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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

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

Table 1
Summary of results of PERMANOVAs testing for differences in assemblage structure related to the investigated source of variability in each case of study (see text for further details). Only tests relevant to hypotheses were reported. Significant results are given in bold. Results of *post hoc* pair-wise comparisons were also provided when appropriate.

Dataset	Source of variability	Pseudo-*F*	*P*	Pair-wise test
OP	Distance	1.12	0.303	300 m = 1000 m = 3000 m
SO	Impact	4.24	**0.001**	–
SB	Area	1.50	**0.037**	–
COR	Impact	2.39	**0.027**	–
HAB	Habitat	8.73	**0.000**	–
NE	Depth	1.78	**0.005**	10 m = 20 m ≠ 50 m
MRR	Depth	4.73	**0.012**	5 m ≠ 15 m = 25 m
PRR	Depth	2.94	**0.030**	5 m ≠ 15 m = 25 m

Table 2
Summary of results of ANOVAs on sample species richness (S), Pielou's evenness (J'), Simpson's diversity ($1 - \lambda'$), and taxonomic diversity (Δ) for each dataset. Only tests relevant to hypotheses were reported. Significant results are given in bold.

Dataset	Source of variability	S		J'		$1 - \lambda'$		Δ	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
OP	Distance	0.16	0.852	2.75	0.104	0.39	0.684	0.43	0.660
SO	Impact	0.05	0.832	10.91	**0.016**	5.13	0.064	7.81	**0.031**
SB	Area	0.05	0.950	0.03	0.967	0.00	0.998	0.18	0.837
COR	Impact	6.36	**0.027**	0.08	0.799	0.41	0.536	0.34	0.569
HAB	Habitat	5.59	0.077	39.64	**0.003**	3.27	0.145	21.36	**0.010**
NE	Depth	0.93	0.403	2.20	0.127	1.89	0.167	2.72	0.081
MRR	Depth	0.26	0.821	1.61	0.292	1.16	0.393	1.75	0.285
PRR	Depth	2.03	0.248	1.07	0.469	3.11	0.149	0.01	0.969

different sampling methods (see Appendix A for further details). All analyses were based on Bray–Curtis similarity on untransformed data, and each term in the analysis was tested by 4999 random permutations of appropriate units (Anderson, 2001b; Anderson and ter Braak, 2003). *Post hoc* pair-wise comparisons using PERMANOVA *t* statistic and 999 permutations were conducted when necessary.

For all datasets, ANOVAs on species richness (S), Pielou's evenness (J'), Simpson's diversity ($1 - \lambda'$), and taxonomic diversity (Δ, Warwick and Clarke, 1995) were also carried out, with the same design used for multivariate analyses, to test for effects of the investigated sources of variability on patterns of α-diversity.

Tests for differences in β-diversity as variation were conducted for all datasets using both classical and distance-based multivariate dispersion measures. In the first case, values of the three indices (i.e., β_W, β_{Add}, and $\beta_{Shannon}$) were calculated for each sample, and classical ANOVAs were conducted to test for differences in mean values. Prior to analyses the homogeneity of variance were tested by Cochran *C* test (Winer et al., 1991). *Post hoc* pair-wise comparisons among means were done through SNK tests when necessary.

As far as dispersion, for each species × sample dataset, we obtained different sample × sample resemblance matrices using the aforementioned set of resemblance measures (see above). Then, permutational tests of multivariate dispersion (PERMDISP, Anderson, 2006) based on such resemblance matrices were carried out for terms of interest, to test for differences in $\bar{d}_{cen}$ related to the

investigated sources of variability. *Post hoc* pair-wise comparisons were performed when necessary. Patterns of sample dispersion were visualized through an n-MDS ordination of replicates. When significant differences in multivariate dispersion emerged with more than one resemblance measure, ordination of data was provided only for the resemblance measure showing the highest statistically significant result in the PERMDISP analysis, as an example. Due to the high number of points in ordinations, 3d-plots were used to decrease stress values, providing a better representation of multivariate patterns (Clarke and Gorley, 2006).

3. Results

For the offshore platform study case (OP), multivariate analysis did not show significant differences in assemblage structure at increasing distance from platform (Table 1), indicating no impact of platform on surrounding polychaete assemblages. Also, ANOVA did not detect significant effects of factor Distance on any of the diversity indices employed (Table 2), showing no effects of platform in modifying patterns of α-diversity (Fig. 1). In contrast, univariate (Table 3) and multivariate measures (Table 4) of β-diversity as variation showed a significant decrease of assemblage heterogeneity at the nearest distances (generally at 300 m, and in one case also at 1000 m) than further away from platform (see Table 5 for values).

Table 3
Summary of results of ANOVAs on β-diversity as variation calculated using classical measures (see text for details). Only tests relevant to hypotheses were reported. Significant results are given in bold. Results of *post hoc* pair-wise comparisons were also provided when appropriate. Distances or depths in pair-wise comparison section are expressed in meters.

Dataset	Source of variability	β_W			β_{Add}			$\beta_{Shannon}$		
		F	*P*	Pair-wise test	*F*	*P*	Pair-wise test	*F*	*P*	Pair-wise test
OP	Distance	0.87	0.504	300 = 1000 = 3000	9.97	**0.001**	300 < 1000 = 3000	2.74	**0.029**	300 = 1000 < 3000
SO	Impact	1.98	0.156	–	4.08	**0.044**		40.76	**0.000**	–
SB	Area	1.41	0.264	–	14.78	**0.000**	–	0.22	0.806	–
COR	Impact	0.11	0.741	–	2.52	0.357	–	38.56	0.101	–
HAB	Habitat	4.07	**0.046**	–	13.40	**0.001**	–	16.11	**0.000**	–
NE	Depth	1.62	0.216	10 = 20 = 50	1.70	0.207	10 = 20 = 50	1.33	0.292	10 = 20 = 50
MRR	Depth	3.14	**0.032**	15 > 5 = 25	16.70	**0.000**	15 > 25 > 5	1.40	0.268	5 = 15 = 25
PRR	Depth	0.84	0.446	5 = 15 = 25	4.78	**0.016**	5 = 15 > 25	0.89	0.421	5 = 15 = 25
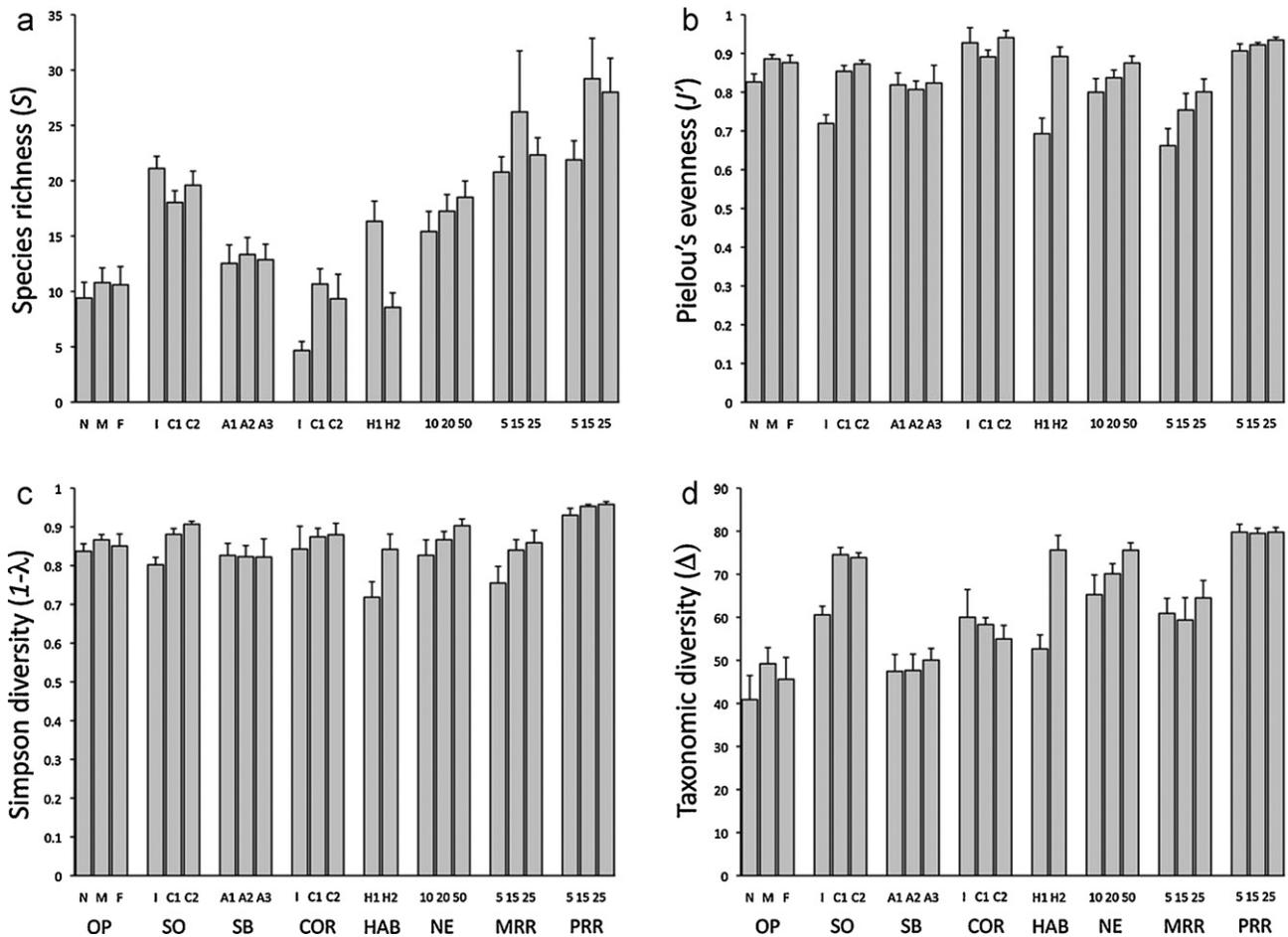
Fig. 1. Mean (±SE) values of (a) species richness (*S*), (b) Pielou's evenness (*J'*), (c) Simpson's diversity (1 − λ'), and taxonomic diversity (Δ) for each study case. For OP, *N* = 300 m, *M* = 1000 m, *F* = 3000 m. For SO and COR, I = impact location, C1, C2 = Control locations 1 and 2. For SB, A1, A2, and A3 indicate the three investigated areas. For HAB, H1 = *P. oceanica* beds, H2 = coralligenous formations. For NE, MRR, PRR, numbers indicate depths in meters.
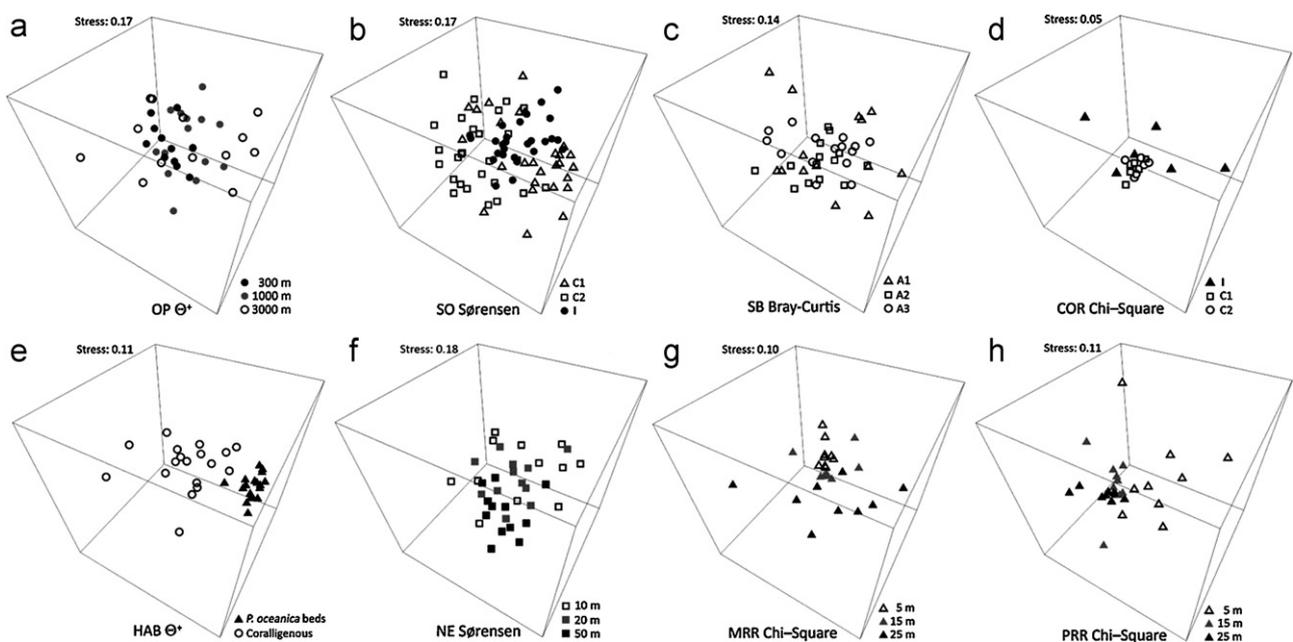
Fig. 2. 3-d nMDS ordination of sample centroids for each study case. (a) OP, offshore platform, three distances from platform; (b) SO, sewage outfall, discharge location (I) and two control locations (C1, C2); (c) SB, soft bottoms, three areas (A1, A2, A3); (d) COR, coralligenous formations, impacted location (I) and two control locations (C1, C2); (e) HAB, habitats, *P. oceanica* beds and coralligenous formations; (f) NE, nematodes, three depths; (g) MRR, mollusc on rocky reefs, three depths; (h) PRR, polychaetes on rocky reefs, three depths. Resemblance measures used are given in the graph, as well as symbols' legends.

Table 4
Summary of results of tests on multivariate dispersion (PERMDISP, see text for further details) based on different resemblance measures for each dataset. Results of *post hoc* pair-wise comparisons were also provided when appropriate. Depths in pair-wise comparison section are expressed in meters. For OP, $N = 300$ m, $M = 1000$ m, $F = 3000$ m.

Dataset	Source of variability	Sørensen		Jaccard		Bray–Curtis		Chi-square		Θ^+	
		F	Pair-wise test	F	Pair-wise test	F	Pair-wise test	F	Pair-wise test	F	Pair-wise test
OP	Distance	8.90**	$N < M = F$	11.14**	$N < M = F$	9.67**	$N < M = F$	3.42ns	$N = M = F$	9.21***	$N < M = F$
SO	Outfall	17.32***	–	17.44**	–	45.96***	–	60.66***	–	12.74**	–
SB	Area	2.21ns	–	2.25ns	–	7.26**	–	2.37ns	–	0.50ns	–
COR	Impact	4.65ns	–	2.55ns	–	12.65**	–	42.80**	–	9.56**	–
HAB	Habitat	5.51*	–	5.80*	–	2.16ns	–	83.33***	–	16.07***	–
NE	Depth	4.01*	$10 = 20 > 50$	4.01*	$10 = 20 > 50$	3.68*	$10 = 20 > 50$	2.57ns	$10 = 20 = 50$	3.35ns	$10 = 20 = 50$
MRR	Depth	3.71*	$5 < 15 = 25$	4.19*	$5 < 15 = 25$	1.10ns	$5 < 15 = 25$	11.94**	$5 = 15 < 25$	1.43ns	$5 = 15 = 25$
PRR	Depth	1.14ns	$5 = 15 = 25$	1.20ns	$5 = 15 = 25$	1.67ns	$5 = 15 = 25$	10.31**	$5 > 15 = 25$	0.56ns	$5 = 15 = 25$

ns, not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Differences in patterns of multivariate dispersion of sample among distances were clearly depicted in the n-MDS ordination (Fig. 2a).

PERMANOVA detected significant differences between the putatively impacted location and controls (*I*-v-*Cs*) in the SO study case, showing a significant effect of sewage discharge on the structure of mollusc assemblages (Table 1). ANOVA also showed significant differences on J' and Δ, indicating reduced evenness and taxonomic diversity at the outfall location (Table 2 and Fig. 1b,c). All β-diversity measures, except β_W, showed significant differences in *I*-v-*Cs* (Tables 3 and 4), demonstrating a significant effect of sewage discharge in modifying patterns of β-diversity at the impacted location, which generally showed lower heterogeneity with respect to control locations (Table 5 and Fig. 2b).

In the SB study case, multivariate analysis showed significant differences in the structure of crustacean assemblage among areas (Table 1), which, instead, showed comparable α-diversity (Table 2 and Fig. 1). Significant differences in β-diversity as variation emerged only when analyzing β_{Add} (Table 3) and $\bar{d}_{cen}$ using Bray–Curtis similarity (Table 4), showing that A1 was characterized by higher heterogeneity than the others two areas (Table 5 and Fig. 2c).

PERMANOVA showed significant differences in polychaete assemblage structure between the impacted location and controls for the COR dataset (Table 1). As far as α-diversity, ANOVA on diversity indices showed significant differences only for species richness (Table 2), which was lower in *I* than in *Cs* (Fig. 1a). Unlike ANOVAs on all classical measures of β-diversity as variation (Table 3), results of PERMDISPs using Bray–Curtis similarity, Chi-square distance, and taxonomic dissimilarity (Θ^+) showed significant differences in *I*-v-*Cs* (Table 4), indicating that changes in patterns of β-diversity were mostly driven by assemblage heterogeneity in relative abundance of species, especially of rare ones, and their taxonomic relatedness. Inspection of n-MDS plot (Fig. 2d) revealed a higher dispersion of samples in *I* with respect to *Cs*, which is consistent across resemblance measures (Table 5).

In HAB study case, PERMANOVA highlighted strong differences in mollusc assemblages between *P. oceanica* beds and coralligenous formations (Table 1). Mollusc assemblages of *P. oceanica* beds also showed significantly lower mean values of J' and Δ than those inhabiting coralligenous formations (Table 2 and Fig. 1b,c), indicating that the former habitat was characterized by lower evenness and more closely related species. Inspection of graph in Fig. 1a also showed a lower sample species richness, although not significant (Table 2), of coralligenous assemblages with respect to those from *P. oceanica*. All β-diversity measures, except $\bar{d}_{cen}$ based on Bray–Curtis similarity, showed significant differences between the two habitats (Tables 3 and 4), revealing a generally lower heterogeneity of mollusc assemblages of *P. oceanica* beds (Table 5 and Fig. 2e).

PERMANOVA on nematode assemblages along the depth gradient in the NE study case detected significant differences among depths (Table 1). Pair-wise comparisons showed that nematode assemblages at 50 m differed from those at the two shallower depths, which, in turn, were comparable (Table 1). None of the analyzed diversity indices showed significant differences in α-diversity among depths (Table 2 and Fig. 1). Similar results were obtained analyzing β-diversity using classical measures (Table 3). PERMDISPs based on Sørensen, Jaccard, and Bray–Curtis resemblance showed that multivariate dispersion of nematode assemblages was significantly lower at 50 m than at 20 m and 10 m (Table 5 and Fig. 2f), indicating a higher heterogeneity in species composition and abundance of shallower assemblages.

PERMANOVA on MRR dataset detected significant differences among depths, showing that mollusc assemblages at 5 m significantly differed from those at 15 m and 25 m, which, in turn, did not differ (Table 1). None of the investigated diversity indices showed significant differences imputable to the depth gradient (Table 2

Table 5
Mean values of classical β-diversity indices and multivariate dispersion based on different resemblance measures for each study case. Values of total species richness are also provided. For OP, $N = 300$ m, $M = 1000$ m, $F = 3000$ m. For SO and COR, I = impacted location, Cs = control locations.

	OP			SO		SB			COR		HAB		NE			MRR			PRR		
	N	M	F	I	Cs	A1	A2	A3	I	Cs	Pos	Cor	10 m	20 m	50 m	5 m	15 m	25 m	5 m	15 m	25 m
Classical β-diversity measures																					
β_W	3.3	4.5	5.0	5.2	5.8	4.1	3.0	3.4	4.9	3.6	6.8	11.9	6.6	5.4	5.0	2.7	4.6	3.1	3.1	3.1	2.6
β_{Add}	25.2	32.4	30.8	83.9	80.2	31.6	20.7	25.1	14.3	18.0	64.7	56.4	70.6	67.8	66.5	33.2	60.8	43.7	43.1	48.8	36.0
$\beta_{Shannon}$	2.5	2.6	3.9	1.4	2.8	2.4	2.1	1.8	3.7	2.1	1.4	4.6	3.9	3.9	3.0	1.3	1.2	3.0	2.4	2.2	1.9
Multivariate dispersion ($\bar{d}_{cen}$)																					
Sørensen	27.5	36.4	45.1	38.5	44.4	41.8	33.1	35.5	51.0	41.1	44.2	49.7	53.5	50.4	45.6	28.4	34.2	33.3	34.3	34.1	30.7
Jaccard	38.6	46.9	53.5	49.2	53.9	50.9	43.8	46.0	56.0	50.8	53.4	57.3	59.4	57.5	54.1	39.6	44.8	44.1	44.9	44.7	41.7
Bray–Curtis	35.7	44.6	52.8	38.0	50.1	52.4	40.3	47.2	56.0	43.5	46.2	50.3	56.4	55.5	50.1	36.5	42.6	39.8	43.0	39.7	37.8
Chi-square	1.4	1.9	2.0	1.4	2.6	2.0	1.4	1.6	3.1	1.5	1.7	5.0	2.7	2.5	2.3	1.1	1.1	2.0	1.8	1.3	1.2
Θ^+	13.9	18.4	22.0	21.2	25.3	16.2	14.1	15.2	30.2	21.4	20.6	31.1	28.5	25.7	22.0	15.9	16.8	17.6	14.8	14.5	13.3
γ-Diversity	37	44	43	105	125	45	35	38	19	41	81	65	86	85	85	54	87	66	65	78	64

and Fig. 1), indicating no effect of depth in modifying patterns of α-diversity. Among classical β-diversity measures, only β_W and β_{Add} showed significant differences among assemblages at different depths although not compatible with a depth gradient (Table 3), with assemblages at 15 m exhibiting higher heterogeneity than those at 5 m and 25 m (Table 5). Among dispersion measures, only PERMDISPs based on Sørensen, Jaccard, and Chi-square resemblance showed a significant effect of depth on β-diversity (Table 4), indicating a general decrease in heterogeneity in species composition, and especially of rare species, at decreasing depth (Table 5 and Fig. 2g).

A significant effect of depth on assemblage structure was detected also for polychaete assemblages in PRR, which showed patterns of variation at increasing depth consistent with those occurring for mollusc assemblages in MRR (Table 1). No effects of depth in modifying patterns of α-diversity of polychaete assemblages were detected (Table 2 and Fig. 1). Significant differences in β-diversity as variation emerged only when analyzing β_{Add} (Table 3) and $\bar{d}_{cen}$ using Chi-square distance (Table 4), showing lower assemblage heterogeneity at shallower depths (Table 5 and Fig. 2h).

4. Discussion

Investigating β-diversity as variation can be relevant to many ecological issues, providing a comprehensive view of natural or human-driven changes in assemblage structure. Human impacts, for example, may induce changes in the multivariate structure of assemblages affecting mean, variance, or both (Terlizzi et al., 2005b), which, in turn, may determine differences in the average location of sampling units in the multivariate space defined by species variables and/or variation in the dispersion of sampling units around their average location (Anderson et al., 2006). Thus, when human impacts affect the spatial heterogeneity of assemblages rather than their average multivariate structure, as in the OP case of study, quantifying β-diversity as variation is crucial in detecting the effect of human disturbance, which may remain otherwise unnoticed. However, even though impacts are evident both on assemblage structure and α-diversity, as in SO case of study, exploring changes in β-diversity as variation could provide complementary information about more subtle effects of human disturbance, such as changes in small-scale patchiness.

Assemblages' homogenization as one of the general outcomes of human impacts (Balata et al., 2007a,b; Claudet and Fraschetti, 2010; Donohue et al., 2009), as confirmed by two impact study cases here reported (i.e. OP and SO). This consequence of human impacts was particularly evident for SO, where the lower heterogeneity in the impacted location, associated to lower evenness and taxonomic diversity, clearly highlighted a biotic homogenization (Olden and Rooney, 2006) likely driven by an increased frequency of few dominant closely related species as a result of sewage discharge. However, assemblage heterogeneity could also denote environmental degradation, especially if accompanied by reduced α- and γ-diversity. As an example, in the COR case of study, assemblages in the impacted location were characterized by significant higher heterogeneity in term of abundance of common species, rare species, and taxonomic relatedness of species than control locations. This changes in β-diversity as variation, coupled with lower total and sample diversity, could be a symptom of ongoing habitat degradation, as a consequence of the effects of multiple human stressors acting on coralligenous formations or the result of recovery from past disturbance events (Ballesteros, 2006). The ecological meaning of changes in β-diversity as variation is, therefore, strongly context-dependent. The magnitude, in terms of intensity, frequency, and duration, of disturbance, whatever natural or anthropogenic, is

likely to play a major role in determining community homogeneity, or heterogeneity, and the ensuing ecological consequences (Fraschetti et al., 2001; Levin and Paine, 1974; Watling and Norse, 1998). Measures of total and local diversity associated with multiple metrics of β-diversity as variation could be of great help in depicting human-driven patterns of assemblage heterogeneity/homogeneity, contributing to outline undesired outcomes of anthropogenic disturbance, such as biotic homogenization.

Factors other than disturbance, such as non-directional environmental and/or biological variability in space (e.g. differences in substrate complexity) and time (e.g. seasonality), or directional variations along natural gradients (e.g. changes in light penetration and hydrodynamic regime with depth), could also affect β-diversity as variation (e.g. Davidar et al., 2007; Ellingsen and Gray, 2002; Hewitt et al., 2005). Different areas, or habitats, or positions along a natural gradient, can exhibit different levels of assemblage heterogeneity, which could not be necessarily accompanied to differences in small-scale diversity, total species richness, or in the overall assemblages structure. In such cases, additional information on β-diversity as variation could provide potential explanations or suggest hypotheses to test about mechanisms involved in determining the observed patterns. Nematode assemblages in the NE case of study, for instance, showed almost equal γ-diversity at the three investigated depths, and comparable patterns of α-diversity at increasing depth, although, on average, assemblages at shallower depths were quite distinct from deepest ones. In this case, significantly higher heterogeneity of nematodes assemblages, in terms of species composition and relative abundance, at 10 m and 20 m with respect to those characterizing 50 m seems to indicate that the effects of local factors in influencing regional nematode diversity, such as variability in vegetation, food supply, organic enrichment, natural and human disturbance (Leduc and Probert, 2011; Mirto et al., 2002; Schratzberger et al., 2006; Urban-Malinga et al., 2006), are likely to be smoothened at the higher depth. Furthermore, substrates at 50 m in the region were characterized by a greater homogeneity in granulometry and silt content (De Leonardis et al., 2008), which likely influenced patterns of distribution of nematodes diversity (Schratzberger et al., 2007) reducing assemblage heterogeneity. Comparable total and sample diversity also characterized crustacean assemblages in different areas in the SB study case. Significant differences in β_{Add} and $\bar{d}_{cen}$ with Bray–Curtis similarity, suggested that changes in diversity among areas, in term of species richness and relative abundance, were mostly due to the β rather than to the α component of diversity. Such differences were likely to reflect changes in the heterogeneity of resource availability and substrate composition (e.g. Gallmetzer et al., 2005; Levin, 1994; MacNeil et al., 2001), since the three different areas were characterized by different levels of small-scale patchiness in the proportion of seagrass detritus, organogenic debris, and coarse sand contained in sediments (Authors' *personal observation*).

Spatial variability of habitat structure is one of the most important factors in generating and maintaining high assemblage heterogeneity (Hewitt et al., 2005; Veech and Crist, 2007; Matias et al., 2011), and, in heterogeneous environments, quantifying the relative contribution of β-diversity in determining the global diversity in a given area or region could provide valuable information particularly useful for conservation purposes (Crist et al., 2003; Nekola and White, 2002; Pressey et al., 1993). In this perspective, the heterogeneity in species distribution gains high relevance, being crucial in guiding the spatial displacement, size, and number of sites for conservation (Gering et al., 2003; Harborne et al., 2006; Thrush et al., 2010). Also, since differences between the regional species pool (γ-diversity) and local species richness (α-diversity) are representative of the ecological connectivity of the system (Chase and Ryberg, 2004; Hastings and Gavrilets, 1999; Mouquet

and Loreau, 2002; Thrush et al., 2010), the assessment of β-diversity as variation could help the establishment of effective networks of reserves promoting region-wide resilience of protected ecosystems (Fernandes et al., 2005; Steneck et al., 2009).

The major role of β-diversity in setting up suitable sites for conservation has also been pointed out when conservation units to target other than species, such as habitats, are used as surrogates of species diversity (Mumby, 2001; Ward et al., 1999). In the HAB example, we showed that assemblage heterogeneity could drastically vary between habitats, even in the same taxonomic group. In this case, the high topographic complexity of coralligenous concretions is probably at the basis of the observed higher heterogeneity of coralligenous mollusc assemblages (Ballesteros, 2006) with respect to those inhabiting sediments of *P. oceanica* beds. In the same habitat, moreover, different groups of organisms can exhibit completely opposite patterns of β-diversity along an environmental gradient, although showing similar pattern of variation in assemblage structure, as in the MRR and PRR study cases. Habitat-based protection initiatives, therefore, should take into account this variability among habitats and/or among taxa; moreover, they should consider that processes originating assemblage heterogeneity can vary for different organisms (McKnight et al., 2007).

In most of study cases here reported, significant variation in assemblage heterogeneity emerged examining the additive expression of β-diversity (β_{Add}) and dispersion around centroids of sampling units ($\bar{d}_{cen}$) using the Chi-square distance. Such findings reinforce the idea that distinct areas or habitat could participate differently in determining regional diversity (Prendergast et al., 1993), serving as diversity hotspots or coldspots, and stress the importance of rare species in structuring spatial patterns of biodiversity (Magurran, 2003) and, consequently, their relevance in environmental impact assessment and conservation planning (Cao et al., 1998; Margules and Usher, 1981). However, there are no preferable measures to use when analyzing β-diversity as variation. Multiple metrics are recommendable because of different effects of natural and human-driven processes on assemblage heterogeneity, but the choice of metric(s) should be dictated by its ecological meaning, which, in turn, should conform to the ecological hypotheses to test (Anderson et al., 2011). Our results suggest the potential of β-diversity as variation to unravel patterns of change in assemblages that could not be necessarily evident analyzing local diversity, or even the whole multivariate assemblage structure. It could be argued, however, that analyses on diversity indices might be biased by an high probability of type II error, due to the reduced sample size of some of the datasets. Therefore, any attempt to compare the performance among indices of α- and β-diversity could be misleading. Moreover, since all analyzed datasets involved single taxonomic groups, our results may apply to environmental assessments involving taxonomic indicators and generalization to whole assemblages still need further investigations. Above all, β-diversity as variation could provide complementary information crucial to the understanding the effects of natural and anthropogenic drivers of change.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2011.11.006.

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