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Mapping biodiversity in three-dimensions challenges marine conservation strategies: The example of coralligenous assemblages in North-Western Mediterranean Sea

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ABSTRACT

Multi-facet diversity indices have been increasingly widely used in conservation ecology but congruence analyses both on horizontal and vertical axes have not yet been explored. We investigated the vertical and horizontal distributions of α and β taxonomic (TD), functional (FD) and phylogenetic diversity (PD) in a three-dimensional structured ecosystem. We focused on the Mediterranean coralligenous assemblages which form complex structures both vertically and horizontally, and are considered as the most diverse and threatened communities of the Mediterranean Sea. Although comparable to tropical reef assemblages in terms of richness, biomass and production, coralligenous assemblages are less known and more rarely studied, in particular because of their location in deep waters. Our study covers the entire range of distribution of coralligenous habitats along the French Mediterranean coasts, representing the most complete database so far developed for this important ecosystem. To our knowledge, this is the first analysis of spatial diversity patterns of marine biodiversity on both horizontal and vertical scales.

Our study revealed that taxonomic diversity differed from functional and phylogenetic diversity patterns at the station level, the latter two being strongly structured by depth, with shallower stations generally richer than deeper ones. Considering all stations, phylogenetic diversity was less congruent to taxonomic diversity (Pearson's correlation of $r = 0.48$) but more congruent to functional diversity ($r = 0.69$) than randomly expected. Similar congruence patterns were revealed for stations deeper than 50 m ($r = 0.44$ and $r = 0.84$, respectively) but no significantly different congruence level than randomly expected was revealed among diversity facets for more shallow stations. Mean functional α- and β-diversity were lower than phylogenetic diversity and even lower than taxonomic α- and β-diversity for both vertical and horizontal scales. Low FD and PD values at both α- and β-diversity indicated functional and phylogenetic clustering. Community dissimilarities (β-diversity) increased over depth especially in central and eastern part of the French Mediterranean littoral and in northern Corsica, indicating coralligenous vertical structure within these regions. Overall horizontal β-diversity was higher within the 50–70 m depth belts.

We conclude that taxonomic diversity alone is inadequate as a basis for setting conservation goals for this ecosystem and additional information, at least on phylogenetic diversity, is needed to preserve the ecosystem functioning and coralligenous evolutionary history. Our results highlight the necessity of considering different depth belts as a basis for regional scale conservation efforts. Current conservation approaches, such as the existing marine protected areas, are insufficient in preserving coralligenous habitats. The use of multi-facet indices should be considered, focusing on preserving local diversity patterns and compositional dissimilarities, both vertically and horizontally.

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1. Introduction

A wide range of animal and plant species exhibit a vertically stratified distribution pattern in terrestrial ecosystems, with most documented examples treating variations in species distributions along the vertical gradient from canopy to understory (ex. small mammals (Pardini et al., 2005), butterflies (Walla et al., 2004; Molleman et al., 2006) ants (Vasconcelos and Vilhena, 2006) and saproxylic species (Wermelinger et al., 2007)). Similar vertical stratification has been documented along the water column in marine ecosystems, for fish larvae and zooplankton groups (Pilar Olivar et al., 2010), as well as in bacterial and archaeal communities (Ghiglione et al., 2008; Ye et al., 2009; Zinger et al., 2011). In marine ecosystems, most of the key abiotic factors (light, water movement, nutrient availability, sedimentation and temperature) vary strongly along bathymetric (vertical) as well as horizontal gradients, thus structuring species' community composition (Bonecker et al., 2014). Whether vertical and/or horizontal gradients structure more species communities may significantly influence conservation efficiency but such aspects still remain poorly documented.

In addition to being a proxy of environmental gradients and structuring species' ecological niche, depth is also related to human pressure. In the Mediterranean basin, most human activities that may have an impact on marine ecosystems are depth-related; recreational fishing, navigation and/or diving activities, for instance, take place in relatively shallow waters (less than 50 m), thus making some depth belts more exposed to disturbances than others (Meinesz and Blanfuné, 2015). However, other sources of disturbances, such as professional fishing, mechanistic destruction (ex. installation of underwater cables) and pollution from terrestrial or marine sources can act as a disturbance in even deeper zones (especially in >50 m depth belts) (Grall and Hall-Spencer, 2003; Meinesz and Blanfuné, 2015). Finally, as recently reviewed in a 30-year survey, depth remains an important factor for marine conservation efforts in the Mediterranean basin, with more focus being recently given to ecosystems deeper than 50 m (Meinesz and Blanfuné, 2015). However, the network of marine protected areas (MPAs) lacks a sufficiently specific planning focus and specific ecological criteria for the selection of the target depth belts. Most Mediterranean MPAs were established on the basis of limited ecological, social, and economic data (Claudet and Pelletier, 2004; Claudet et al., 2006).

While some taxonomic groups, such as fish and seagrass meadow communities, have been studied extensively within the Mediterranean basin (Ruíz et al., 2009; Mouillot et al., 2011) and used as indicators for European environmental policies (Devlin et al., 2007; Gobert et al., 2009; Personnic et al., 2014), deeper marine ecosystems remain poorly known (Cartes et al., 2004). Among the most vulnerable and diverse ecosystems within the Mediterranean basin, coralligenous outcrops are comparable in species richness and abundance to tropical reef assemblages (Bianchi and Morri, 2000; Ballesteros, 2006). Coralligenous reefs are found between 20 and 120 m depth and are composed of a hard substrate of concretions of biogenic origin, produced mainly by the accumulation of encrusting algae growing at low light levels (Garrabou and Ballesteros, 2000). Little was known about this highly diverse ecosystem until recently (Ballesteros, 2006), and it is only during the last few years that technical diving improvements have enabled their systematic surveying over extended spatial zones (Deter et al., 2012a,b). As they have little to no resilience against disturbances, due to their particularly low rate of development of only 0.006–0.83 mm/yr in the western Mediterranean Sea (Littler, 1991; Sartoretto et al., 1996), the risk of extinction may be high, given current and future global changes. However, no regional diversity analysis has been conducted to date on this important Mediterranean habitat.

Although taxonomic indices have traditionally been, widely used in conservation, recent research shows that other biodiversity facets, such as species ecological traits (functional diversity) and species evolutionary history (phylogenetic diversity) are important to ecosystem functioning (Hooper et al., 2005; Mouquet et al., 2012; Srivastava et al., 2012). More importantly, the spatial patterns of these two biodiversity facets are often not congruent with taxonomic diversity patterns (Forest et al., 2007; Devictor et al., 2010a), since the three facets result from different processes in community assembly, and in turn provide relevant inputs for the identification of conservation targets (Devictor et al., 2010b; Mouillot et al., 2011). It has thus been increasingly widely acknowledged that conservation planning should focus on preserving ecosystem processes and functions and more effort should be made to identify areas that preserve functional traits and evolutionary legacies at various spatial scales (Abdulla et al., 2009; Coll et al., 2012). However, the multidimensionality of diversity is not yet reflected in existing conservation planning. MPAs, for instance, used as one of the main conservation tools worldwide, are designated on the basis of a few charismatic taxa (e.g. fish, mammals), not via an integrated ecosystemic approach (Fraschetti et al., 2005).

Exploring the vertical vs horizontal distribution patterns for all three diversity facets is a completely unexplored field. We chose to address these questions with regard to the Mediterranean coralligenous assemblages because of their complex structure, both vertically and horizontally, and their high level of richness and vulnerability. In order to understand and preserve the three-dimensional nature of these high diversity assemblages, it is urgent to examine compositional dissimilarity levels along both vertical and horizontal gradients, especially since all previous and existing conservation efforts have focused on rather shallow coastal areas (<40 m), disregarding deeper ecosystems (Abdulla et al., 2009). To address this conservation issue, a preliminary step is to combine measures of diversity distribution (community diversity = α diversity and between-community dissimilarities = β diversity) (Legendre et al., 2009; Veech and Crist, 2010) in the three dimensions. To our knowledge, this has to date never been done using the three facets of diversity for any studied terrestrial or marine ecosystem.

We assessed the taxonomic, functional and phylogenetic diversity of North-Western Mediterranean coralligenous assemblages along both horizontal (1700 km) and vertical (73 m) gradients, which represents the entire distribution of coralligenous habitats in the French Mediterranean. In comparison with previous studies (Balata et al., 2006; Piazzi et al., 2009; Piazzi and Balata, 2011), which considered a small fraction of the possible depths (30–40 m) at which one may encounter the coralligenous concretions, our database represents the most complete distribution range ever used for the studied organisms. Our aim is to answer the following questions: (1) How are the three facets of diversity spatially distributed and what is their degree of congruence? (2) How does spatial distribution of biodiversity vary from the horizontal to the vertical axis? (3) To what extent does the existing network of marine protected areas encapsulate the multidimensionality of coralligenous biodiversity (vertical/horizontal, taxonomic/functional/phylogenetic)? Our results have important implications not only for the conservation biology of coralligenous assemblages but also for any kind of ecosystem organised along both horizontal and vertical axes.

2. Materials and methods

2.1. Study area and coralligenous assemblages monitoring

The coralligenous monitoring programme started in 2010 and is still ongoing. Three regions, composing the French coralligenous distribution area, are surveyed: (i) eastern Provence-Alpes-Côte

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