucial components of diversity because they still use a species-centered approach for optimization or ignore the basic principle of minimum area requirement. Thus, the spatial optimization of the Mediterranean MPA system, taking into account all biodiversity components and both political and social constraints (conflicts with fisheries, country policies, etc.), still requires conceptual developments and further data.

Given the exceptional biodiversity of the Mediterranean and the major threats that it faces, protecting the diversity of its biological traits as well as its evolutionary heritage should be viewed as a priority. To reach the COP10 target 11, we need to rapidly turn a much larger surface area into MPAs. To optimize future conservation efforts, i.e., number, size, and spacing of MPAs, we may rely on many criteria, among which connectivity and biodiversity patterns are essential. Connectivity among MPAs, the extent to which populations in different MPAs are linked by exchange of larvae, recruits, juveniles, or adults [40], may promote regional persistence particularly for exploited species within a context of global change [41]. By highlighting the spatial mismatching between the different components of fish biodiversity, our study poses new challenges for the design of a “true” MPA network in the Mediterranean Sea, i.e., a system of interconnected MPAs designed to protect all the components of fish biodiversity and integrating the potential impacts of climatic change [42] and connectivity among populations [22].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.05.005.

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References

1. Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., et al. (2010). The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLoS ONE* 5, e11842.
2. Bianchi, C.N., and Morri, C. (2000). Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. *Mar. Pollut. Bull.* 40, 367–376.
3. Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., and Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040.
4. Fady, B., and Conord, C. (2010). Macroecological patterns of species and genetic diversity in vascular plants of the Mediterranean basin. *Divers. Distrib.* 16, 53–64.
5. Garcia-Charton, J.A., Perez-Ruzafa, A., Marcos, C., Claudet, J., Badalamenti, F., Benedetti-Cecchi, L., Falcon, J.M., Milazzo, M., Schembri, P.J., Stobart, B., et al. (2008). Effectiveness of European Atlanto-Mediterranean MPAs: Do they accomplish the expected effects on populations, communities and ecosystems? *J. Nat. Conserv.* 16, 193–221.
6. Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., Murenu, M., Pais, A., Spano, N., Balzano, R., Agardy, T., Boero, F., et al. (2008). Italian marine reserve effectiveness: Does enforcement matter? *Biol. Conserv.* 141, 699–709.
7. Abdulla, A., Gomei, M., Hyrenbach, D., Notarbartolo-di-Sciara, G., and Agardy, T. (2009). Challenges facing a network of representative marine protected areas in the Mediterranean: Prioritizing the protection of underrepresented habitats. *ICES J. Mar. Sci.* 66, 22–28.
8. Francour, P., Harmelin, J.G., Pollard, D., and Sartoretto, S. (2001). A review of marine protected areas in the northwestern Mediterranean region: Siting, usage, zonation and management. *Aquat. Conserv.* 11, 155–188.
9. Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., Da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., et al. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature* 428, 640–643.
10. Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., and DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33.
11. Mouillot, D., Culioli, J.M., Pelletier, D., and Tomasini, J.A. (2008). Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve. *Biol. Conserv.* 141, 1569–1580.
12. Mace, G.M., Gittleman, J.L., and Purvis, A. (2003). Preserving the tree of life. *Science* 300, 1707–1709.
13. Redding, D.W., DeWolff, C.V., and Mooers, A.O. (2010). Evolutionary distinctiveness, threat status, and ecological oddity in primates. *Conserv. Biol.* 24, 1052–1058.
14. Purvis, A., and Hector, A. (2000). Getting the measure of biodiversity. *Nature* 405, 212–219.
15. Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., et al. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016–1019.
16. Rodrigues, A.S.L., and Gaston, K.J. (2002). Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biol. Conserv.* 105, 103–111.
17. Cadotte, M.W., Cardinale, B.J., and Oakley, T.H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci. USA* 105, 17012–17017.
18. Clemente, S., Hernandez, J.C., Rodriguez, A., and Brito, A. (2010). Identifying keystone predators and the importance of preserving functional diversity in sublittoral rocky-bottom areas. *Mar. Ecol. Prog. Ser.* 413, 55–67.
19. Lasram, F.B., Guilhaumon, F., and Mouillot, D. (2009). Fish diversity patterns in the Mediterranean Sea: Deviations from a mid-domain model. *Mar. Ecol. Prog. Ser.* 376, 253–267.
20. Wood, L.J., Fish, L., Laughren, J., and Pauly, D. (2008). Assessing progress towards global marine protection targets: Shortfalls in information and action. *Oryx* 42, 340–351.
21. Spalding, M.D., Fish, L., and Wood, L.J. (2008). Toward representative protection of the world's coasts and oceans—progress, gaps, and opportunities. *Conserv. Lett.* 1, 217–226.
22. Weeks, R., Russ, G.R., Alcalá, A.C., and White, A.T. (2010). Effectiveness of marine protected areas in the Philippines for biodiversity conservation. *Conserv. Biol.* 24, 531–540.
23. Russ, G.R., Cheal, A.J., Dolman, A.M., Emslie, M.J., Evans, R.D., Miller, I., Sweatman, H., and Williamson, D.H. (2008). Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Curr. Biol.* 18, R514–R515.
24. Jackson, S.F., Walker, K., and Gaston, K.J. (2009). Relationship between distributions of threatened plants and protected areas in Britain. *Biol. Conserv.* 142, 1515–1522.
25. Maiorano, L., Falcucci, A., and Boitani, L. (2006). Gap analysis of terrestrial vertebrates in Italy: Priorities for conservation planning in a human dominated landscape. *Biol. Conserv.* 133, 455–473.
26. Mora, C., Andréfouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., Gaston, K.J., and Myers, R.A. (2006). Coral reefs and the global network of Marine Protected Areas. *Science* 312, 1750–1751.
27. Tognelli, M.F., Fernandez, M., and Marquet, P.A. (2009). Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. *Biol. Conserv.* 142, 3147–3153.
28. Vanewright, R.I., Humphries, C.J., and Williams, P.H. (1991). What to protect? Systematics and the agony of choice. *Biol. Conserv.* 55, 235–254.
29. Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Procheş, S., van der Bank, M., et al. (2007). Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757–760.
30. Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10.
31. Faith, D.P. (2008). Threatened species and the potential loss of phylogenetic diversity: Conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conserv. Biol.* 22, 1461–1470.
32. Prinzing, A., Durka, W., Klotz, S., and Brandl, R. (2001). The niche of higher plants: Evidence for phylogenetic conservatism. *Proc. Biol. Sci.* 268, 2383–2389.
33. McNyset, K.M. (2009). Ecological niche conservatism in North American freshwater fishes. *Biol. J. Linn. Soc. Lond.* 96, 282–295.
34. Somerfield, P.J., Clarke, K.R., Warwick, R.M., and Dulvy, N.K. (2008). Average functional distinctness as a measure of the composition of assemblages. *ICES J. Mar. Sci.* 65, 1462–1468.
35. Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B., and Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458, 1167–1170.
36. Hargrave, C.W. (2009). Effects of fish species richness and assemblage composition on stream ecosystem function. *Ecol. Freshwat. Fish* 18, 24–32.
37. Villéger, S., Ramos Miranda, J., Flores Hernández, D., and Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of

- tropical fish communities after habitat degradation. *Ecol. Appl.* *20*, 1512–1522.
38. Stelzenmuller, V., Maynou, F., and Martin, P. (2009). Patterns of species and functional diversity around a coastal marine reserve: A fisheries perspective. *Aquat. Conserv.* *19*, 554–565.
39. Bowker, M.A., Miller, M.E., Belnap, J., Sisk, T.D., and Johnson, N.C. (2008). Prioritizing conservation effort through the use of biological soil crusts as ecosystem function indicators in an arid region. *Conserv. Biol.* *22*, 1533–1543.
40. Moffitt, E.A., White, J.W., and Botsford, L.W. (2011). The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. *Biol. Conserv.* *144*, 306–318.
41. Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J., Enríquez, S., Iglesias-Prieto, R., Cherubin, L.M., and Stevens, J.R. (2011). Reserve design for uncertain responses of coral reefs to climate change. *Ecol. Lett.* *14*, 132–140.
42. McLeod, E., Salm, R., Green, A., and Almany, J. (2009). Designing marine protected area networks to address the impacts of climate change. *Front. Ecol. Environ* *7*, 362–370.