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Measuring more of β-diversity: Quantifying patterns of variation in assemblage heterogeneity. An insight from marine benthic assemblages

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ABSTRACT

β-Diversity is currently receiving increasing attention, after being neglected for a long time, especially in marine environments. Recent works introduced the distinction within β-diversity between turnover and variation. The former relates to directional changes in β-diversity along any gradient, the latter to non-directional changes, or, in other words, to the heterogeneity of assemblages within any spatial, temporal, or environmental extent. However, the quantification of assemblage heterogeneity in assessing patterns of β-diversity is still largely unexplored. Here, we investigate the potential of classical and multivariate measures of β-diversity in highlighting patterns of assemblage heterogeneity examining eight cases of study from Mediterranean Sea, involving different marine organisms and a variety of environmental settings. Multivariate analyses were employed to assess differences in assemblage structure imputable to the investigated source of variability. ANOVAs on a set of diversity indices were also performed to test for effects on patterns of α-diversity. Differences in assemblage heterogeneity were tested using both classical and distance-based multivariate dispersion measures of β-diversity as variation. Mean values of classical β-diversity metrics were analyzed using ANOVA, whereas, for distance-based multivariate dispersion, permutational tests based on a set of resemblance measures were carried out. In all study cases, analyses of β-diversity as variation showed significant effects of the investigated source of variability in modifying patterns of assemblage heterogeneity, even when no effects on the multivariate structure of assemblages and/or α-diversity were detected. The assessment of β-diversity as variation could potentially unveil patterns of change in assemblages that could remain unnoticed analyzing other components of diversity, providing complementary information crucial to the understanding of the effects of natural and anthropogenic disturbances on natural assemblages.

1. Introduction

As for terrestrial environments, investigations on marine biodiversity have been traditionally focused on α- and γ-diversity (e.g. Soininen et al., 2007), largely neglecting β-diversity (Gray, 2000). Indeed, β-diversity is essential in estimating and mapping diversity, in identifying its relevant scales of change, and in understanding processes underlying the formation and evolution of biological systems (Vellend, 2010). β-Diversity in marine systems is currently receiving renewed interest due to its central role in linking local and regional diversity (Witman et al., 2004), exploring variations across environmental and biogeographical gradients (Ellingsen and Gray, 2002), understanding ecological processes such as connectivity and meta-community assembly (Thrush et al., 2010), assessing processes of ecological homogenization related to anthropogenic activities (Balata et al., 2007a), and designing representative networks of marine reserves (Hewitt et al., 2005; Winberg et al., 2007).

Since its first formulation by Whittaker (1960, 1972), the notion of β-diversity evolved in a plethora of approaches (e.g. Tuomisto, 2010a,b, for extensive reviews) that often raised contrasting opinions on their correctness (e.g. Jurasinski et al., 2009; Koleff et al., 2003; Vellend, 2001), generating a growing confusion about the appropriate metric to use when measuring β-diversity. Recently, Anderson et al. (2011) provided a clear user-friendly guide in approaching β-diversity concepts and analyses. The most interesting aspect raised by the authors concerns the distinction between directional and non-directional changes in β-diversity (as originally conceived by Vellend, 2001). The former are those occurring among communities along a gradient. Gradients imply the existence of a direction of change and, in this case, β-diversity expresses the extent of change in community composition (i.e. *turnover*) at varying position along the gradient. Non-directional variations, instead, are those occurring in community composition among a set of sample units within a given spatial, temporal, or environmental

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extent. In this last case, variations do not have any direction, and β-diversity represents a measure of heterogeneity in assemblage structure.

Both types of changes are aligned with β-diversity concepts originally made by Whittaker (1960, 1972), representing complementary views of changes in species composition between two or more communities. While β-diversity as *turnover* measures the extent of change in species composition *between* two communities, β-diversity as *variation* measures the heterogeneity in species composition *within* communities. Thus, the measurement of species turnover generally leads to a single value (Izsak and Price, 2001) that could be, at the best, modelled against corresponding changes in continuous variables generating the environmental gradient of interest (Anderson et al., 2011). In contrast, the measurement of β-diversity as variation enables to obtain multiple values that allow to formally test for differences among groups of assemblages, either using classical statistical analyses or recently developed tests for multivariate dispersion (Anderson, 2006).

β-Diversity as variation could provide further insights into β-diversity patterns and processes driving species distribution and community structure, since the effect of environmental and/or biological drivers of change could not significantly affect species turnover only, but also the heterogeneity in species composition. However, due to its relatively recent introduction (Anderson et al., 2011; Vellend, 2001), the application of the concept of variation in investigating β-diversity in marine communities is still largely uncharted (Terlizzi et al., 2009). Here, we explored the potential of classical and multivariate measures of β-diversity as variation in highlighting patterns of marine assemblage heterogeneity induced by a variety of environmental drivers, including natural gradients, spatial variability, habitat variability, and human impacts.

2. Methods

2.1. Study cases

Eight datasets from Mediterranean marine benthic assemblages were analyzed (see Appendix A in Supporting Information for details). Datasets involved different organisms and habitat types, and were representative of a range of environmental settings, providing a wide record of study cases to investigate the performances of different measures of β-diversity as variation (hereafter we referred to this type of β-diversity also as *assemblage heterogeneity*). Three of them regarded different sources of human impact, namely, an offshore platform on sandy-detritic bottoms at 20–40 m depth (OP), a sewage outfall on rocky reefs at about 5 m depth (SO), and general anthropogenic disturbance (i.e., urbanization, commercial harbouring, industrial pollution) on coralligenous formation (COR) (see Ballesteros, 2006 for a definition of the Mediterranean coralligenous habitat). In OP, soft bottom polychaete assemblages were sampled along a gradient of increasing distance (300 m, 1000 m, 3000 m) from a four-legs gas production platform located in the Ionian Sea, in five sites for each distance ($n = 3$) (Terlizzi et al., 2008). In this case, the aim was to determine if there were significant changes in the heterogeneity of assemblages at increasing distance from platform. In the SO study case, mollusc assemblages of rocky reefs in SW Apulia (SE Italy, N Ionian Sea) were sampled in three sites ($n = 9$) within one location impacted by sewage discharge, and two control locations (Terlizzi et al., 2005a). Here, interest lies in testing for significant differences in heterogeneity of assemblages between impact and control locations. Finally, the COR dataset, concerned polychaete assemblages of coralligenous concretions at 20–25 m depth (SE Italy, S Adriatic Sea), sampled in two sites ($n = 3$) within three locations, one of them close to an urban centre hosting a huge commercial harbour and several on-shore industrial facilities, and two control locations.

Other two study cases considered natural variability among spatial units. One of them, namely SB, investigated differences among crustacean assemblages from three areas of sandy bottom at 20–40 m depth (SW Italy, N Ionian Sea), 1–3 km apart, each sampled in five sites with $n = 3$ replicates. In this case, interest lies in investigating natural spatial pattern in assemblage heterogeneity among areas. The second one (HAB) referred to mollusc assemblages of two different habitats, namely coralligenous formations and *Posidonia oceanica* seagrass beds from SE Apulia (SE Italy, S Adriatic Sea). In each of the two habitats, assemblages were sampled in three replicates in two sites within three locations. In this case, the aim was to investigate differences in heterogeneity of assemblages between the two habitats.

The last three study cases focused on depth gradients. In one of them (NE), soft bottom nematode assemblages were sampled at three depths (10 m, 20 m, 50 m) ($n = 12$) along 100 km of coast in S Apulia (SE Italy, N Ionian and S Adriatic Sea; Sandulli et al., 2002). In the remaining two study cases, namely MRR and PRR respectively, mollusc and polychaete assemblages from rocky reefs in SE Apulia (SE Italy, S Adriatic Sea) were sampled at three depths (5 m, 15 m, 25 m) in three sites with $n = 3$ replicates (Giangrande et al., 2003; Terlizzi et al., 2003). In all these cases interest lies in investigating differences in heterogeneity of assemblages along a depth gradient.

2.2. Measures of β-diversity as variation

For all datasets, β-diversity as variation was analyzed using both classical and distance-based multivariate measures of β-diversity (Anderson et al., 2006, 2011). Among the classical indices, we employed $\beta_W = \gamma/\bar{\alpha}$ (Whittaker, 1960), and $\beta_{Add} = \gamma - \bar{\alpha}$ (Crist and Veech, 2006; Lande, 1996), which both focus on species identities alone. A further β-diversity measure based on the Shannon–Wiener diversity index, $\beta_{Shannon}$ (Jost, 2007), which accounts for species identities and relative abundances, was also used.

As far as distance-based multivariate dispersion estimate of β-diversity, we employed the average distance to the group centroid of sampling units in the space defined by a resemblance measure $\bar{d}_{cen}$ (see Anderson et al., 2006 for full details). We calculated $\bar{d}_{cen}$ using an array of resemblance measures to take into account distinct aspects of variation. The Sørensen similarity and the Jaccard dissimilarity were used to investigate change in assemblage heterogeneity from a strict compositional point of view. Both indices consider species identities only but, while Sørensen index focus on commonalities in species composition among sampling units, Jaccard dissimilarity considers also distinctive species. Two quantitative resemblance measures on untransformed data were used in order to check for differences in heterogeneity among assemblages taking into account the relative abundance of species. One of them, the Chi-square distance, was employed to give emphasis to rare species, whereas the Bray–Curtis similarity to consider mainly the contribution of most abundant species. Finally, taxonomic dissimilarity (Θ^+, Clarke et al., 2006) was used to account for differences in assemblage heterogeneity associated to taxonomic relatedness of species.

2.3. Statistical analyses

A distance-based permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001a) was carried out for each dataset, to test for differences in assemblage structure imputable to the investigated source of variability. Experimental designs for analyses are provided in Appendix A. For NE and HAB datasets, data were standardized prior to analyses since samples from different habitats (HAB) with varying depths (NE) were collected using