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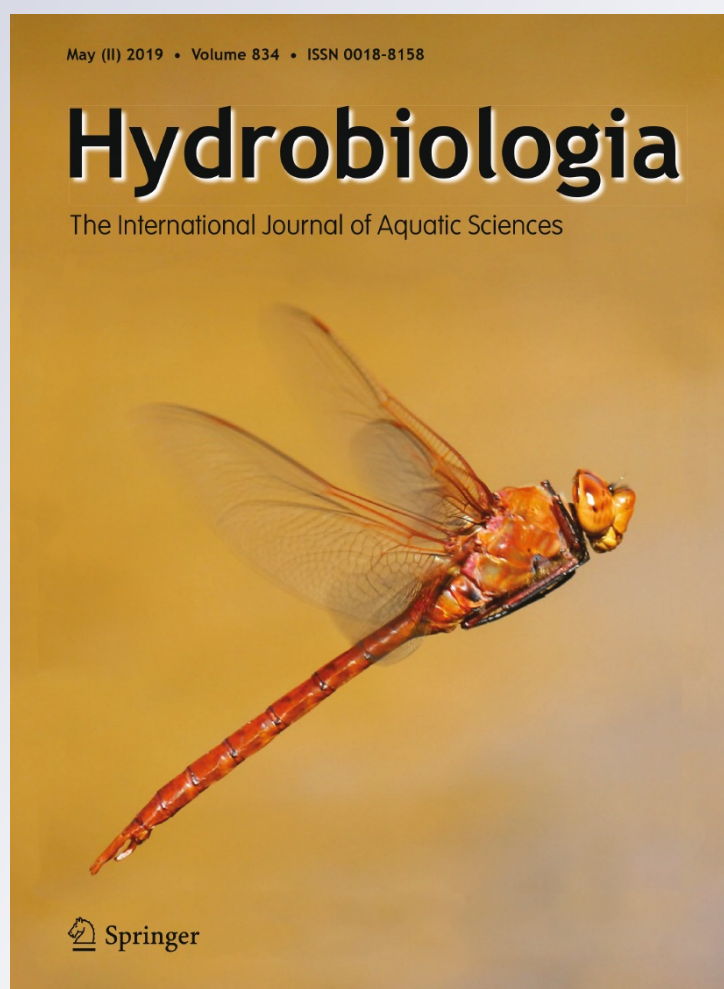
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Partitioning multiple diversity dimensions of nearshore fish assemblages within a coastal seascape

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Abstract The conservation of coastal seascapes requires a better understanding of how different dimensions of biodiversity are represented between juxtaposed habitats. We explored patterns of taxonomic, functional, and phylogenetic diversity of fishes between four habitats (sandy bottoms, rocky reefs of high and low relief, and mixed bottoms) within a semi-lagoon seascape (Las Canteras beach) in Gran Canaria Island. Data on fish presence in each habitat were provided by weekly snorkeling tours, at day and night, from August 2015 to August 2018. Indices that measured ‘how much’ biodiversity, i.e., ‘how many

species’ (species richness), ‘how much functional dissimilarity’, and ‘how much evolutionary history’ were larger on rocky bottoms. However, indices that measured phylogenetic differentiation, i.e., ‘how different’, via the taxonomic distinctiveness and the Mean Pairwise Distance index were particularly high on sandy bottoms, because of the presence of elasmobranchs, which were absent from rocky bottoms. The ‘phylogenetic signal’, whether phylogenetically related species are functionally similar, was significant on rocky bottoms, but non-significant on sandy bottoms, reflecting phylogenetic ‘overdispersion’ on sandy bottoms and phylogenetic ‘clustering’ on hard bottoms. From a conservation perspective, sandy bottoms cannot be underrated, particularly in the context of maximizing indices that measure ‘how phylogenetically different’ biodiversity is.

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Introduction

Coastal seascapes typically include a mosaic of reticulated habitats of varying structure and complexity, e.g., rocky reefs, coral reefs, seagrass meadows, unvegetated sediments, etc. (Dorenbosch et al., 2005; Tuya et al., 2010). The size, arrangement, and

structure of these habitats often play a key role on the abundance and composition of associated nearshore assemblages (Curdia et al., 2015; Cacabelos et al., 2016). Typically, complex habitats containing a large number of structural elements (e.g., fronds, crevices, drops) support a larger number of species and greater abundances of organisms (Matias et al., 2010; Ferreira et al., 2014; Carvalho et al., 2017). This pattern has been linked to increase availability of ecological niches and colonisable surface (species-area relationships), as well as increased availability of refuges against predators (Buhl-Mortensen et al., 2012; Kovalenko et al., 2012; Ferreira et al., 2014). For example, a larger species richness and abundances of nearshore fishes is found on rocky reefs relative to sandy bottoms across a range of scales and biogeographic areas (Jenkins & Wheatley, 1998; Guidetti, 2000; La Mesa et al., 2011; Rees et al., 2018). It is expected that a larger number of available ecological niches translate into a more diverse range of functional traits. For instance, specialization in functional traits (morphology, diet, etc.) in marine and freshwater fishes enables niche complementarity, a key aspect in ecosystem integrity and functioning (Mouillot et al., 2007; Mason et al., 2008).

Understanding patterns of biodiversity through scales of spatial and temporal variation has attracted major interest by community ecologists (Fraschetti et al., 2005; Meynard et al., 2011; Tuya et al., 2011). Traditionally, ecological studies have addressed biodiversity from a mere and reductionist—taxonomic perspective; for example, through the number of species (species richness) and change (turnover) in species composition (beta-diversity). Taxonomic diversity (TD) indices assume that all species contribute equally to ecosystem functioning, regardless of their relatedness and role in the community functions. Ecosystem functions, however, arise from the functional traits of species rather than by their taxonomic identity (Petchey & Gaston, 2006; Cadotte, 2011). In fact, the term biodiversity cannot be viewed as a single unidimensional component but rather with varying 'dimensions', such as functional (trait) and phylogenetic diversity. A multidimensional approach to quantifying biodiversity may help to unravel the relevance of mechanisms driving community assembly (Meynard et al., 2011; Cadotte et al., 2012). In this context, several functional (FD) and phylogenetic (PD) diversity metrics have been developed to account

for the relatedness of species in a community based on functional traits—attributes such as morphology, physiology, trophic ecology, etc. that influence organisms' performance (Petchey & Gaston, 2002)—and accumulated evolutionary history (Cadotte et al., 2010). An important property of some of these indices is that they are invariant of species richness, enabling unbiased evaluations of the effects of stressors on complementary dimensions of biodiversity (Tolimieri & Anderson, 2010; Villéger et al., 2010; Purschke et al., 2013).

Phylogenetically related species are expected to be functionally comparable (Webb et al., 2002; Swenson et al., 2007), according to the 'niche conservatism hypothesis' (Harvey & Pagel, 1991). Hence, both the phylogenetic and functional structure of an assemblage are often considered as surrogates of each other. However, this assumption, so-called as the 'phylogenetic signal', warrants further investigation and types of assemblages as a result of inconsistent results (Munkemuller et al., 2015; Tanaka & Sato, 2015). Connections between different dimensions of biodiversity are sometimes unexpected and system-specific (Perronne et al., 2014); this is particularly the case between taxonomic, functional, and phylogenetic diversity patterns of reef fishes at both global (Stuart-Smith et al., 2013) and local scales (Villéger et al., 2010; Bosch et al., 2017; Tuya et al., 2017). Within this framework, combining TD, FD, and PD is very valuable to test predictions on the balance between processes governing community assembly, e.g., competition versus environmental filtering. Communities under strong environmental filtering tend to show 'phylogenetic clustering', i.e., species belong to the same evolutionary lineages. In contrast communities under strong competition show 'phylogenetic overdispersion'. Notably, however, the spatial scale can alter this rule (Gomez et al., 2010; Arnan et al., 2016; Xu et al., 2017).

Since it is challenging to preserve biodiversity due to limited conservation budgets, it remains critical to understand how diversity dimensions are related. In this study, we explored patterns of taxonomic, functional, and phylogenetic diversity of nearshore fishes across four juxtaposed habitats (sandy, mixed, high relief rocky bottoms, and low relief rocky bottoms) interspersed within a shallow-water seascape of a subtropical island. We initially partitioned rocky bottoms between high and low relief because they provide

different niches, for example, in terms of available refuges (Tuya et al., 2011). We firstly hypothesized that fish biodiversity, in terms of ‘how much’ taxonomic, functional and phylogenetic diversity, would differ between the four habitats. In particular, we expected a larger diversity on rocky reefs relative to sandy bottoms. Secondly, we hypothesized that strong correlations between FD and PD should lead to ‘phylogenetic signal’ between habitat types. We finally hypothesized that varying patterns of phylogenetic differentiation should affect the balance between phylogenetic ‘overdispersion’ and ‘clustering’ of lineages between habitats.

Materials and methods

Study site

This study was carried out at Las Canteras beach, a nearshore semi-lagoon system located at the city of Las Palmas de Gran Canaria, in the northern side of Gran Canaria Island (north-eastern Atlantic), a subtropical island of volcanic origin (Fig. 1a). Sandy bottoms and rocky reefs of varying structural complexity are found interspersed as irregular mosaics, typically between zero and four m depth (Supplementary Fig. 1). An offshore sedimentary bar (ca. 1.6 km long) delimitate the system seaward (Fig. 1b, Supplementary Fig. 1, 0.42 km²). At low tide, the bar is majorly above the surface, providing protection against oceanographic forces (e.g., waves and currents), and so delimitating a clear semi-lagoon system. At high tide, however, the system is open to offshore waters. For the purpose of this study, four habitat types were defined (Fig. 2): sandy bottoms with no vegetation, low relief rocky bottoms (rocky flat platforms and large boulders covered by photophilous vegetation), high relief rocky bottoms (rocky areas of abrupt topography, including caves, overhangs, and crevices), and mixed bottoms, encompassing sandy-rocky transitions. Delimitation of habitats was quite straightforward in situ. Rocky bottoms, either of low or high relief, are > 25 m away from adjacent sandy bottoms. The study site is protected within the framework of a ‘Special Area of Conservation’ (code ES7010037), under the EU ‘Natura 2000’. Recreational and commercial fishing is banned within the system.

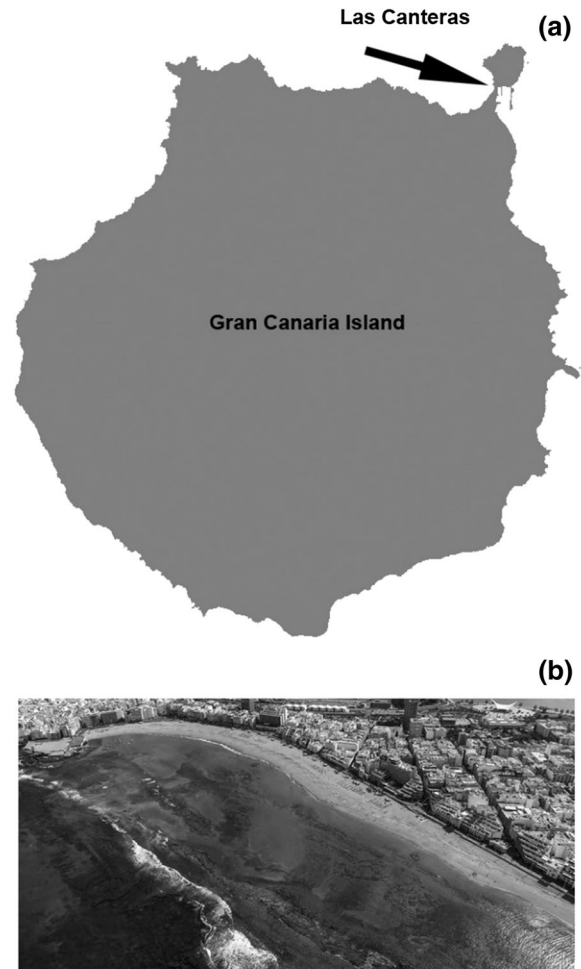


Fig. 1 Location of (a) the study site (Las Canteras beach) at Gran Canaria Island (eastern Atlantic), including (b) an aerial view of the semi-lagoon system

Data collection

Data on fish presence in each habitat were provided by tours carried out by the ecotourism enterprise Snorkeling Experience (www.snorkelingexperience.com) from August 2015 to August 2018, including all seasons throughout each year (Supplementary Fig. 2). Normally, 2–3 tours, both at day and night, are performed per week, except in seasons of rough seas. On each tour, the four habitats are visited, as part of a standard underwater path (Supplementary Fig. 3). Group snorkeling guides (authors: F.T., M.A., and A.N.) annotated fish species observed on each habitat. Typically, each tour passed through each type of habitat several times, as these habitats are connected at

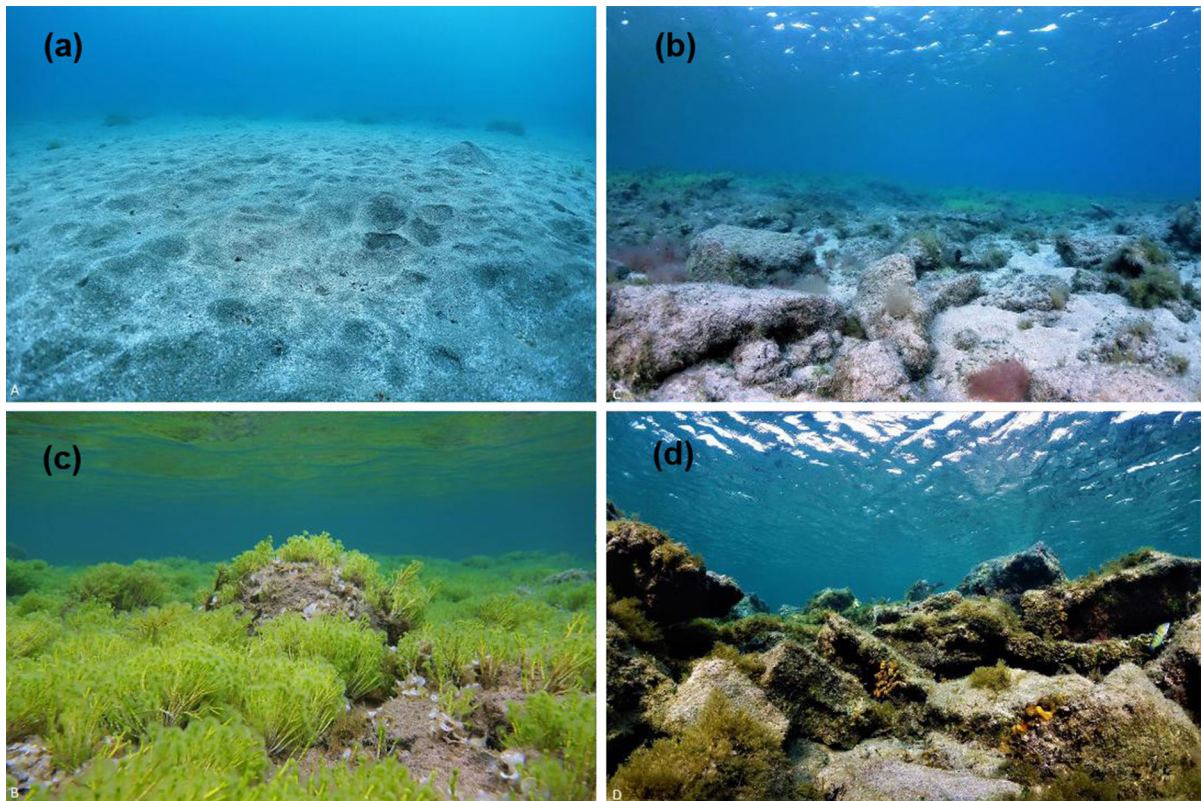


Fig. 2 Habitat types within the coastal seascape at the study site (Las Canteras beach), including **a** sandy bottoms, **b** mixed bottoms, **c** low relief rocky bottoms and **d** high relief rocky bottoms

small scales (Supplementary Fig. 1). The snorkeling tracks start and end at different points of the beach. During this period, a total of 308 tours (229 at daytime and 79 at night-time, for a total of ca. 500 h of underwater observation) were carried out. Seawater visibility typically ranged between 8 and 25 m. Night-time excursions facilitated the identification of species of nocturnal habits with the help of underwater torches. At the same time, we compiled information from free-diving underwater photography competitions carried out at the study site (www.fotosublaspalmasgc.com) on 2015, 2016 and 2017, which cover the four considered habitats. In particular, this provided complementary information for very cryptic species (e.g., small-sized blennies and gobies). In both cases, taxonomic identification of fishes was based on previous fish checklists from Gran Canaria Island (Tuya et al., 2004; Bosch et al., 2017) and the Canary Islands (Brito et al., 2002). A presence-absence matrix was then assembled and taxonomically validated via the World Register of Marine Species (WoRMS) ‘match taxa’

tool (www.marinespecies.org) (Table 1). The conservation status of each species, according to the IUCN Red List of Threatened Species (www.iucnredlist.org), was also considered.

Biodiversity patterns

The R-package EcoIndR (Guisande, 2017) was used to calculate a range of diversity indices from presence-absence data for each habitat (Table 1), including: species richness (an index of TD), the Rao and the functional evenness indices (indices of FD) and the taxonomic distinctiveness, a proxy of PD. To assess FD, a fish-traits matrix was initially assembled following the classification of Bosch et al. (2017) for the study region. Six functional traits, representing key aspects of the ecological performance of fish species in terms of habitat and resource use, were considered: trophic (niche) level, trophic breadth, trophic group (detritivorous, planktivorous, herbivorous, omnivorous, micro-invertebrate feeder, macro-invertebrate

Table 1 Presence of fish species on each habitat type within the study site

Species	Authority	Sandy bottoms	Mixed bottoms	HR rocky bottoms	LR rocky bottoms
E = <i>Myliobatis aquila</i> (DD)	(Linnaeus, 1758)	1	1	0	0
E = <i>Dasyatis pastinaca</i> (DD)	(Linnaeus, 1758)	1	1	0	0
E = <i>Taeniura grabata</i> (DD)	(Geoffroy Saint-Hilaire, 1817)	1	1	1	1
E = <i>Gymnura altavela</i> (VU)	(Linnaeus, 1758)	1	1	0	0
E = <i>Aetomylaeus bovinus</i> (DD)	(Geoffroy Saint-Hilaire, 1817)	1	1	1	1
E = <i>Squatina squatina</i> (CE)	(Linnaeus, 1758)	1	1	0	0
E = <i>Torpedo marmorata</i> (DD)	Risso, 1810	1	0	0	0
E = <i>Mustelus mustelus</i> (VU)	(Linnaeus, 1758)	1	1	1	1
<i>Sphyræna viridensis</i> (LC)	Cuvier, 1829	0	1	1	1
<i>Belone belone</i> (LC)	(Linnaeus, 1760)	0	1	1	1
<i>Atherina presbyter</i> (LC)	Cuvier, 1829	0	1	1	1
<i>Engraulis encrasicolus</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Boops boops</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Sardinella maderensis</i> (VU)	(Lowe, 1838)	0	1	1	1
<i>Trachinotus ovatus</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Pomatomus saltatrix</i> (VU)	(Linnaeus, 1766)	0	1	1	1
<i>Pseudocaranx dentex</i> (LC)	(Bloch & Schneider, 1801)	0	1	1	1
<i>Seriola rivoliana</i> (LC)	Valenciennes, 1833	0	0	1	1
<i>Chelon auratus</i> (LC)	(Risso, 1810)	1	1	1	1
<i>Chelon labrosus</i> (LC)	(Risso, 1827)	1	1	1	1
<i>Dicentrarchus labrax</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Dicentrarchus punctatus</i> (LC)	(Bloch, 1792)	0	1	1	1
<i>Pagrus auriga</i> (LC)	Valenciennes, 1843	0	1	0	1
<i>Lithognathus mormyrus</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Pagellus erythrinus</i> (LC)	(Linnaeus, 1758)	1	1	0	0
<i>Diplodus puntazzo</i> (LC)	(Walbaum, 1792)	0	0	1	1
<i>Diplodus sargus</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Diplodus vulgaris</i> (LC)	(Geoffroy Saint-Hilaire, 1817)	0	1	1	1
<i>Diplodus cervinus</i> (LC)	(Lowe, 1838)	0	1	1	1
<i>Diplodus annularis</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Sparus aurata</i> (LC)	Linnaeus, 1758	0	1	1	1
<i>Oblada melanura</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Sarpa salpa</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Pomadasys incisus</i> (LC)	(Bowdich, 1825)	0	1	1	1
<i>Parapristipoma octolineatum</i> (LC)	(Valenciennes, 1833)	0	0	1	0
<i>Spondyliosoma cantharus</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Kyphosus sectatrix</i> (LC)	(Linnaeus, 1758)	0	0	1	1
<i>Sciaena umbra</i> (NT)	Linnaeus, 1758	0	0	1	1
<i>Mycteroperca fusca</i> (EN)	(Lowe, 1838)	0	0	1	1
<i>Epinephelus marginatus</i> (EN)	(Lowe, 1834)	0	0	1	0
<i>Serranus scriba</i> (LC)	(Linnaeus, 1758)	0	1	1	1

Table 1 continued

Species	Authority	Sandy bottoms	Mixed bottoms	HR rocky bottoms	LR rocky bottoms
<i>Sparisoma cretense</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Symphodus trutta</i> (LC)	(Lowe, 1834)	0	0	1	1
<i>Coris julis</i> (LC)	(Linnaeus, 1758)	0	0	1	1
<i>Thalassoma pavo</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Xyrichtys novacula</i> (LC)	(Linnaeus, 1758)	1	1	0	0
<i>Labrisomus nuchipinnis</i> (LC)	(Quoy & Gaimard, 1824)	0	0	1	1
<i>Mullus surmuletus</i> (LC)	Linnaeus, 1758	1	1	0	1
<i>Trachinus draco</i> (LC)	Linnaeus, 1758	1	1	0	0
<i>Synodus synodus</i> (LC)	(Linnaeus, 1758)	1	1	0	1
<i>Synodus saurus</i> (LC)	(Linnaeus, 1758)	1	1	0	1
<i>Scorpaena porcus</i> (LC)	Linnaeus, 1758	0	1	1	1
<i>Scorpaena maderensis</i> (LC)	Valenciennes, 1833	0	0	1	1
<i>Balistes capriscus</i> (LC)	Gmelin, 1789	0	1	1	1
<i>Stephanolepis hispidus</i> (LC)	(Linnaeus, 1766)	0	1	1	1
<i>Abudefduf luridus</i> (LC)	(Cuvier, 1830)	0	1	1	1
<i>Abudefduf saxatilis</i> (LC)	(Linnaeus, 1758)	0	0	1	1
<i>Chromis limbata</i> (LC)	(Valenciennes, 1833)	0	0	1	0
<i>Apogon imberbis</i> (LC)	(Linnaeus, 1758)	0	1	1	1
<i>Tripterygion delaisi</i> (LC)	Cadenat & Blache, 1970	0	0	1	1
<i>Ophioblennius atlanticus</i> (LC)	(Valenciennes, 1836)	0	0	1	1
<i>Parablennius parvicornis</i> (LC)	(Valenciennes, 1836)	0	0	1	1
<i>Parablennius pilicornis</i> (LC)	(Cuvier, 1829)	0	0	1	1
<i>Parablennius incognitus</i> (LC)	(Bath, 1968)	0	0	1	1
<i>Parablennius goorensis</i> (LC)	(Valenciennes, 1836)	0	0	1	1
<i>Coryphoblennius galerita</i> (LC)	(Linnaeus, 1758)	0	0	1	1
<i>Scartella cristata</i> (LC)	(Linnaeus, 1758)	0	0	1	1
<i>Lipophrys pholis</i> (LC)	(Linnaeus, 1758)	0	0	1	1
<i>Lipophrys trigloides</i> (LC)	(Valenciennes, 1836)	0	0	1	1
<i>Gobius paganellus</i> (LC)	Linnaeus, 1758	0	1	1	1
<i>Gobius niger</i> (LC)	Linnaeus, 1758	0	1	0	0
<i>Mauligobius maderensis</i> (LC)	(Valenciennes, 1837)	0	1	1	1
<i>Vanneaugobius canariensis</i> (LC)	Van Tassell, Miller & Brito, 1988	0	1	1	1
<i>Gnatholepis thompsoni</i> (LC)	Jordan, 1904	0	1	1	1
<i>Lepadogaster lepadogaster</i> (LC)	(Bonnaterre, 1788)	0	0	1	1
<i>Opeatogenys cadenati</i> (DD)	Briggs, 1957	0	0	0	1
<i>Canthigaster capistrata</i> (LC)	(Lowe, 1839)	0	1	1	1
<i>Sphoeroides marmoratus</i> (LC)	(Lowe, 1838)	0	1	1	1
<i>Microchirus azevia</i> (DD)	(de Brito Capello, 1867)	1	1	0	0
<i>Bothus podas</i> (LC)	(Delaroche, 1809)	1	1	0	0
<i>Myrichthys pardalis</i> (LC)	(Valenciennes, 1839)	0	1	1	1
<i>Gymnothorax unicolor</i> (LC)	(Delaroche, 1809)	0	0	1	0

Table 1 continued

Species	Authority	Sandy bottoms	Mixed bottoms	HR rocky bottoms	LR rocky bottoms
<i>Muraena augusti</i> (LC)	(Kaup, 1856)	0	0	1	0
<i>Muraena helena</i> (LC)	Linnaeus, 1758	0	0	1	0
<i>Ariosoma balearicum</i> (LC)	(Delaroche, 1809)	1	1	0	0
<i>Apterichtus caecus</i> (LC)	(Linnaeus, 1758)	1	1	0	0
<i>Facciolella oxyrhyncha</i> (LC)	(Bellotti, 1883)	1	1	0	0
<i>Syngnathus typhle</i> (LC)	Linnaeus, 1758	0	0	0	1
<i>Hippocampus hippocampus</i> (DD)	(Linnaeus, 1758)	0	0	0	1

The status of each species, according to the IUCN Red List of Threatened Species, is included

DD data deficient, LC least concern, NT near threat, VU vulnerable, EN endangered, CR critically endangered. Elasmobranchs are denoted with an ‘E’

feeder and piscivorous, piscivorous), maximum body length, body shape (elongated, fusiform, depressed, compressed, and eel-like), and water-column position (benthic, benthopelagic, pelagic non-site attached). Most values and attributes were obtained from Fishbase (www.fishbase.org), but also from existing literature. When information on particular species was not available, we then used values from sibling species, often within the same genus and geographic area. In addition to the Rao index of FD (Villéger et al., 2008), we calculated an index of functional evenness, a measure of the spread of species across the range of functional trait values present in a community—the so-called ‘functional space’ (Villéger et al., 2008). The taxonomic distinctiveness estimates the taxonomic extent of a sample from a presence-absence checklist. The taxonomic distance between each pair of species is considered through a classification tree based on the classical Linnean taxonomy. Then, the average taxonomic distinctness ($\Delta +$) is calculated, as the mean of all pairwise distances throughout the tree (Clarke & Warwick, 2001).

A phylogenetic tree for all recorded species (Supplementary Fig. 4) was constructed, using the PhyloT online platform (www.phylot.biobyte.de), which is based on the NCBI taxonomy (www.ncbi.nlm.nih.gov/guide/taxonomy). The NCBI taxonomy classifies organisms from public sequence databases. For seven species: *Apterichtus caecus* (Linnaeus, 1758), *Myrichthys pardalis* (Valenciennes, 1839), *Sphoeroides*

marmoratus (Lowe, 1838), *Canthigaster capistrata* (Lowe, 1839), *Symphodus trutta* (Lowe, 1834), *Parablennius goorensis* (Valenciennes, 1836), and *Opeatogenys cadenati* Briggs, 1957, there was no public sequences; their phylogenetic relatedness was considered from sibling species instead. A nexus file containing the topology of the phylogenetic tree was provided and then converted to a ‘phylo’ object, and subsequently visualized, using the ‘ape’ R-package (Paradis & Schliep, 2018). By using the ‘picante’ R-package (Kembel et al. 2010), we calculated the Faith’s index of PD, which is defined as the total branch length spanned by the tree including all species in a local community, here each habitat. In addition, we calculated the Mean Pairwise Distance (MPD) index between all species in each community (here, habitat). These two indices reflect the ‘richness’ and ‘divergence’ of a phylogenetic tree respectively; ‘how much’ evolutionary diversity and ‘how different’ is their evolutionary history, respectively (Tucker et al., 2017). Measures of the ‘standardized effect size’ of the phylogenetic community structure were calculated, for each habitat, by comparing the observed phylogenetic relatedness, via the MPD, to patterns of random (null) communities. Standardized effect sizes estimate the divergence between phylogenetic distances in the observed *versus* null communities, through 999 randomizations, divided by the standard deviation of phylogenetic distances in the null data (Webb et al., 2002). Such calculations allow to infer

patterns of community assembly (Xu et al., 2017). The 'picante' R-package provides functions in this regard. We obtained a correlation matrix between each pair of biodiversity indices in R 3.5.1 to address connections between the different biodiversity dimensions (Supplementary Table 1).

A matrix of pairwise phylogenetic distances, using tree branch lengths, was obtained from the phylogenetic topology of each habitat (Supplementary Fig. 5). A mantel test, via Pearson correlation, then tested for the significance, through 999 permutations, of correlations between the matrices of phylogenetic distances for each habitat and their corresponding matrices of dissimilarities according to functional traits. This procedure, which was implemented using the 'vegan' R-package (Oksanen et al., 2018), allowed to infer variation in the intensity of the 'phylogenetic signal' between habitats; the longer the correlation, the stronger the 'phylogenetic signal'.

Patterns in taxonomic beta-diversity were assessed by testing for compositional differences between habitats through Jaccard dissimilarities; the 'vegan' R-package (Oksanen et al., 2018) was used in this regard. We also evaluated patterns in phylogenetic beta-diversity, i.e., patterns of phylogenetic relatedness, between communities using the 'picante' R-package (Kembel et al., 2010).

Results

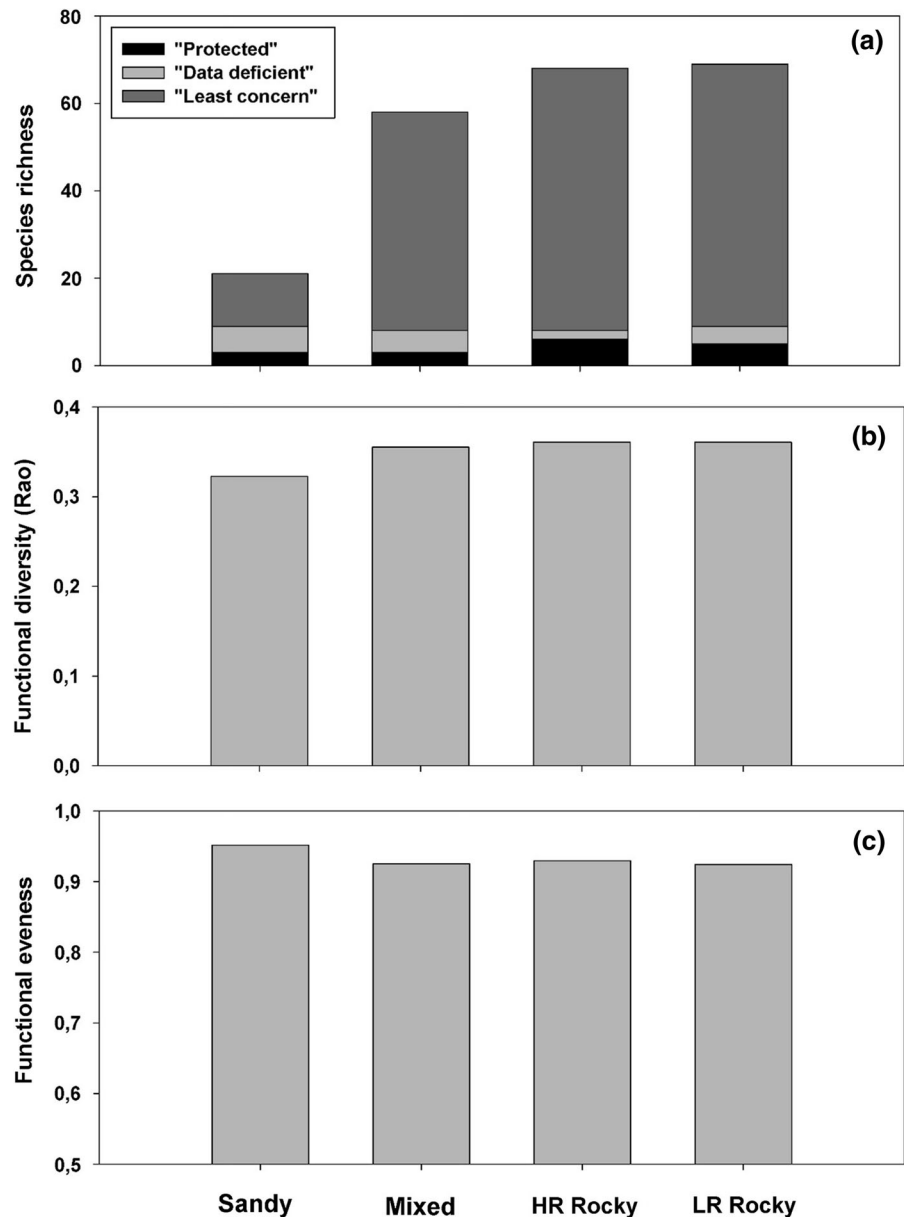
A total of 89 fish species (8 elasmobranchs and 81 teleosts) were recorded from the study site (Table 1). A larger number of fish species were observed from rocky bottoms of both low (69) and high relief (68), relative to mixed (58) and sandy (21) bottoms (Fig. 3a). These differences in TD, however, were minor in terms of FD (through the Rao index), as FD slightly peaked in rocky bottoms, of low and high relief, relative to both mixed and sandy bottoms (Fig. 3b). In fact, despite sand communities encompassed a narrow range of functional traits compared to rocky and mixed bottoms, species were evenly spread across the functional trait space, resulting in a larger functional evenness value (Fig. 3c).

Despite low fish species richness on sandy bottoms, the taxonomic distinctiveness of fish assemblages was particularly high in this habitat (Fig. 4a). This result reflects the major presence of elasmobranchs in sandy

and mixed bottoms relative to rocky bottoms, where several elasmobranchs were absent (Table 1). In any case, sandy bottoms harbored a small part of the total evolutionary history of the phylogenetic tree, as the Faith's index of PD was particularly low in sandy bottoms relative to the other habitats (Fig. 4b). However, species inhabiting sandy bottoms were phylogenetically distinct, as the MPD (Fig. 4c) was larger in sandy bottoms relative to the other habitats. This phylogenetic 'overdispersion' (or evenness) of fishes inhabiting sandy bottoms was, in turn, demonstrated according to measures of the 'standardized effect size' of phylogenetic community structure, when patterns of the MPD were compared to patterns of null models of phylogeny (random communities, Table 2). On sandy bottoms, positive 'standardized effect size' (MPD.obs.z > 0) and high quantiles (MPD.obs.p > 0.95) provided evidence of phylogenetic 'overdispersion' or, at least, a greater phylogenetic distance between occurring species than expected by chance (Table 2). On the contrary, the negative 'standardized effect size' (MPD.obs.z < 0) found on rocky habitats and the low quantiles (MPD.obs.p < 0.05) are clearly suggesting phylogenetic 'clustering' of lineages, or reduced phylogenetic distances between species, on rocky bottoms (Table 2). The degree of 'phylogenetic signal' was particularly accentuated on rocky bottoms (Pearson $r_s = 0.519$ and 0.517 , $P = 0.01$, for high and low relief reefs, respectively) and mixed bottoms (Pearson $r_s = 0.502$, $P = 0.01$) relative to sandy bottoms (Pearson $r_s = 0.055$, $P = 0.34$). In other words, there was no relationship between the functional and phylogenetic structure of the fish community on sandy bottoms.

Finally, analysis of beta-diversity revealed a clear turnover of species between habitats (Fig. 5a), while turnover of phylogenies was less accentuated (Fig. 5b). High and low relief rocky bottoms shared the highest number of species and phylogenetic history, and there was also high similarity between these habitats and mixed bottoms. On the other hand, sandy bottoms supported distinct communities both based on species composition and phylogenetic history.

Fig. 3 Diversity of fish species on each habitat, according to the **a** total number of species (species richness, TD), **b** the Rao index of FD and **c** the evenness index of FD. The total number of species was partitioned according to the IUCN conservation categories: 'least concern', 'data deficient' and 'protected' species, which included vulnerable, endangered, and critically endangered species



Discussion

This study has demonstrated that patterns of fish diversity between adjoining habitats within a coastal seascape are considerably influenced by the way diversity is defined and, therefore, mathematically calculated. Initially, our study revealed a certain degree of consistency between indices that measured 'how much' biodiversity; indices that measured 'how many species' (species richness, TD), 'how much

functional diversity' (Rao index, FD) and 'how much phylogenetic history' (Faith's PD) showed a similar pattern. However, indices that measured 'how different' fish communities are, taxonomically and phylogenetically, showed an opposing pattern; the taxonomic distinctiveness and the MPD of fishes was particularly large for the fish community of lower TD, here sandy bottoms. Typically, different habitats offer different resources (e.g., food or shelter) and the use of these habitats may be part of species' life cycle

Fig. 4 Diversity of fish species on each habitat, according to the **a** the taxonomic distinctness of PD, **b** Faith's PD and **c** the mean phylogenetic distance (MPD) index

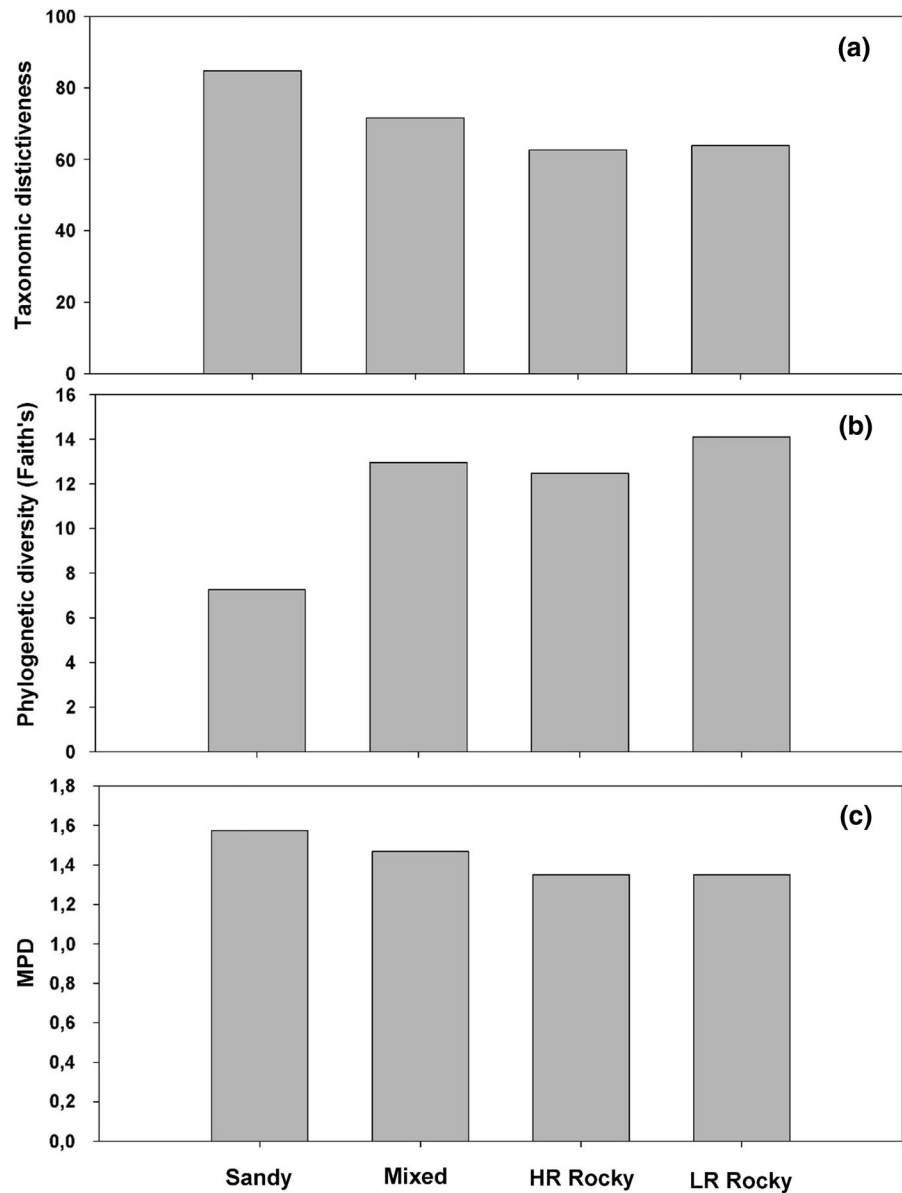
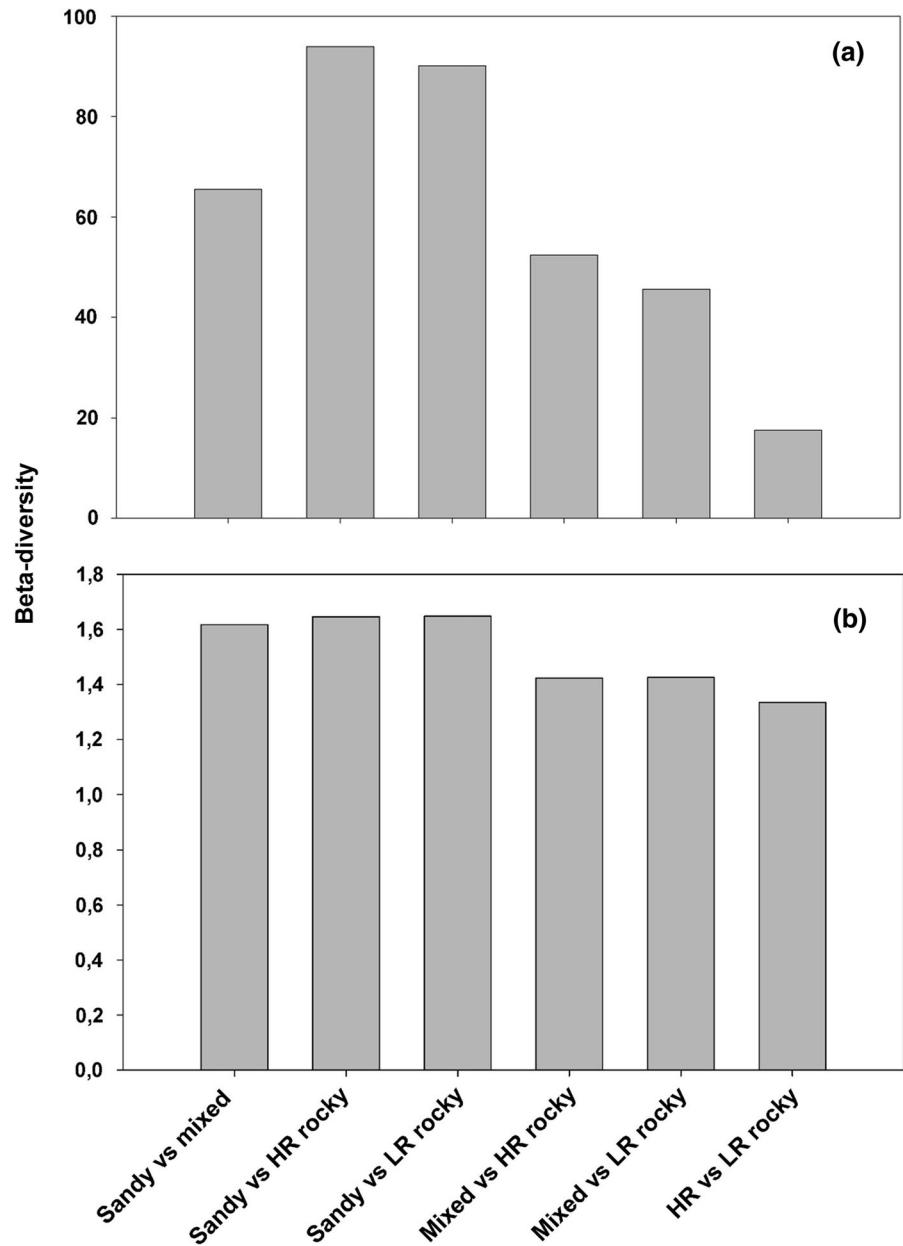


Table 2 Mean phylogenetic distance (MPD) of fish species on each habitat and those from null (random) communities to test for patterns of community assembly; MPD.rand.mean: mean MPD in null communities; MPD.rand.sd: standard deviation of

MPD in null communities; MPD.obs.rank: rank of observed MPD vs. null communities; MPD.obs.z: standardized effect size of MPD versus null communities; MPD.obs.p: *P* value (quantile) of observed MPD versus null communities

Habitat	MPD	MPD.rand.mean	MPD.rand.sd	MPD.obs.rank	MPD.obs.z	MPD.obs.p
Sandy	1.5735	1.4536	0.0796	952	1.5054	0.952
Mixed	1.4683	1.4525	0.0317	667	0.5004	0.667
HR rocky	1.3505	1.4523	0.0241	1	- 4.2272	0.001
LR rocky	1.3509	1.4519	0.0237	1	- 4.2704	0.001

Fig. 5 Beta-diversity of fish species, according **a** dissimilarities in species composition and **b** phylogenetic relatedness, between habitats



or be associated to a particular life history stage (e.g., nourishment vs. reproductive areas). This is particularly common for nearshore fishes, where ontogenetic habitat shifts have been widely documented (Espino et al., 2015; Costa Azevedo et al., 2017). This seems to be plausible at the study system, because can easily move between adjoining habitats connected at small scales. At the same time, adaptation of fish species to the peculiarities of the spatial architecture/configuration of each habitat may concurrently affect functional

traits, e.g., variations in morphology and position in the water column for fishes (Farré et al., 2015). In species-rich ecosystems, high structural complexity increase niche availability, reducing competition and predation (Almany, 2004; Richardson et al., 2017). This allows phylogenetically related fish species to locally coexist, playing a key role in the evolution of traits within lineages (Bellwood et al., 2014a, b; Floeter et al., 2018).

As expected, our study initially detected a larger number of species (richness) and a different composition of nearshore fishes on rocky reefs (of both high and low relief) relative to sandy bottoms (Jenkins & Wheatley, 1998; Guidetti, 2000; La Mesa et al., 2011; Rees et al., 2018). The positive correlation between measures of TD (here, species richness) and measures of functional differentiation (here, Rao index of FD) (Supplementary Table 1) supports previous expectations that the presence of more species promote a larger representation of functional traits just 'by chance' (Schleuter et al., 2010). However, this pattern might be reversed in situations where harsh environmental conditions promote the coexistence of species that are functionally similar, independently of changes in species richness (Villéger et al., 2010; Purschke et al., 2013). In this study, the sandy bottom fish community encompassed a narrow range of functional traits compared to rocky and mixed bottoms, as a result of the predominance of species with depressed bodies and carnivorous diets. For example, most elasmobranchs, as well as other representative species of sandy bottoms, e.g., *Bothus podas* (Delaroche, 1809), *Microchirus azevia* (de Brito Capello, 1867) shared these traits, which are majorly absent in species inhabiting rocky bottoms. For example, the nine species with depressed bodies only occurred on sandy and mixed bottoms. Here, species are more evenly distributed (higher functional evenness) across the functional space (i.e., across the range of functional traits), suggesting a better utilization of the niche space (Mason et al., 2005).

We recorded a low number of fish species on sandy bottoms relative to the other habitats, as registered elsewhere (Jenkins & Wheatley, 1998; Guidetti, 2000; La Mesa et al., 2011; Rees et al., 2018). However, we observed an unexpected high diversity of fish species on sandy bottoms according to their taxonomic distinctiveness (see also Supplementary Table 1). Indices of taxonomic distinctness quantify diversity as a measure of the taxonomic relatedness of species within a sample (here, a habitat), based on the distances between species in a classification tree, i.e., the Linnean classification (Clarke & Warwick, 2001), which is a simple approximation to a full phylogeny. A relevant number of fish inhabitants of sandy and mixed bottoms were elasmobranchs, which were otherwise majorly absent from rocky bottoms. As the Linnean classification is only based in 5 taxonomic nodes

(species, genus, family, order, and class), and the high-order level is the 'class', the large presence of elasmobranchs in sandy and mixed bottoms notably conditioned the outcomes of the taxonomic distinctness. The importance of elasmobranchs driving patterns in taxonomic distinctiveness has also been found in other ecological systems (Rogers et al., 1999; Tolimieri & Anderson, 2010); this has been linked to the clustering of specialist species in habitats under severe environmental conditions, such as the deep ocean (Zinten et al., 2011). Other studies have also shown that communities with low species richness do not necessarily have a smaller taxonomic distinctiveness relative to communities with many species (Ellingsen et al., 2005), whereas species richness and taxonomic distinctness of fishes may otherwise behave in the same way (Bosch et al., 2017).

The use of phylogenies in modern ecology and conservation is becoming increasingly common (Winter et al., 2013), enlarging our understanding of biological diversity and ecosystem functions (Webb et al., 2002; Tucker et al., 2017). Our study revealed contrasting outcomes, according to the way phylogenetic diversity is perceived and measured. In particular, sandy bottoms accumulated a reduced amount of the total fish evolutionary history of the study seascape, here demonstrated by a low Faith's index of PD. However, species inhabiting sandy bottoms were considerably dissimilar from a phylogenetic point of view, as revealed by a high MPD. In turn, our study demonstrated 'phylogenetic overdispersion' (= evenness) of fishes in sandy bottoms, relative to rocky bottoms, where 'phylogenetic clustering' of species tend to occur. Most likely, the high structural complexity of reefs results in increased niche availability, reducing competition, and so favoring the coexistence ('clustering') of phylogenetically similar species sharing similar traits. On the contrary, we detected a lack of 'phylogenetic signal' on sandy bottoms. In other words, on sandy bottoms, phylogenetically dissimilar species can have similar traits and/or phylogenetically similar species can have very dissimilar traits. For example, two phylogenetically dissimilar inhabitants of sandy bottoms, the Angel shark *Squatina squatina* (Linnaeus, 1758), and the wide-eyed flounder *Bothus podas*, have both depressed bodies and are located in the same position in the column (benthic); both species tend to somehow be functionally similar, despite their large

phylogenetic differentiation. On the contrary, two phylogenetically similar inhabitants of sandy bottoms, here two elasmobranchs, the smooth-hound *Mustelus mustelus* (Linnaeus, 1758) and the common stingray *Dasyatis pastinaca* (Linnaeus, 1758) hardly share similar traits. *Mustelus mustelus* has an elongated body with a benthopelagic position in the water column, whereas *D. pastinaca* has a depressed body and occurs on the benthos. On sandy bottoms, evolutionary adaptation of species to a bidimensional habitat seems to promote functional convergence, at least of certain traits, of phylogenetically different species (MacArthur & Levins, 1967). The absence of phylogenetically related species that share common traits on sandy bottoms has likely arisen as a result of intense competition (for food) between species in this relatively homogenous and resource-poor habitat (Farré et al., 2015). Typically, resource shortage produce higher interspecific competition, resulting in phylogenetic overdispersion, which is common from harsh habitats (e.g., deep reefs), where the availability of resources is limited, so species must specialize to maximize their fitness (Gomez et al., 2010). ‘Environmental filtering’ tend to decrease functional and phylogenetic distances between species (‘PD or FD clustering’) for a given level of TD, whereas competition tend to otherwise increase these distances (‘PD or FD overdispersion’) (Webb et al., 2002; Kraft et al., 2007).

Conservation implications

Typically, preserving biodiversity via protection of species richness has been an explicit aim of management and conservation policies. The functional and phylogenetic associations between species, however, have been gradually incorporated to grasp a more holistic understanding of biodiversity, particularly in the context of thoughtful functional or evolutionary lineages (Winter et al., 2013; Grenié, 2018). Indices of FD and PD are attractive because, firstly, they may be based on presence/absence data, as our case-study, and are unaffected by the sampling effort. In this study, for example, elasmobranchs, which majorly inhabit sandy and mixed bottoms of the study seascape, largely contributed to the functional and phylogenetic distinctiveness of fishes between habitats. This was particularly highlighted by PD indices that measured ‘how different’ biodiversity was, rather than by

indices that estimated ‘how much’ biodiversity. Importantly, over and above topological (and mathematical) connotations linked with the calculations of biodiversity indices, most elasmobranchs are included in different categories of concern according to the IUCN Red List (3 out of 8 species, while the remaining five species are ‘Data Deficient’, Table 1). Certain areas of the world are rich in terms of the diversity of elasmobranchs with a high frequency of observations along nearshore waters. The Canary Islands are a clear example; large aggregations of elasmobranchs are spotted near the shore (Narváez, 2013), even linked to human facilities (Tuya et al., 2006).

When working with pooled compositional (presence-absence) data, lack of replication at the habitat-scale avoids proper statistical inferences. Despite this limitation, our results support the idea that sandy bottoms cannot be initially underrated in terms of conservation. In summary, data from this study indicate that protection of coastal habitats is greatly benefited when a range of habitats are included to maximize biodiversity indices that assess both ‘how much’ and ‘how different’ biodiversity varies across habitats. This seems to be particularly pertinent when depressed-body elasmobranchs are a key conservation element.

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