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Multi-scale functional and taxonomic β -diversity of the macroinvertebrate communities in a Mediterranean coastal lagoon

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Abstract

Benthic macroinvertebrate communities form the basis of the intricate lagoonal food web. Understanding their functional and taxonomic response, from a β -diversity perspective, is essential to disclose underlying patterns with potential applicability in conservation and management actions. Within the central lagoon of Messolonghi, we studied the main environmental components structuring the macroinvertebrate community. We analyzed the β -taxonomic and β -functional diversity across the main habitats and seasons, over a year time frame. Our results outline habitat type and vegetation biomass as the major factors structuring the communities. We found environmental variability to have a positive correlation with functional β -diversity; however, no correlation was found with taxonomic β -diversity.

Across the seasons, an asynchronous response of the functional and taxonomic β -diversity was identified. The taxonomic composition displayed significant heterogeneity during the driest period and the functional composition during the rainy season. Across the habitats, the unvegetated ones presented higher taxonomic homogeneity and functional heterogeneity, contrary to the vegetated habitats that present higher taxonomic variability and functional homogeneity. Across the seasons and habitats, a pattern of functional redundancy and taxonomic replacement was identified. Moreover, high functional turnover versus low taxonomic turnover was documented in an anthropogenic organically enriched habitat

We conclude that habitats display independent functional and taxonomic seasonal patterns and, thus, different processes may contribute to their variability. The framework presented here highlights the importance of studying both β -diversity components framed in a multi-scale approach for a better understanding of ecological processes and variability patterns. These results are important for understanding macroinvertebrate community assembly processes and are valuable for conservation purposes.

Keywords: Beta diversity, Benthic macroinvertebrates, Functional diversity, Biological trait analysis, Habitats, Seasons, Coastal lagoon.

Introduction

Benthic macroinvertebrate communities respond to the natural variability of the environment and to the interference of human activities. The study of biological diversity is necessary as species richness cannot account in detail for the levels of community variation. The extent of change in community composition in relation to an environmental gradient or pattern of environments is defined as β -diversity (Whittaker, 1960, 1972). Beta diversity (β -diversity) is the effective number of distinct compositional units in the area of study, and indicates the degree of differentiation among biological communities (Tuomisto, 2010). Patterns of β -diversity are the consequence of multiple processes operating at different spatial and temporal scales. Understanding the variation in species composition provides a better view of the processes driving biodiversity (Tuomisto & Ruokolainen, 2006). Communities of different taxonomic compositions are likely to have different trait diversity. The extent to which diversity influences the functioning of an ecosystem depends on the traits and niches occupied by

species. Thus, the study of functional diversity composition may provide additional information other than what species richness or diversity can explain (Cadotte *et al.*, 2011). The combination of both functional and taxonomic diversity may contribute to a better understanding of the ecological processes governing both β -diversity patterns.

Variation in environmental conditions, habitat heterogeneity and the degree of isolation are the main processes allowing species with different functional and ecological requirements to occur across a set of sites, thus increasing β -diversity (Anderson *et al.*, 2011; Fitzpatrick *et al.*, 2013). Understanding the processes and their operative scale structuring the benthic communities is crucial for marine conservation and resource management (Hewitt *et al.*, 2005).

Coastal lagoon ecosystems are sheltered and shallow, transitional water bodies, where continental and coastal waters meet (Kjerfve, 1994). Mediterranean coastal lagoons differ from each other according to their size, salinity and tidal ranges, exposure, mixing characteristics and depth (Guelorget *et al.*, 1983). Due to their geomorphological conditions, these ecosystems are very sus-

ceptible to morphological changes throughout the year. Temporal and spatial variability occurs due to seasonal or stochastic process (Ghionis *et al.*, 2015). Thus, the study of various spatial and temporal scales is essential to understand the main principles of community variability.

Researchers studying Mediterranean coastal lagoons have identified several different drivers influencing the structure of macroinvertebrate communities. The degree of communication with the sea, temperature, salinity, sediment type, carbon content, habitat type and dystrophic events are the main factors determining the distribution and composition of benthic communities (Reizopoulou & Nicolaidou, 2004; Galuppo *et al.*, 2007; Vignes *et al.*, 2010; Basset *et al.*, 2013; Cladas *et al.*, 2016). Yet, studies that make comparisons across the main lagoonal habitat types, in an effort to account for the degree of variability of macroinvertebrate communities from a β -diversity perspective, are rare. Since different habitats present different spatial, structural and physicochemical components, related with the level of nutrients and sediment type, it is likely that ecological patterns and processes will differ. Additionally, if a particular habitat regulates the variability of the macroinvertebrate community, we might also expect some type of functional traits organization and variability at this level.

Little is known about how those two ecological components (functional and taxonomic diversity) perform whilst framed in a β -diversity perspective. Thus, in this study we aim to identify how functional and taxonomic β -diversity respond to environmental variables and habitat type, both spatially and temporally. We hypothesized that both components may respond similarly if framed in the same spatial and temporal scale. Also, we predicted that both taxonomic and functional β -diversity respond similarly to environmental heterogeneity. We hypothesized that the findings of this work may assist managers of Mediterranean lagoonal ecosystems to implement targeted habitat protection plans.

Methods

Study area

The lagoon system of Messolonghi is located on the Greek Ionian coast, on the northern side of the Patraikos Gulf, between the Acheloos and Evinos rivers. It is the largest lagoon complex in Greece, covering approximately 15,000 ha and consisting of 6 different basins. The lagoonal complex, part of the National Park of Messolonghi, is also a Marine Protected Area, a Ramsar Site, an Important Bird Area (IBA), and part of the Natura 2000 network. The region is characterized by a typical Mediterranean climate. During 2013, the sampling year, annual precipitation was 1016 mm, of which the 73% (741.6 mm) were registered in 3 months (January, February and November). Mean annual temperature was 18.4°C, fluctuating between the mean monthly minimum

of 10.3°C in January, and the mean monthly maximum, 28.5°C in August (<http://www.meteo.gr>).

This study was carried out in the main lagoon of Messolonghi, which is an open lagoon communicating with the sea through a shallow and wide frontal area. Throughout the year, the lagoon presents a range of salinity and temperature values, as a result of its shallowness (mean depth about 1 m). Climatic factors such as rainfall and wind rapidly affect the temporal variations of the abiotic parameters of the water masses (Gianni *et al.*, 2011). Depending on the presence or absence of vegetation, we can distinguish vegetated habitats, characterized by the dominant vegetation (*Cymodocea nodosa*, *Rytiphlaea tinctoria* and *Valonia aegagropila*) and unvegetated habitats. In order to assess the β -diversity of the lagoon, sampling stations were selected in a way as to represent all habitats: *Cymodocea nodosa* in a marine environment (M1), *Valonia aegagropila* (M3), *Rytiphlaea tinctoria* and *Cymodocea nodosa* (M5), *Rytiphlaea tinctoria* (M6), and unvegetated (M4, M7 and M8) (Fig. 1). The M8 unvegetated site is located next to a sewage treatment plant outflow.

Data collection

Data was collected four times during 2013 (January, April, July and November). For the analysis of benthic macroinvertebrates, sediment samples (3 replicates) were collected with a box corer (0.023m² surface area) at each sampling site throughout the main benthic habitats. The samples were sieved through a 0.5 mm mesh sieve and stored in a 4% formalin solution with Rose Bengal. At the laboratory, the collected organisms were sorted, identified to the lowest possible taxonomic level (typically species level) and counted. Their maximal length was measured under the stereoscope using a stage micrometer. An additional sediment sample was collected at each site, the uppermost 2 cm of which were kept for granulometry and total carbon analysis. For the granulometric analysis, the samples were originally separated to coarse grained (N63 μ m) and fine grained (b63 μ m) fractions by wet sieving. Further classification of the sand and mud fractions was accomplished with standard sieves and a Sedigraph 5100 grain size analyzer. Total carbon was measured using an elemental (CHN) analyzer following the methodology of Verardo *et al.* (1990). At each sampling site, salinity, temperature, pH and dissolved oxygen were monitored close to the bottom using a multi-probe meter (YSI 600QS).

Analysis of biological traits

We selected seven traits (19 states), which are associated with biological adaptations to habitats and to physicochemical conditions and that describe the functional composition of the benthic macroinvertebrate communities. These are: mobility, position in the sediment or water column, trophic mode, exoskeleton mate-

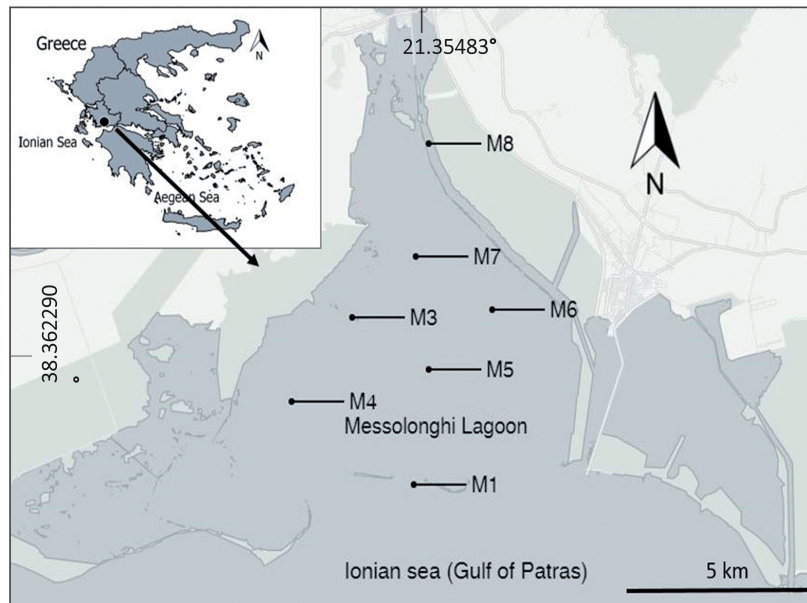


Fig. 1: Lagoon of Messolonghi (Greece). Seven sampling sites across the main lagoon covering the main habitats, sampled 4 times in 2013.

rial, development mode, reproduction mode, and average body size (Table 1). The traits for each taxon, except for body length, were derived from literature sources, such as publications (Pearson & Rosenberg, 1978; Fauchald & Jumars, 1979) and databases such as <http://polytraits.lifewatchgreece.eu>. Body length was obtained directly by measuring each organism. Individual taxa were coded according to the extent to which they display each category using a fuzzy-coding procedure (Chevenet *et al.*, 1994), which allows assessment of the affinity of a taxon

to multiple categories, using discrete scores from 0 (no affinity) to 3 (total affinity). Trait category scores for each taxon present at a station were weighted (multiplied) by their abundance at that station. These abundance-weighted trait category scores were then summed over all taxa presenting that code at the station, to provide a measure of the frequency of occurrence of trait categories over the whole assemblage (Charvet *et al.*, 2000). This weighting procedure was repeated for each station in the dataset, thus producing a station-by-trait table. This matrix was

Table 1. Main selected traits and corresponding states for the functional composition calculation by means of biological traits analysis (BTA).

Traits	States
Mobility. Describes the general locomotion of the organisms	Sessile/tube building Semi-mobile/Crawling Mobile/free swimming
Water column/sediment position. Describes whether the organism spends most of its time at the bottom or in the water column or amongst the vegetation.	Epifauna Surface Subsurface
Trophic mode. General description of the method through which resources are acquired.	Suspension feeder Deposit feeder Predator Scavenger Grazer
Exoskeleton material. The primary material in the exoskeleton matrix.	Calcium Chitin
Reproduction mode. Describes the state of having just one of at least two distinct sexes in any one individual organism.	Gonochoastic Hermaphrodite
Development mode. Describes whether offspring have or do not have a larval form and the type of form.	No Planktotrophic Lecitotrophic
Average body length	Body length (mm)

subjected to multivariate analysis. Biological Trait Analysis (BTA) uses multivariate ordination to describe patterns of functional composition over entire assemblages. Several ordination tools are available for this purpose. The choice of analytical tool is a balance between the capabilities of the tool to describe changes in trait composition and the ease with which results can be interpreted (Bremner *et al.*, 2006).

Data analysis

All the multivariate analyses were carried out using the PRIMER V6 (Clarke & Gorley, 2006) packages with PERMANOVA+ (Anderson *et al.*, 2008).

Initially, we performed non-metric Multidimensional Scaling (nMDS), using the Bray-Curtis similarity measure, to visualize the relative dispersion of sample units in relation to site, habitat and season. The ordinations of both macroinvertebrate abundance and functional diversity were based on the whole set of samples.

To test the relationship between a set of environmental variables (sand content, total carbon in sediment, temperature, salinity and dissolved oxygen in the water column, and weight of vegetation) with both taxonomic and functional composition, we performed the distance-based linear model (DISTLM), (McArdle & Anderson, 2001). The skewness of the environmental variables was checked by means of draftsman plots and the data was square root transformed accordingly. An Information Criterion routine (AIC) was used as a selection criterion, and the contribution of each independent variable was described by the amount of explained variation.

Differences in taxonomic and functional composition was tested using permutational multivariate analysis of variance, PERMANOVA (Anderson, 2001). We analyzed the differences in taxonomic and functional composition across all 7 sampling sites, and between any distinct cluster identified by the MDS: Unvegetated (*Unv*), Vegetated (*Veg*), Unvegetated-Sewage (*UnvSw*) and Vegetated-Marine (*Mar*). We estimated and compared the sizes of each component of variation, which correspond to the different spatial scales.

In analyzing the differences in β -diversity, we considered the definition given by Anderson *et al.* (2006), which explains β -diversity as the variability in species and trait composition among sample units at a given scale. The scales used were both spatial (distinct habitats identified by the MDS plot), and temporal (month).

By means of the Jaccard compositional similarity index (based on presence or absence) and the PERMDISP routine, for testing the homogeneity of multivariate dispersion (Euclidean distances), we tested for differences in functional and taxonomic β -diversity among the studied habitats (see above) at three levels.

- First level (spatial): β -diversity of each habitat for a given season (explains the spatial variability of the samples within a given habitat).

- Second level (temporal): β -diversity of each habitat across the 4 seasons (explains the temporal variability of a given habitat over all four sampling periods)

- Third level (spatial-temporal): β -diversity of a given habitat with reference to the other habitats over all four seasons.

In order to test the correlation between environmental variability and β -diversity variability, we tested the null hypothesis of homogeneity in the multivariate dispersions among the habitats in terms of the environmental variables. The test is based on Euclidean distances to the centroids for normalized data by means of the PERMDISP routine. We also tested the null hypothesis of homogeneity in the multivariate dispersions among the sites using the Jaccard dissimilarity measure for the taxonomic and functional diversity matrices. We then related by linear regression the distances to the centroids of environmental variables to the biological measurements.

The contribution of each species to the habitats was investigated using SIMPER analysis for both the taxonomic and functional composition (Clarke & Warwick, 1994).

Results

Environmental variables

The DISTLM marginal test for the studied variables showed no statistical significance for temperature ($P=0.056$) in the taxonomic composition and temperature and salinity ($P=0.125$ and $P=0.058$ respectively) for the functional composition. The non-significant variables were then excluded from the final model to determine the best predictor variables. The DISTLM models significantly explained 35% of macroinvertebrate composition and 50% of functional composition, (Table 2). The macroinvertebrate community is explained by Total Carbon>Sand content>Vegetation biomass>Salinity>Dissolved Oxygen and the biological traits by Vegetation biomass>Sand content>Total Carbon (Table 3).

Table 2. Best DISTLM fitting models for the studied environmental variables, and taxonomic and functional composition. AIC: Log-likelihood associated with the model; R^2 : coefficient of determination; RSS: residual sum of squared deviation; # Variables: Number of variables. Salinity (S), Dissolved Oxygen (DO), Sand content (S %), Total Carbon (TC), Vegetation biomass (VB).

BEST fitting model	AIC	R^2	RSS	# Variables	Variables
Taxonomic composition	655.13	0.345	177570	5	S, DO, S%, TC, VB
Functional composition	501.14	0.498	29780	3	S%, TC, VB

Benthic macroinvertebrate communities

In total, 24046 macroinvertebrate individuals, belonging to 194 taxonomic groups (94% to Spp. level), were identified in this study. Annelida, mainly Polychaeta were the most diverse group followed by Crustacea and Mollusca. The structure of taxonomic composition varied amongst habitats.

The MDS analysis used for the visualization of taxonomic composition suggests a fair separation amongst the different habitat groups (Fig. 2 A). A neat separation in the lower part of the plot occurs between M8 (*Unvegetated Sewage*) and M1 (*Marine*) and at the top of the plot between M7 and M4 (*Unvegetated*) and M3, M5 and M6 (*Vegetated*). Additionally, a clear separation of unvegetated locations in the left part of the plot occurs versus the vegetated ones on the right. The effect of season added little differentiation to the two-dimensional representations.

The MDS visualization for the functional composition is less differentiated than the taxonomic composition. The maximum distinction occurs along one dimension and runs from left, with the unvegetated group (M7 and M4), to right with the vegetated group (M3, M5 and M6). In between and overlapping with both groups, lies

the marine station (M1) and the unvegetated area next to the sewage outflow (M8).

The taxonomic composition similarities test, sites across seasons (PERMANOVA, Table 4), and habitats across seasons (PERMANOVA, Table 5), presented significant dissimilarities for each factor. The components of variation determined by the PERMANOVA routine show that the greatest variation occurs at habitat level, followed by season and site. Thus, the lowest component of variation occurred at replicate level (Table S1).

The functional composition similarities test, sites across seasons (PERMANOVA, Table 6) and habitats across seasons (PERMANOVA, Table 7), presented significant dissimilarities for each of the studied factors. Regarding the components of variation determined by the PERMANOVA routine, the greatest variation occurs at habitat level, followed by sample level (Residual) and season, the variation of which is comparable in size to the interactions (Table S2).

Different biological traits, states and taxonomic groups dominated across the studied habitats. As regards the biological traits, SIMPER analysis revealed the average length of the organisms to hold the overall higher contribution to the habitats. The *Mar* habitat is dominated

Table 3. Set of studied variables that significantly contribute to the model ($p < 0.01$), to better explain taxonomic and biological composition. AIC: Log-likelihood associated with the model; SS: Sum of squares; Pseudo-F: F-ratio from a distance-based permutational MANOVA; Prop.Cont: percentage of variance explained. Salinity (S), Dissolved Oxygen (DO), Sand content (S %), Total Carbon (TC), Vegetation biomass (VB).

	Variable	AIC	SS	Pseudo-F	Prop. Cont.
Taxonomic composition	S	677.74	15406	4.942	0.057
	DO	677.39	7029	2.2902	0.026
	S%	670.67	24517	8.7529	0.090
	TC	661.03	28997	11.742	0.107
	VB	655.13	17516	7.6943	0.065
Functional composition	S %	542.46	8229.5	13.213	0.139
	TC	530.15	7997.7	15.039	0.135
	VB	501.14	13295	35.717	0.225

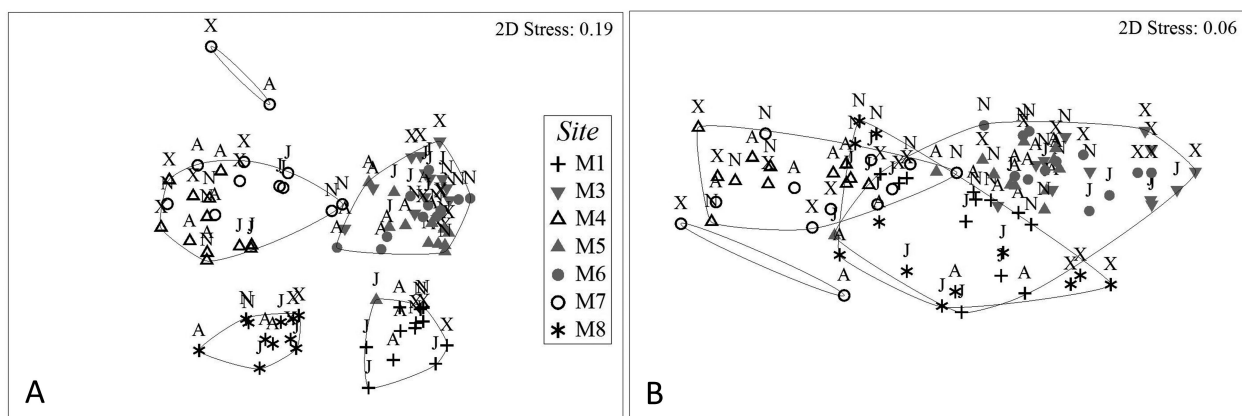


Fig. 2: (A) MDS scaling for taxonomic composition. (B) MDS scaling for functional diversity composition. MDS integrates the four seasons; January (J), April (A), July (X) and November (N). Grey symbols for vegetated sites and black symbols for unvegetated sites. Contour lines enclose samples with 20% Bray-Curtis similarity.

Table 4. PERMANOVA to test the hypothesis of no differences in taxonomic composition across sites and seasons, significantly statistical interactions are noted in bold. P: values passed on 9999 permutations. df: degrees of freedom; SS: sum of squares; MS: mean sum of squares; Pseudo-f: f value per permutation; P(perm): P value per permutation.

Source	df	S.S.	MS	Pseudo-f	P (perm)
Seasons	3	1.9642E7	6.5473E6	78.145	0.0001
Site	6	1.317E8	2.195E7	261.98	0.0001
Season*Site	18	1.3684E6	76022	0.907	0.4127
Residual	55	4.6081E6	83784		
Total	82	1.5834E8			

Table 5. PERMANOVA to test the hypothesis of no differences in taxonomic composition across habitats and seasons. P: values passed on 9999 permutations, significantly statistical interactions are noted in bold. df: degrees of freedom; SS: sum of squares; MS: mean sum of squares; Pseudo-f: f value per permutation; P(perm): P value per permutation.

Source	df	S.S.	MS	Pseudo-f	P(perm)
Seasons	3	1956000	4651900	11.145	0.0316
Habitat	3	8644300	41018000	14.695	0.009
Site(Habitat)	3	-2509900	2881400	34.391	0.0001
Season*Habitat	9	-2509900	-278880	-0.661	0.6619
Season*Site(Habitat)	9	3878300	430920	5.1432	0.0933
Residual	55	4608100	83784		
Total	82	158340000			

Table 6. PERMANOVA to test the hypothesis of no differences in functional diversity composition across sites and seasons. P: values passed on 9999 permutations, significantly statistical interactions are noted in bold. df: degrees of freedom; SS: sum of squares; MS: mean sum of squares; Pseudo-f: f value per permutation; P(perm): P value per permutation.

Source	df	SS	MS	Pseudo-f	P(perm)
Season	3	3089.1	1029.7	7.0929	0.0001
Site	6	36360	6059.9	41.743	0.0001
Season*Site	18	11724	651.33	4.4865	0.0001
Residual	55	8129.8	145.17		
Total	82	59302			

Table 7. PERMANOVA to test the hypothesis of no differences in functional composition across habitats, groups (from MDS) and seasons. P: values passed on 9999 permutations, significantly statistical interactions are noted in bold. df: degrees of freedom; SS: sum of squares; MS: mean sum of squares; Pseudo-f: f value per permutation; P(perm): P value per permutation.

Source	df	SS	MS	Pseudo-f	P(perm)
Season	3	2895.5	965.16	2.2177	0.0181
Habitat	3	33090	11030	10.12	0.004
Site(Habitat)	3	3269.9	1090	7.5079	0.0001
Season*Habitat	9	7807	867.44	1.9931	0.0348
Season*Site(Habitat)	9	3917	435.22	2.9979	0.0001
Residual	56	8129.8	145.17		
Total	83	59302			

by deposit feeders and semi-mobile organisms, the *Veg* habitat by sessile and suspension feeders and the *Unv* and *UnvSw* habitats by deposit feeders and subsurface organisms (Table S3).

As regards the contribution of the taxonomic groups, SIMPER analysis revealed differences across habitats. The *Mar* habitat is dominated by polychaetes from the

family Capitellidae, the *Veg* habitat by polychaetes *Janua pagenstecheri* and amphipods from the family Aoridae. The *Unv* habitat is dominated by the bivalve mollusc *Abra segmentum* and the polychaetes *Nephtys hombergii* and *Armandia cirrhosa*, and the *UnvSw* habitat by the polychaetes *Spio decoratus* and the bivalve mollusc *Abra segmentum* (Table S4).

Beta diversity

Habitat heterogeneity and β -diversity

We did not find support for the predicted taxonomic and functional β -diversity similar response to environmental heterogeneity. There were no statistically significant differences in environmental heterogeneity across seasons, as deviation to the centroid, among habitats for all 4 sampling periods (*PERMDISP*; F : 1.604, $P(\text{perm})$: 0.372). The correlation between environmental heterogeneity and taxonomic diversity was not significant (Fig. 3 A), while a weak but significant ($P < 0.05$) positive correlation was found with functional diversity, (Fig. 3 B), thus indicating that the habitats with higher environmental heterogeneity had higher functional variability.

Multiscale β -diversity

We did not find support for our hypothesis that both diversity components would respond similarly if framed in the same spatial and temporal scale. The variation of the β -diversity, as variance of the deviation to the centroid, of the functional and taxonomic composition differed across habitats and sampling period to different extents.

1st Level. Spatial variability of β -diversity within habitats during the same season.

Taxonomic β -diversity varied significantly in July (*PERMDISP*, F : 64.136, df_1 : 3, df_2 : 17, $P(\text{perm})$: 0.0001) and November (*PERMDISP*, F : 32.59, df_1 : 3, df_2 : 17, $P(\text{perm})$: 0.0002), but no significant β -diversity variation was found in January and April. Conversely, functional β -diversity varied significantly in January (*PERMDISP*, F : 7.3151, df_1 : 3, df_2 : 17, $P(\text{perm})$: 0.017), April (*PERMDISP*, F : 18.598, df_1 : 3, df_2 : 17, $P(\text{perm})$: 0.001) and November (*PERMDISP*, F : 10.106, df_1 : 3, df_2 : 17, $P(\text{perm})$: 0.043). No significant variation in functional β -diversity was found in July.

Taxonomic β -diversity was significantly higher in the *Unv* habitat while *Mar* and *UnvSw* held the lowest, with

no significant difference between them (Pairwise comparisons; July, $P(\text{perm})$: 0.101 and November, $P(\text{perm})$: 0.123), (Fig. 4).

Functional β -diversity was significantly higher in *UnvSw* in January and April and *Unv* in November (Fig. 5). The lowest functional β -diversity was found in the *Veg* habitat in January and November and in the *Mar* habitat in April. Pairwise comparisons indicate that the differences between maximum and minimum β -diversity are significant ($P < 0.05$)

2nd Level. Temporal variability of β -diversity within habitats.

Taxonomic β -diversity (distance to centroid) varied significantly across the four seasons within the *Veg* (*PERMDISP*, F : 5.0756, df_1 : 3, df_2 : 32, $P(\text{perm})$: 0.010) *Mar* (*PERMDISP*, F : 18.845, df_1 : 3, df_2 : 8, $P(\text{perm})$: 0.015), and *UnvSw* habitats (*PERMDISP*, F : 18.702, df_1 : 3, df_2 : 7, $P(\text{perm})$: 0.046). No significant variation was found for the taxonomic β -diversity of the *Unv* habitat. Additionally, the functional β -diversity did not present significant variation at this level.

Overall, significantly higher taxonomic β -diversity is recorded in April across the *Veg* and *UnvSw* habitat types and in July across the *Mar* habitat type (Fig. 6). The lowest taxonomic β -diversity was recorded in November for every habitat; nonetheless, no significant difference was found between November and July (P : 0.3421) in the *Veg* habitat and between November and January (P : 0.1002) in the *Mar* habitat (Fig. 6).

3rd Level. Spatial-temporal variability of β -diversity within habitats in 2013.

Taxonomic and functional β -diversity varied significantly across the habitats and sampling months (*PERMDISP*, F : 4.224, df_1 : 3, df_2 : 80, $P(\text{perm})$: 0.024) and (*PERMDISP*, F : 30.247, df_1 : 3, df_2 : 80, $P(\text{perm})$: 0.0001) respectively.

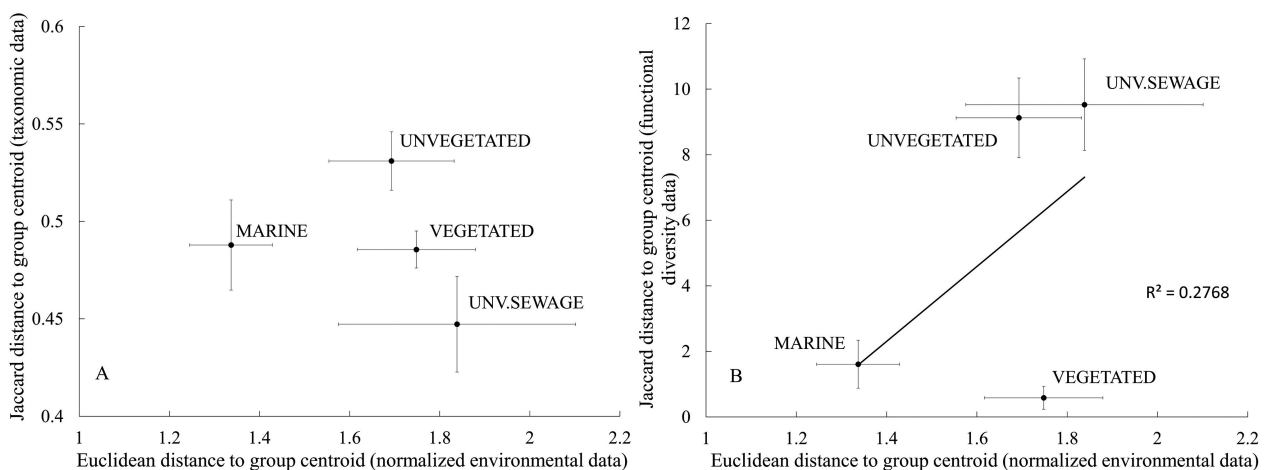


Fig. 3: Jaccard distance to group centroids on taxonomic (A) and functional (B) data vs. Euclidean distances to group centroids on normalized environmental data, for the studied habitats. Regression line for significant correlations ($P < 0.05$).

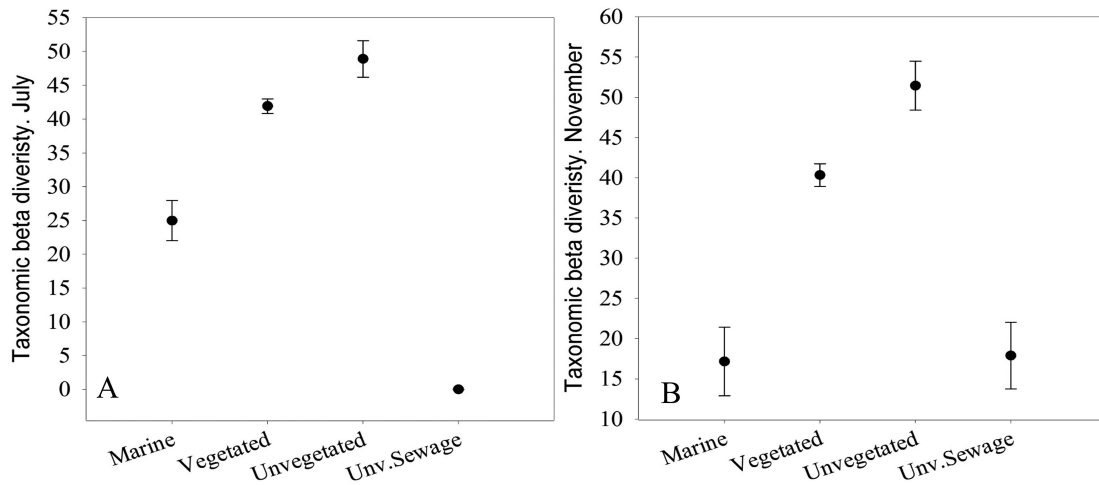


Fig. 4: β -diversity, as variation in the distribution of distance to the centroid, for each habitat in July (A) and November (B), explaining the spatial variability of the samples within a given habitat. July, $P < 0.05$ and November, $P < 0.001$.

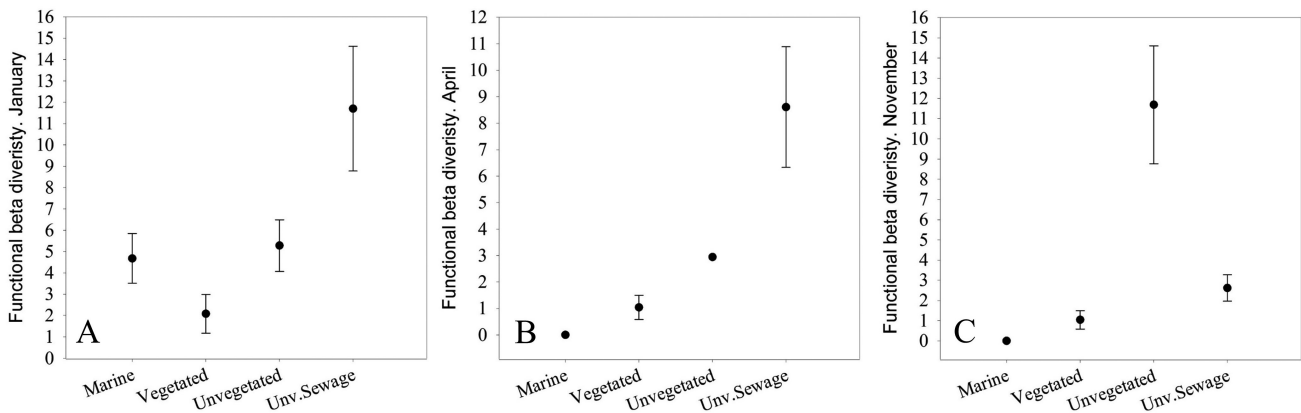


Fig. 5: β -diversity, as variation in the distribution of distance to the centroid, for each habitat within a given season (explains the spatial variability of the samples within a given habitat). January (A), November (B) and April (C). January and November, $P < 0.001$, and April $P < 0.05$.

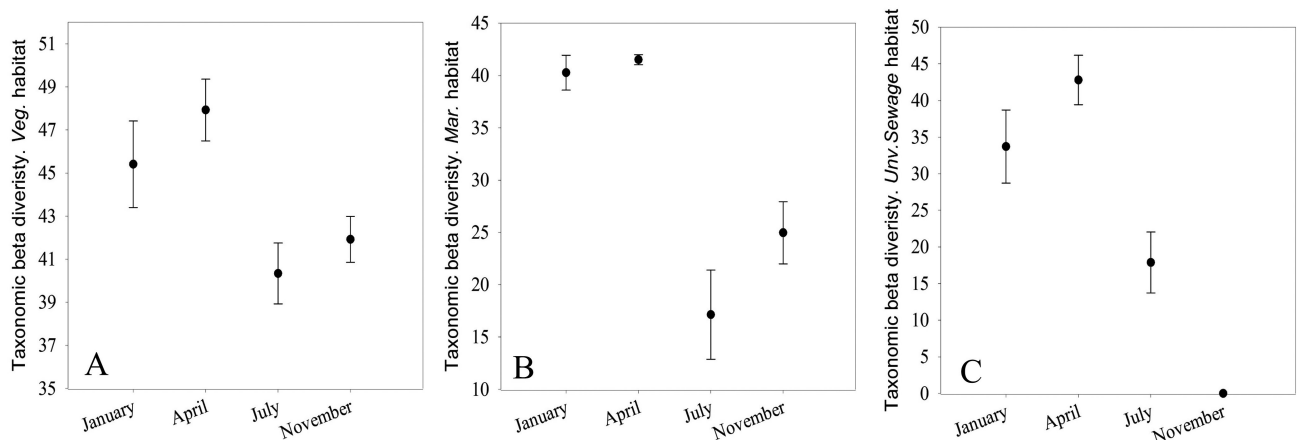


Fig. 6: β -diversity, as variation in the distribution of distance to the centroid, for a given habitat type among the 4 seasons (explains the internal variability of a given habitat over the four seasons). Vegetated (*Veg*) and Marine (*Mar*) habitat $P < 0.01$, Unvegetated Sewage (*Unv.Sewage*) $P < 0.001$. Vegetated habitat (A), Marine habitat (B) and Unvegetated Sewage habitat (C).

As regards taxonomic β -diversity, the lowest variation was observed in *UnvSw* and the highest in *Unv* (Fig. 7 A). The pairwise comparison did not reveal significant differences between *Veg* and *Mar* ($P: 0.930$).

As regards functional β -diversity, the lowest variation was observed in the *Veg* and the highest in *UnvSw* (Fig. 7 B). The pairwise comparison did not reveal significant differences in *Mar* vs *Veg* habitats ($P: 0.460$) and *Unv* vs *UnvSw*, ($P: 0.861$).

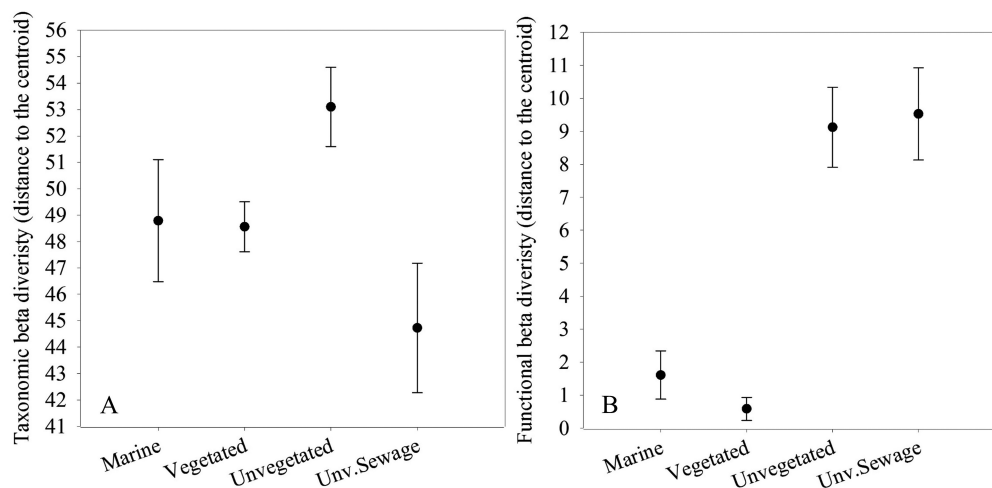


Fig. 7: Spatial and temporal variation of β -diversity. Variation in the distribution of distance to centroid among habitats in 2013. (A); taxonomic β -diversity and (B) functional β -diversity.

Discussion

Ecological requirements and stochastic processes are the main β -diversity drivers, and both act simultaneously to shape benthic communities (Chase & Leibold, 2003). Amongst the ecological requirements, habitat type is a key environmental filter for macroinvertebrate communities, determining both functional and taxonomic composition (Galuppo *et al.*, 2007; Verdonschot *et al.*, 2012; St Pierre & Kovalenko, 2014). Other environmental variables, such as salinity and temperature, have also been proved to structure macroinvertebrate, planktonic, and algal communities in transitional waters (Remane, 1934; Telesh & Khlebovich, 2010; Schubert *et al.*, 2011). Significant differences in the benthic composition across space and time may indicate different levels of variability with reference to ecological patterns and processes. A better understanding of β -biodiversity patterns will help in the design of effective conservation plans for Mediterranean coastal lagoons.

In this paper, we studied the benthic macroinvertebrate communities focusing, in particular, on identifying the degree of variation by means of both functional and taxonomic β -diversity across the main benthic habitats and seasons during 2013. Additionally, we studied the main environmental variables structuring the communities and the extent to which these factors and their variability contribute to drawing β -diversity patterns.

Benthic macroinvertebrate communities

Amongst the spatial and temporal factors (i.e. seasons, habitats and sites), habitat ranked as the highest component of variation for structuring both the functional and taxonomic composition in Messolonghi lagoon (Tables S1 and S2 and Fig. 2 A, B). Conversely, the lowest contribution to the structure of the community was

attributed to the season, also differentiated, but to a lesser degree, in the two-dimensional MDS.

Within each habitat, total carbon, vegetation biomass and sand content in sediment, contributed significantly to the structure of both taxonomic and functional diversity. The vegetation acting as an ecosystem engineer and habitat former (Jones *et al.*, 1997), plays a key role in structuring the functional (22.5%) and taxonomic (6.5%) composition in Messolonghi lagoon (Table 3). A similar response, i.e. lack of seasonality in benthic communities and a key role played by the vegetation biomass in structuring a benthic community, has also been described by Nicolaidou (2007) in a neighbouring Greek lagoon. Benthic vegetation slows down the currents, thus facilitating sedimentation of fine sediment and organic particles (Ginsburg & Lowenstam, 1958; de Boer, 2007). Besides, the presence of vegetation is related with the provision of food, habitat and refuge (Ferreiro *et al.*, 2014). The filtering capacity of vegetated habitats leads to increased species richness and more significantly to clustering of biological traits, as demonstrated by the functional redundancy. In vegetated habitats, the highest contribution was attributed to tube building, suspension feeders, deposit feeders and epifauna organisms. Conversely, the unvegetated habitats harbour larger sized individuals, deposit feeders, subsurface and surface organisms (Table S3). However, the length of the macroinvertebrates could possibly introduce bias, due to the different shapes and morphologies. The use of length per weight equations might increase accuracy but such data for Mediterranean lagoons are scarce in available literature (Rosati *et al.*, 2012).

Beta diversity

The combination of both spatial and temporal scales permitted us to identify patterns that are not observable at a single scale. Overall, our results suggest a set of dissimilar patterns at each studied level in relation to both func-

tional and taxonomic β -diversity. In general, major variability has been associated with taxonomic β -diversity, whereas functional β -diversity is more homogeneous.

Beta diversity and environmental heterogeneity

Higher environmental variation among sites within a region leads to an increased number of niches (Leibold *et al.*, 2004). The PERMDISP routine indicated that environmental heterogeneity predicted significantly (but moderately) functional β -diversity but did not explain taxonomic β -diversity (Fig. 3 A, B). A partially similar response, where environmental fluctuation induced variability in functional trait composition at local and regional scale, has been described by Dimitriadis *et al.* (2012). Here, higher functional β -diversity was associated with the unvegetated habitats, *Unv* and *UnvSw*, which are subject to high physicochemical changes across the four seasons (Fig. 7 B). Habitats with higher physicochemical variability and less refuge available, linked to the lack of vegetation, display higher variation in trait composition (Townsend *et al.*, 1997). Thus, environmental variation and habitat heterogeneity allow the occurrence of species with different ecological requirements, thus increasing functional β -diversity.

In this work, temporal variability is determined within a yearly term and covering the main seasons. Accordingly, our results need to be interpreted with caution. Increased sampling effort would help in gaining a better understanding of the intensity of variability and thus increased confidence to support the hypothesis that major environmental variability is associated with higher functional β -diversity.

1st Level

Functional and taxonomic β -diversity asynchronicity

We tested the relationship between functional and taxonomic β -diversity across different habitats in a given season. Our findings describe a general asynchronous pattern: while taxonomic β -diversity varies significantly, functional β -diversity remains homogeneous. Considering relatively short distances across the whole lagoon of Messolonghi, a similar functional and taxonomic β -diversity response was expected across habitats and seasons. Also, a relatively slight variation in species composition, due to a low dispersal constraint, was anticipated (Leibold *et al.*, 2004). Nonetheless, taxonomic composition displayed significant heterogeneity in July and November (Fig. 4) and functional heterogeneity in January, April and November (Fig. 5). Overall, during the rainy period (January and April), the homogeneity of taxonomic β -diversity is higher. This could be explained by a reduction in taxonomic groups linked to the major input of fresh water into the main lagoon (Cañedo-Argüelles & Rieradevall, 2010). On the contrary, greater taxonomic β -diversity was recorded during the dry period (July). Thus, across the main lagoon of Messolonghi, a low taxonomic and high functional vari-

ability were recorded during January and April. On the other hand, low functional and high taxonomic variability was recorded in July. In this respect, our study provides evidence of an asynchronous response of functional and taxonomic diversity to seasonal factors across Messolonghi. This kind of pattern has not been previously described for benthic macroinvertebrate communities. Spatial and temporal scales are inherently linked and, thus, exploring both patterns and processes in ecological studies provides the benefit of testing new ecology theories (White *et al.*, 2010).

At this level the unvegetated habitats, *UnvSw* and *Unv*, support a reduced number of species and are the most functionally heterogeneous. Thus, the variation in a restricted number of species may result in a high impact for the functional β -diversity (Lake, 2011). Thus, in habitats with high environmental heterogeneity and low species abundance, a change in environmental conditions can eliminate some species thus causing loss of unique traits (Schriever *et al.*, 2015). Similar results were also obtained by Faulwetter *et al.* (2015) by means of computer-simulated scenarios in a set of Mediterranean coastal lagoons.

2nd Level

Functional redundancy (functional stability vs taxonomic replacement)

None of the habitats presented significant variation in functional β -diversity at this level. Conversely, high taxonomic variability was identified. Therefore, we have to reject the hypothesis that both components, i.e. taxonomic and functional β -diversity might respond similarly if framed in the same spatial and temporal dimension. It is worth noting that taxonomic replacements do not always lead to variations in functional diversity and, consequently, in ecological functioning. The lack of significant variability in functional composition discloses a pattern of functional redundancy, profusely described for macroinvertebrate communities (Sigala *et al.*, 2012; Bogan *et al.*, 2013). Functional redundancy may be a result of environmental filtering, which restricts trait diversity (Heino, 2005) and is an indicator of relative resilience of the traits and may help in maintaining the functions of an ecosystem after disturbance (Schmera *et al.*, 2012). Thus, the loss or gain of taxonomic groups does not cause significant variability in functional diversity.

On the other hand, taxonomic β -diversity follows heterogeneous patterns across seasons and habitats. Across habitats, the *Unv* is the most taxonomically resilient throughout the year, while the vegetated habitats (*Veg* and *Mar*) presented significant taxonomic variability (Fig. 6). This pattern might be explained by a contribution of the vegetation to increasing structural complexity and heterogeneity, which triggers taxonomic richness (St Pierre & Kovalenko, 2014) and β -diversity (Astorga *et al.*, 2014). Besides, the dominant lagoonal vegetation un-

dergoes seasonal cycles of growth and decay, which may contribute to an increase in the availability of habitat and thus ecological niches (Leibold *et al.*, 2004).

3rd level

Year based resilience. High functional turnover vs low taxonomic turnover in the *UnvSw* habitat.

The decomposition of β -diversity within the entire study period gives a holistic perspective where annual patterns can be outlined, (Fig. 7 A, B). At this level, both functional and taxonomic β -diversity displayed dissimilar patterns. Functional β -diversity turnover (functional replacement during the sampling period) was lower in the *Mar* and *Veg* than in the *UnvSw* and *Unv* habitats. On the contrary, taxonomic β -diversity turnover presented the lowest value in the *UnvSw* habitat and the highest in the *Unv*.

The higher functional resilience in *Mar* and *Veg*, is explained by a gain or loss of species with low impact on functional β -diversity, (Fig. 7 B). Conversely, the higher functional turnover in the *Unv* and *UnvSw* habitats is explained by the existence of a reduced number of taxonomic groups, which enclose the whole set of functions of the given habitat. Consequently, the loss or gain of one taxonomic group can drastically modify functional diversity (O’Gorman *et al.*, 2010).

Over the studied period, the *UnvSw* habitat, adjacent to the Aitoliko sewage treatment plant outflow, displays the highest functional turnover and the lowest taxonomic turnover. The dominance of organisms, classified as tolerant in biotic indices such as the BENTIX index (Simboura & Zenetos, 2002), i.e. *Spio decoratus*, *Abraxsegmentun*, *Capitella capitata* and *Microdeotopus gryllotalpa*, form a very resilient community able to tolerate high levels of organic load. Due to the reduced number of taxonomic groups with these characteristics, the loss of a single species may have a high impact on functional β -diversity (Lake, 2011) (Table S4).

Thus, even though a homogeneous community across the year may indicate some degree of resilience, from a conservation perspective the weight of this community in lagoonal biodiversity is rather low. Thus, for conservation purposes, characteristics other than resilience need to be considered. The information retrieved shows that studying every habitat across the spatial and temporal scale is imperative for conservation purposes.

Conclusions

In the lagoon of Messolonghi, habitat type and vegetation biomass are the major elements contributing to the structure of both the functional and taxonomic composition of macroinvertebrate communities. Despite the anticipated similar response of functional and taxonomic β -diversity, this work determined different patterns. Functional and taxonomic β -diversity respond asynchronously, while dis-

similar variability was also identified across habitats at relatively short distances. We conclude that different processes may contribute to shaping the composition of a community. This study underlines the importance and complementarity of studying both taxonomic and functional diversity for gaining a better understanding of ecological processes. It highlights the importance of studying different spatial and temporal scales, which adds perspective when framing the variability of macroinvertebrate communities in naturally stressed ecosystems such as Mediterranean coastal lagoons. These results are important for understanding macroinvertebrate community assembly processes and are valuable for conservation purposes.

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