Parallel assemblage structures in Mediterranean marine amphipods revealed by beta diversity partitioning

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Abstract

Relying on a purely taxonomic view of diversity may ignore the fact that ecological communities can be constituted of species having both distinct evolutionary histories and functional characteristics. Thus, considering how the multiple facets of diversity vary along environmental and geographic gradients may provide insights into the role of historic processes and current environmental changes in determining the divergence or convergence of lineages and functions, ultimately influencing the way species assemble across space. However, analyses can be somehow flawed by the choice of traits being analysed, as they should capture the whole functional variability of species in order to assess the relationship between phylogenetic and functional diversity along a gradient. When continuous measures of functional diversity based on a variety of different traits are absent, the use of functional traits known to show strong phylogenetic signal can help elucidating such relationship.
By using distributional, traits and taxonomic-distance information, we explored how the taxon, functional and phylogenetic community composition (co)vary along spatial and environmental gradients in seagrass amphipod metacommunity within the Mediterranean Sea. We used beta diversity partitioning and null models to determine the role of deterministic and stochastic processes on the replacement and the net loss/gain of species, lineages and highly conserved β-niche traits. We showed that dispersal-based processes are the main determinants of the high taxonomic and phylogenetic beta diversity, while niche-based processes explain the low functional dissimilarity among assemblages. Moreover, phylogenetic and functional beta diversity showed contrasting patterns when controlling for the underlying taxonomic composition, with the former being not significantly different and the latter significantly lower than expected. Our results suggest the key role of historical and biogeographic processes in determining the present-day patterns of community assembly and

species turnover, providing also evidence for parallel assemblage structures in Mediterranean seagrass amphipods.

Keywords: Dispersal limitation; Niche filtering; Functional diversity; Phylogenetic diversity; Species turnover; Amphipods; Mediterranean Sea

Introduction

Understanding the patterns and mechanisms of species distribution is a central goal in community ecology, having important outcomes for biodiversity conservation. Although classical approaches focused mainly on the quantification of the difference in the number of species across sites and/or time, recent findings have shown the weakness of considering taxonomic diversity (TD) as the unique building block of diversity (Flynn et al. 2011, Cadotte et al. 2012, Craven et al. 2018). Indeed, by using TD as main descriptor of natural communities, one often ignores that the different evolutionary history of species (i.e. their phylogenetic diversity, PD) and the diverse array of functional traits (i.e. their functional diversity, FD) constitute a not negligible and complementary part of diversity (Webb et al. 2002, Petchey and Gaston 2006, Graham and Fine 2008). For instance, distinct communities may be characterized by a high taxonomic divergence although showing high levels of functional convergence, signalling the replacement of species performing similar functions across sites (Carvalho et al. 2019). Similarly, communities composed of phylogenetically related species may show high levels of traits divergence, as a signal of the influence of regional and historical processes on local community assembly (Ramm et al. 2018). Biodiversity investigation taking into account phylogenetic and trait-based analyses can thus help disentangling the mechanisms of community assembly, since different processes may influence in a different way and at different spatial and temporal scales the way species assemble and diverge/converge in their phylogeny and functional abilities. Thus, analysing how multiple diversity facets vary over large spatial scales may allow disentangling the role of deterministic and stochastic processes, as well as the differential effects of competition and environmental filtering on the distribution of species, lineages and functions.

Beta diversity, that is, the variation in community composition across space, is a core concept in ecology aimed at determining the degree of dissimilarity in the assemblage of communities along a gradient (Whittaker 1960, Anderson et al. 2011, but see Legendre 2019 and reference therein for a temporal definition of beta diversity). Beta diversity can be decomposed into two additive sources of dissimilarity, replacement (or turnover) and richness difference (i.e. the net loss/gain of species), each reflecting different processes acting on communities. If the loss/gain of species occurs in an ordered manner, then a nested pattern emerges, where the biotas of sites with smaller number of species are subsets of the biotas of richer sites (Atmar and Patterson 1993, Baselga 2010). Independently of the methodological frameworks developed so far for its partitioning, the beta diversity concept has been extended

to include other dimensions of diversity besides taxonomical, namely phylogenetic and functional (Graham and Fine 2008, Leprieur et al. 2012, Cardoso et al. 2014).

Measuring the relative contribution of each component on the overall beta diversity may allow identifying the underlying ecological processes assembling communities. For instance, species turnover may arise from the replacement of species, functions and lineages along a given gradient due to environmental filtering (Saladin et al. 2019), while the net differentiation of assemblages may be given by the selective loss/gain of species with a particular set of traits due to stochastic dispersal or extinction processes (Si et al. 2016). The extent to which beta diversity covaries with environmental and geographic features are thought to be signal of niche filtering or dispersal limitation, two complementary mechanisms in shaping beta diversity patterns (Laliberté et al. 2009, Carvalho et al. 2011). Moreover, it has been noticed how a given degree of correlation between phylogenetic and functional beta diversity should be expected (see Tucker et al. 2018 for a complete review), especially if the functional traits that allow species to persist in the environment are evolutionarily conserved (Webb et al. 2002). Likewise, it is reasonable to expect that functional and phylogenetic beta diversity components will be correlated with their taxonomic counterparts along gradients. Given the dependence between the different facets of beta diversity, the degree to which functional and phylogenetic beta diversity are significantly higher (or lower) than expected with respect to a given taxonomic composition, can be interpreted as signal of their divergence (or convergence), while random values as signal of dispersal limitation (Swenson et al. 2011, Carvalho et al. 2019).

Marine benthic amphipods represent a well-suited group of species to test specific hypotheses relating the complementary role of niche- and dispersal-based processes on the structuring of ecological communities over large scales, due to their limited dispersal ability, their importance for marine trophic webs and their sensitivity to environmental alterations (Pinnegar et al. 2000, Kumagai 2008, Michel et al. 2015). Moreover, it has been found that their assembly pattern is mostly driven by traits related to habitat choice rather than feeding traits, such as body size and mechanisms for attaching to substrate, which are also characterized by a strong phylogenetic signal when compared with other niche-related traits (Best et al. 2013, Best and Stachowicz 2014, Lürig et al. 2016).

In this paper, we aim to test for the relative contribution of the replacement and richness components and the presence of environmental and/or geographic signals on taxon, functional and phylogenetic beta diversity. Here, we used the term taxon *in lieu* of taxonomic diversity, as these terms identify two different but related aspects of diversity, with the first

referring to a partition and the second to a hierarchy (Cardoso et al. 2014). We used taxonomic distance as surrogate for phylogeny and distribution data of amphipods associated with *Posidonia oceanica* (L.) Delile, 1813 Mediterranean seagrass habitat, including information on a restricted array of functional traits having important outcomes for the community assembly process and characterized by a strong phylogenetic signal (i.e. high conserved β-niche traits: body size and tube building ability). We characterized the sampling sites by using distribution data on the occurrence of *P. oceanica* seagrass habitat and information on specific environmental features known to have a direct influence on the distribution of biota in the Mediterranean Sea (Coll et al. 2010). Moreover, as rates of trait evolution and speciation may differ among biogeographic regions (Arnan et al. 2017), we used a previously identified biogeographic partition of the same dataset (Bellisario et al. 2019), to reveal the role of different environmental and historical conditions in determining the pattern of assemblages' differentiation.

Material and methods

Study area

We used a dataset on the presence of amphipods from *P. oceanica* meadows across different regions of the Mediterranean Sea, characterized by comparable data in terms of sampling season, depth and methods. The study area covered a large portion of the Mediterranean Sea, characterized by different geographic, hydrological and geological features, as well as differences in the potential connectivity due to general circulation models (Bianchi 2011, Berline et al. 2014). In a previous work (Bellisario et al. 2019), network analysis was applied to identify the bioregional (aka modular) partition of local assemblages composed of 147 amphipod species from *P. oceanica* meadows in 28 sites (Fig. 1).

Environmental and habitat characterization

We used the Sea Surface Temperature (SST) and Sea Water Salinity (PSU) values as main determinants of the environmental characteristics of sites, since they are both known to co-vary geographically and so influencing the pattern of species diversity throughout the Mediterranean basin (Coll et al. 2010). Data were downloaded from the COPERNICUS Marine Environment Marine Service (CMEMS, https://marine.copernicus.eu), which provides an easy way to access a variety of data from multiple sources (e.g. satellite observations and *in situ* sensors) encompassing different spatial and temporal resolution. SST and PSU were extracted from the Mediterranean Sea Physics Reanalysis, a hydrodynamic model supplied by the Nucleus for European Modelling of the Ocean (NEMO), with a resolution matching the seasonal (Spring/Summer), temporal (1987-2014) and depth coverage (5-20m) of the original papers from which community data were extracted (see Data availability statement section). This model has a variational data assimilation scheme (OceanVAR) for temperature and salinity vertical profiles and satellite sea level anomaly along track data, with an horizontal grid resolution of ~1 km. Reanalysis has been initialized with a gridded climatology for temperature and salinity computed from *in situ* data sampled before 1987, and released as monthly mean (more information about models and data processing can be found at http://marine.copernicus.eu/services-portfolio/access-to-products/).

To describe the habitat characteristic at sites, we used the probability of *P. oceanica* occurrence (PPOMed), downloaded from the EMODnet Seabed Habitat portal (https://www.emodnet-seabedhabitats.eu) with a spatial resolution of ~1km and values ranging in the 0-1 interval. PPOMed expresses the probability of seagrass occurrence from the collation and integration of available habitat distribution models at Mediterranean scale, derived by applying a Machine Learning technique (i.e. Random Forest) to train on data from regions where information was available and then used to predict the probability of occurrence of *P. oceanica* (more information can be found in Cameron and Askew 2011).

To derive a meaningfulness measure of the environmental and habitat characteristics, we performed a geostatistical analysis by superimposing a vector of sampling data points to the SST, PSU and PPOMed rasters in a Geographic Information System (QGIS Development Team 2019), and derived the average (±SD) values within a 1km search radius centred on sampling localities.

Amphipod traits and phylogenetic data

We extended our previous dataset (Bellisario et al. 2019) by including information on the body size and living habit (i.e. free living *vs*. tube builders), which are considered as key functional traits in the community assembly processes of seagrass amphipods and that are characterized by a strong phylogenetic signal when compared to other niche related traits as temperature tolerance and feeding habits (Best et al. 2013, Best and Stachowicz 2014, Lürig et al. 2016).

Traits information were extracted from Ruffo (1982, 1989, 1993, 1998) and current literature (see Ashford et al. 2018 and references herein) and nomenclature was updated following the World Register of Marine Species (WoRMS, last access 29/10/2020). We used the maximum body length (measured from the anterior margin of the head to the posterior end of the telson, in mm) in accordance with the fast-seasonal growth cycle of seagrass amphipods (Spring/Summer breeding period, Best and Stachowicz 2014), taking into account that community data were all referred to these seasons. Since a certain degree of sexual body size dimorphism may exist in amphipods (Longo and Mancinelli, 2014), body size was taken as the average maximum body length between male and female specimens. Information on living habit were extracted at family level and each species was coded as ‘tube’ (tube-dwelling) and ‘free’ (free-living). Traits distance between species was measured with the

Gower distance (Pavoine et al. 2009), by means of the function 'gowdis' in the FD package of R (Laliberté and Legendre 2010, R Development Core Team 2018).

Since a true phylogenetic tree was currently unavailable for all amphipod species recorded in our study, we used a taxonomic distance measure based on the average path lengths in the taxonomic tree (Ricotta et al. 2012, Cardoso et al. 2014). Although the amount of approximation provided by surrogate measures for phylogeny poses serious limits when used for answering strict evolutionary questions (Cardoso et al. 2014), their use is found to be valid in large-scale metacommunity studies (Heino and Tolonen 2017, Hill et al. 2019). Taxonomic information were retrieved from WORMS by using the function 'classification' in the package 'taxize' (Chamberlain and Szocs 2013) of R and the taxonomic distance was calculated by using equal branch lengths between seven taxonomic levels (Species, Genus, Family, Superfamily, Parvorder, Infraorder, Suborder), by using the function 'taxa2dist' in the 'vegan' package of R (Oksanen et al. 2019).

Statistical analyses

We measured the compositional dissimilarity of local assemblages by following the approach proposed by Cardoso et al. (2014), which uses trees as common representation for taxonomic/phylogenetic and functional diversity, according to which part of a global tree is shared by or unique to the compared communities. Traits and phylogenetic distance matrices were converted to trees and then used to quantify the taxon (TDβ), functional (FDβ) and phylogenetic (PDβ) beta diversity and its replacement (turnover) and richness difference components, by using the package 'BAT' of R (Cardoso et al. 2015).

Since taxon diversity intrinsically influences functional and phylogenetic diversity (Arnan et al. 2017), we used null models to address whether FDβ and PDβ were significantly higher or lower with respect to a given TDβ. We therefore generated a null distribution of FDβ and PDβ by randomizing 1,000 times the species name along the functional and phylogenetic dendrograms (Swenson et al. 2011, Carvalho et al. 2019). This allowed keeping actual branch lengths and their distribution, while preserving the spatial structure of species in the system. Departure from random expectation was measured by using the standardized effect size (SES, Gotelli and Graves 1996), SES = $(\beta_{obs} - \beta_{mean}) / \beta_{SD}$, with β_{obs}, β_{mean} and β_{SD} the measured beta diversity components and the average and standard deviation of a null distribution, respectively.

The Mantel and partial Mantel test (Legendre and Legendre 2012) were used to test for a correlation between the different facets of beta diversity components with environmental and geographic variables. We used the Euclidean distance between latitude and longitude to construct the geographic distance matrix. Since salinity and sea surface temperature are known to covary within the Mediterranean Sea and to strongly influence the present distribution of *P. oceanica* (Chefaoui et al. 2017), we performed a Principal Component Analysis (PCA) on the SST, PSU and PPOMed variables, so as to avoid multicollinearity and satisfy the assumption of linearity in (partial) Mantel tests. PCA explained almost 90% of total variation and the first two axes (PCA1 = 70.92%, PCA2 = 18.94%) were used to calculate the Euclidean distance between each pair of sites. Finally, we used the biogeographic (aka modular) partition already derived from our previous study (Bellisario et al. 2019) to account for the biogeographic-level effects in determining the patterns of dissimilarity. We therefore assigned a numeric code to each site corresponding to the bioregion it belonged (Fig. 1), and then calculated the dissimilarity matrix. This matrix was used as covariates in the partial Mantel test to account for the biogeographic-level effect on explanatory variables.

Results

Beta diversity patterns

Assemblages of Mediterranean seagrass amphipods showed a similar pattern of TDβ and PDβ, both showing an average high total beta diversity ($TD\beta_{tot} = 0.799 \pm 0.014$; $PD\beta_{tot} = 0.624 \pm 0.011$). The replacement and richness difference components accounted for a nearly equal contribution of total taxon and phylogenetic beta diversity ($TD\beta_{repl} = 0.418 \pm 0.007$, $TD\beta_{rich} = 0.381 \pm 0.006$; $PD\beta_{repl} = 0.298 \pm 0.005$, $PD\beta_{rich} = 0.326 \pm 0.006$) (Fig. 2). A different pattern was shown for FDβ, where the concentration of points in the left angle of the ternary plot (Fig. 2) highlighted the high similarity in terms of functional composition ($FD\beta_{tot} = 0.226 \pm 0.004$), showing the relatively marginal contribution of the replacement component ($FD\beta_{repl} = 0.084 \pm 0.001$) compared to richness difference ($FD\beta_{rich} = 0.143 \pm 0.002$).

Overall, the replacement and richness difference components accounted for ca 50% each on the total TDβ and PDβ, while richness was the dominant component in FDβ, contributing to ca 64% for the total.

As expected, we found significant correlations between the different facets of beta diversity components. TDβ was positively correlated with PDβ (Mantel r, 0.939, 0.956 and 0.979 for total, replacement and richness, respectively), showing also a significant albeit lower correlation with FDβ (Mantel r, 0.704, 0.629 and 0.784 for total, replacement and richness, respectively). All components of PDβ and FDβ were positively correlated (Mantel r, 0.719, 0.661 and 0.749 for total, replacement and richness, respectively), although their correlation drastically decreased after controlling for TDβ (Mantel r, 0.238, 0.259 and 0.215 for total, replacement and richness, respectively).

Null model analysis (Fig. 3) showed significantly lower values for the total and richness difference components of FDβ when compared to the null expectation given the underlying taxonomic variation (SES = - 1.915, p = 0.033 and SES = - 1.645, p = 0.049), while functional replacement ($FD\beta_{repl}$) did not (SES = - 0.435, p = 0.359). None of the PDβ components differed from the null expectation (SES > 0.271, p > 0.306 for all cases, Fig. 3).

Correlates of beta diversity

Mantel and partial Mantel tests showed marked differences within and between different components of beta diversity facets, highlighting interesting patterns in the relationship with environmental and geographic distances. Total components of TDβ, FDβ and PDβ were all positively correlated with environmental and geographic distances, even after controlling for the biogeographic partition, with the only exception of $FD\beta_{tot}$ that did not show any significant correlation with the environmental distance when controlling for geography (Table 1). The replacement component of TDβ and PDβ showed a significant correlation only with the geographic distance, but not when controlling for the biogeographic partition, while $FD\beta_{repl}$ did not show any significant correlation with environmental nor geographic variables (Table 1). The richness difference components of both TDβ and PDβ were positively correlated with environmental and geographic distance even after accounting for the biogeographic-level effect (Table 1), while the environmental distance alone was correlated with $FD\beta_{rich}$, but not after controlling for the geographic and biogeographic effect (Table 1).

Discussion

In this study, we focused on the beta diversity partitioning of Mediterranean seagrass amphipods to assess the relative importance of niche- *vs*. dispersal-based processes on the replacement and richness difference components of taxon, functional and phylogenetic beta-diversity. Species replacement and richness difference gave a nearly equal contribution to the total taxon and phylogenetic beta diversity, while the net loss/gain of functions overtook the relative contribution of the replacement component in explaining the low functional differentiation of assemblages. We also found marked differences on the influence of environmental and geographic variables in determining the observed patterns of differentiation, especially when considering the biogeographic partition. Overall, our findings show that stochastic and deterministic processes act at different spatial and diversity scales, with dispersal limitation determining the high taxon and phylogenetic beta diversity and environmental niche filtering mostly driving the low functional differentiation of seagrass amphipod assemblages in the Mediterranean Sea. Taken together, our results suggest the key role of historical and biogeographic processes in determining the distribution of species with limited dispersal abilities, ultimately influencing present-day patterns of community assembly and species turnover among assemblages.

Beta diversity patterns

TDβ and PDβ showed a nearly equal contribution of both the replacement and richness difference components, while the net loss/gain of functions mostly drove the functional differentiation (FDβ) of assemblages. Different factors might have drove the dynamics of current distribution of lineages and functions in seagrass amphipods to produce these patterns, mainly related to the complex paleogeographic history and the marked biogeographic structure of the Mediterranean Sea (Bianchi et al. 2011). Indeed, it is well known the role of geological events occurred during the Tertiary and the climatic fluctuations during the Quaternary (especially the most recent cycles of Plio-Pleistocene glaciations; Coll et al. 2010) in determining the distribution of biota in the basin (Bianchi et al. 2011). Moreover, the turbulent geological history of the basin allowed for the creation of a great variety of climatic and hydrologic conditions in fairly isolated sub-basins, subdividing the Mediterranean Sea in many biogeographic sectors characterized by different environmental

and habitat features (Bianchi et al. 2011). This allowed species of different biogeographic origin to enter and settle within the basin, contributing to the high level of α-diversity and endemism rate designating the Mediterranean Sea as one of the world's biodiversity hotspots (Lejeusne et al. 2010, Bianchi et al. 2011). This scenario is also compatible with the high level of β-diversity found in seagrass amphipods in our study. Turnover can be related to the progressive replacement of species of Atlantic origin with Mediterranean endemics along the west-east axis and, to a lesser extent, along the north-south axis (Bianchi et al. 2011). Conversely, the richness difference component can be related to the extremely low affinities of the eastern sectors (i.e. Adriatic and Ionian Sea) with the central-western part of the basin, as evidenced by the reduced occurrence of Mediterranean endemics and number of shared species with other biogeographic sectors (Bianchi et al. 2011, Bellisario et al. 2019). Thus, the balanced contribution of the turnover and the net loss/gain of taxa and lineages would stem from the repeated isolation and contraction of biotas and associated speciation events, which might have contributed to the overall diversity of taxa and the divergence of lineages.

If, on one hand, none of the components overtook the other in determining the overall TDβ and PDβ, on the other hand, the net loss/gain of functions showed a relatively high contribution on total FDβ. The low functional differentiation of assemblages in our study can be the outcome of a combination of a high number of shared traits and the presence in some assemblages of a small subset of the functional variability present in other, more variable assemblages. Therefore, it is likely that the functional differentiation of local assemblages may have been caused by common adaptative trajectories followed by amphipods, resulting in a low turnover of functions from site to site as a response to different niche filtering intensity among assemblages.

Determinants of beta diversity

Overall, our findings show the main role of dispersal-based processes in determining TDβ and PDβ but not of FDβ, a pattern that is consistent throughout the beta diversity components. Interestingly, we found that the replacement component of TDβ and PDβ is not significantly correlated with geographic distance when controlling for the biogeographic level effect. This might suggest the role of dispersal limitation acting at a finer scale in determining the turnover of taxa and lineages, in line with the low dispersal potential of amphipods and the complex spatial and temporal circulation pattern of the Mediterranean Sea (Fernandez et

al. 2005). Indeed, a recent eco-regionalization based on the potential connectivity assessed from ensemble Lagrangian simulations (Berline et al. 2014) provides an in-depth subdivision of the basin in several different regions whose hydrodynamical boundaries can help explaining the spatial distribution of passively transported organisms. Interestingly, some bioregions are completely devoid of any boundaries (e.g. Adriatic and Ionian Sea, ADR and ION in Fig. 1) while others (e.g. Central Tyrrhenian, CWM in Fig. 1) are characterized by a considerable number of boundaries, a scenario that is compatible with the significant influence of biogeographic partition on dispersal processes in determining the observed taxon and phylogenetic beta diversity.

The significant mutual dependence of both spatial and environmental signals on FDβ and the lack of a biogeographic-level effect suggest the key role of niche-based processes on the functional differentiation of assemblages, probably related to spatial differences of both environmental and habitat conditions encompassing different biogeographic sectors. Environmental gradients might be involved in determining spatial patterns in the distribution of functional traits by sorting species according to their environmental requirements. However, we hypothesize a role for biotic interactions as we focused on a single specific habitat (i.e. *P. oceanica* meadows) and on a selected array of functional traits usually associated with large-scale distribution patterns (β-niche traits, Ackerly et al. 2006) known to be strictly related to the competitive ability for habitat-niche partitioning. Such traits are also found to be the most important in driving the assembly of seagrass amphipods in natural communities, besides showing a strong phylogenetic signal when compared with other niche-related traits such as temperature tolerance (Best et al. 2013, Best and Stachowicz 2014).

Relationship between beta diversity facets

We found random values of PDβ given TDβ, meaning that the observed phylogenetic turnover did not differ with respect the given species pool. Conversely, the significant low FDβ observed when controlling for the underlying taxonomic variation, indicates that assemblages are more functionally convergent than expected. Traits convergence in natural communities can be the outcome of habitat filtering, able to select for the optimal trait values to confer appropriate abiotic physiological tolerance to a site (Cornwell et al. 2006, Kraft et al. 2015). However, functional convergence can also be determined by competitive interactions, increasing the similarity among coexisting species by excluding species bearing

traits associated with low competitive ability (e.g. the weaker competitor exclusion, Mayfield and Levine 2010). Although our results do not provide enough evidences on the predominance of one process over the other, it must be emphasized how our analysis of functional beta diversity was focused on specific traits known to be strongly related with the competitive ability of amphipods. Indeed, it is well known how amphipod assemblages in seagrass ecosystems are structured *via* fine-scale microhabitat partitioning in response to an evolved consequence of consistently high predation risk (Duffy and Hay 1991, Lürig et al. 2016). Moreover, the architectural complexity of the host plant and the presence of specific functional traits, as body size and tube-building ability, both determine the successful microhabitat utilization by crustacean mesograzers (Warfe et al. 2008, Kovalenko et al. 2011). Therefore, it is possible that historical and biogeographic processes alongside current environmental conditions may have played a role in determining the complexity of shelters provided by *Posidonia* meadows in the Mediterranean Sea, ultimately influencing the variability of traits associated with the competitive ability of species. However, we cannot exclude that other unmeasured variables, related for instance to habitat fragmentation, may be involved in restructuring the complexity of seagrass meadows, which in turn may promote changes in the functional structure of associated communities.

The observed positive relationship between PDβ and FDβ provides additional information on trait lability, reinforcing the finding that body size and tube dwelling in amphipods are phylogenetically conserved over many taxonomic groups. Besides the identification of the processes and mechanisms behind beta diversity, our results suggest the potential convergent adaptation of high-conserved β-niche traits in distantly related lineages. Despite the significant positive relationship between PDβ and FDβ indicates a strong phylogenetic signal and, therefore, a high level of functional convergence among closely related species, signals of apparent converge adaptation in amphipods have been recently reported. In a recent paper, Ashford et al. (2018) used detailed phylogenetic and functional information to investigate the extent to which interspecific competition or physical environment were implicated in the structuring of macrofaunal assemblages from Northwest Atlantic Ocean continental slopes. Among many, their findings show a certain convergence of functional traits between relatively distantly related crustacean taxa, suggesting that their functional similarity is somehow convergent (Ashford et al. 2018).

Speculations

Despite the significant positive correlation between FDβ and PDβ indicates a strong phylogenetic signal in the selected functional traits, our findings suggest the role of apparent convergent adaptation of distantly related species. We argue that the observed pattern may arise from independent adaptive radiations occurred in different bioregions, so that the same traits may have evolved independently in different clades, allowing for the low trait differentiation between bioregions. Thus, under this scenario, we should expect trait convergence at species level to scale up to the entire assemblage as a consequence of shared geographical distributions among species. Although we lack a real and detailed phylogeny to elucidate the role of shared evolutionary histories in determining the observed pattern of diversity, our results suggest parallel assemblage structures driven by different mechanisms balancing both evolutionary responses to long-term isolation and local adaptation to environment.

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Table 1 – Results of the (partial) Mantel tests between taxon (TDβ), functional (FDβ) and phylogenetic (PDβ) beta diversity components of Mediterranean seagrass amphipods and environmental (ENV) and geographic (GEO) distances, while accounting for the biogeographic-level (BIOREG) effect (see Fig. 1). Bold values highlight the (partial) Mantel correlations (r), with $p < 0.05$.

	TDβ			FDβ			PDβ		
Model	Tot	Repl	Rich	Tot	Repl	Rich	Tot	Repl	Rich
ENV	**0.392**	0.061	**0.184**	**0.214**	0.067	**0.148**	**0.346**	0.023	**0.209**
GEO	**0.482**	**0.139**	**0.165**	**0.293**	0.126	0.178	**0.471**	**0.141**	**0.191**
GEO | ENV	**0.365**	**0.125**	0.091	0.223	0.108	0.124	**0.371**	**0.146**	0.106
GEO | BIOREG	**0.445**	0.181	**0.156**	**0.238**	0.084	0.145	**0.434**	0.113	**0.171**
ENV | GEO	**0.212**	-0.005	**0.123**	0.089	0.007	0.073	**0.158**	-0.049	**0.138**
ENV | BIOREG	**0.332**	0.014	**0.174**	**0.138**	0.013	0.108	**0.284**	-0.013	**0.187**

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Figures 1 – Geographic extension of the study area and sites location. Dotted arrows indicate the main circulation patterns and red lines with circles the main barriers: 1, Gibraltar Strait; 2, Almeria-Oran Front; 3, Ibiza Channel; 4, Balearic Front; 5, Sicily Channel; 6, Otranto Strait. Colours correspond to the biogeographic partition: blue, Tunisian (TUN); yellow, Central Western Mediterranean (CWM); red, Adriatic Sea (ADR); green, Ionian Sea (ION).

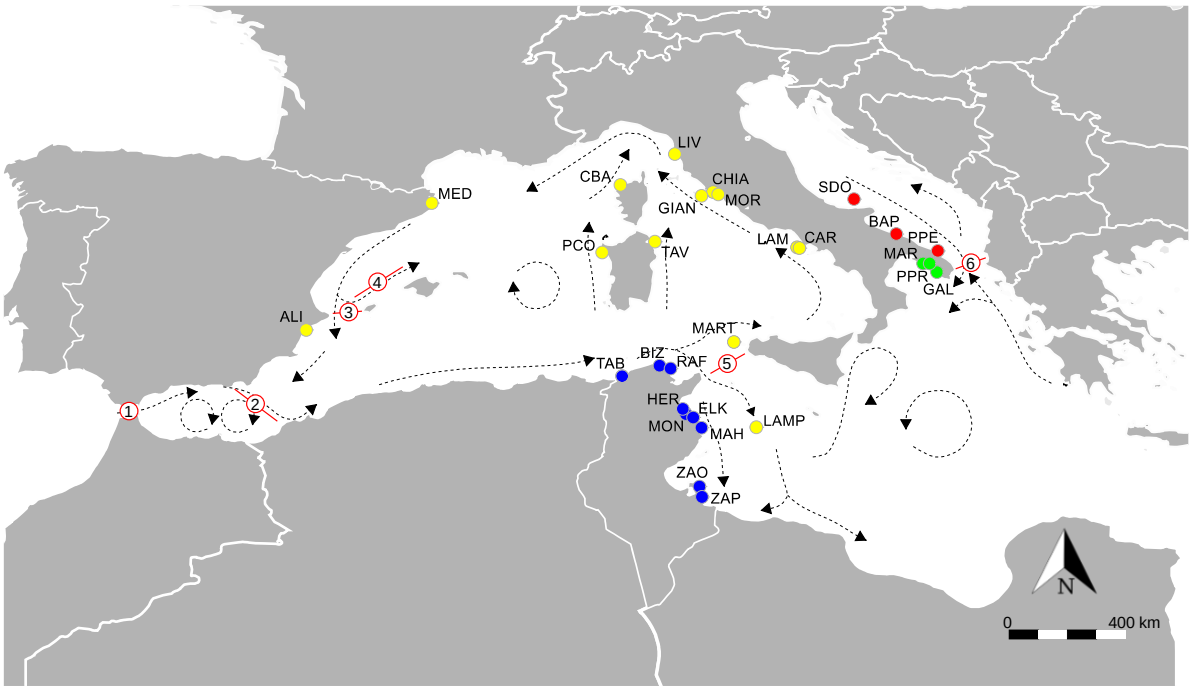


Figure 2 – Ternary plots showing the taxon (TDβ), functional (FDβ) and phylogenetic (PDβ) beta diversity structure of Mediterranean seagrass amphipod communities. Values on the plots are expressed as the mean of 1 - β_{tot} (similarity), β_{repl} (replacement) and β_{rich} (richness difference), with colours indicating the different biogeographic regions (see Fig. 1).

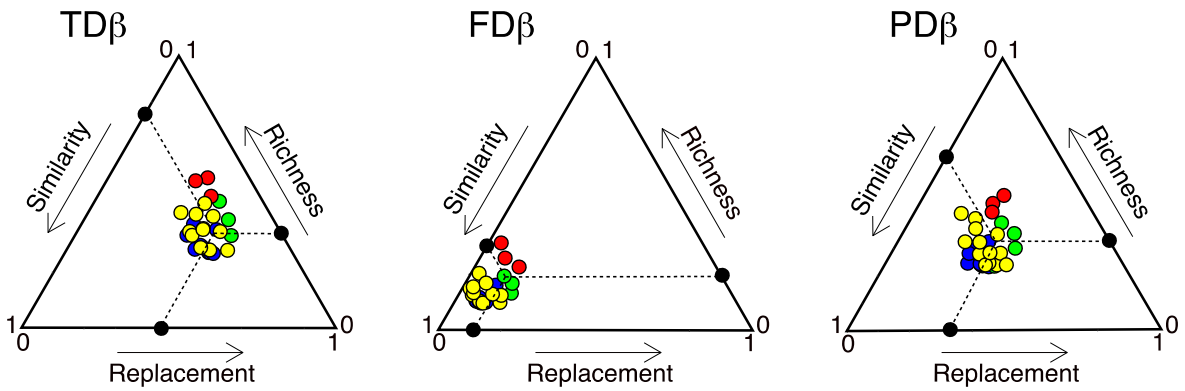
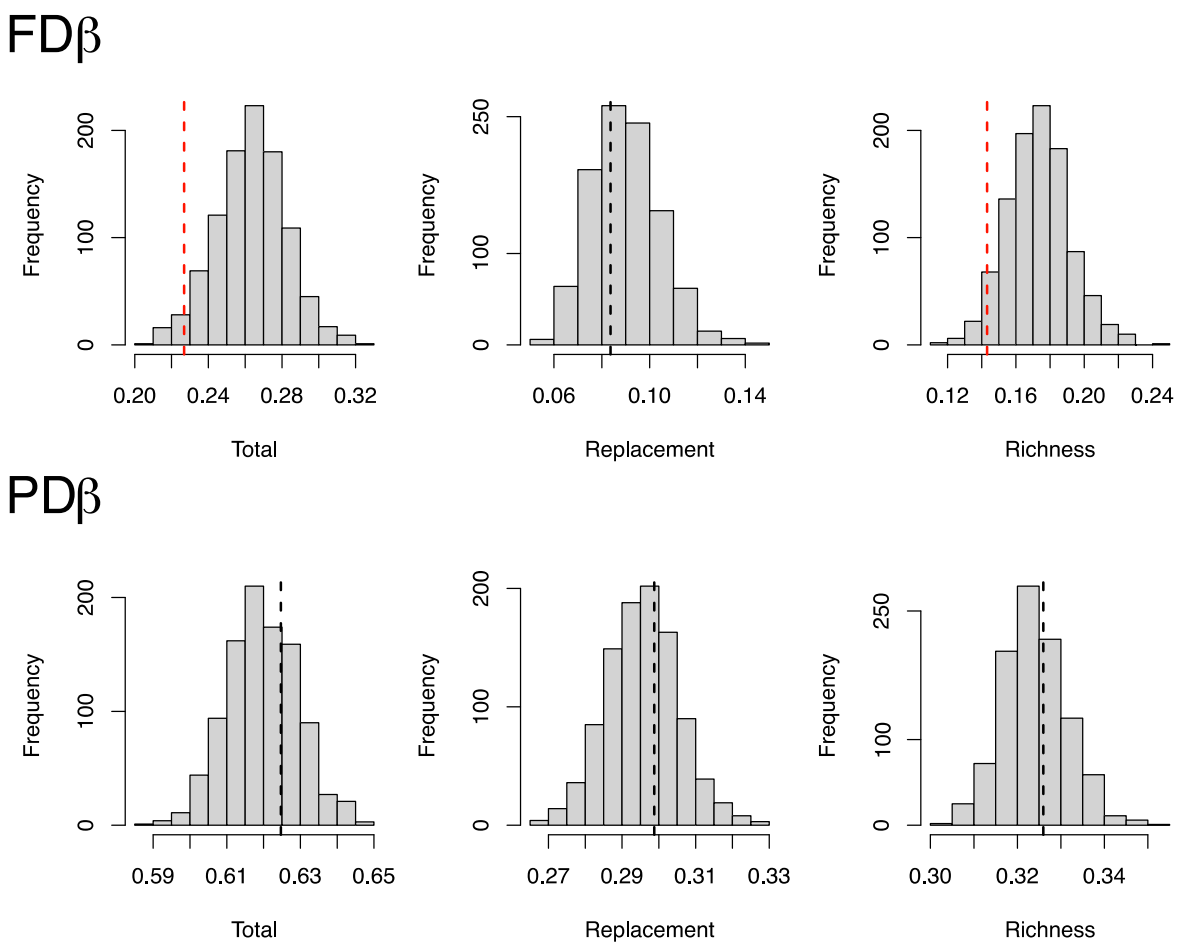


Figure 3 - Histograms showing the distribution of FDβ and PDβ components under the null model expectation given the underlying taxonomic variation, obtained after resampling 1,000 times the species name along the functional and phylogenetic dendrograms. Vertical dotted lines are the measured values for each beta diversity component. Red lines indicate significant differences ($p < 0.05$).



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