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VOJSAVA GJONI, STAMATIS GHINIS, MAURIZIO PINNA, LUCA MAZZOTTA, GABRIELE MARINI, MARIO CIOTTI, ILARIA ROSATI, FABIO VIGNES, SERENA ARIMA, ALBERTO BASSET

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Patterns of functional diversity of macroinvertebrates across three aquatic ecosystem types, NE Mediterranean

Vojsava GJONI[1], Stamatis GHINIS[2], Maurizio PINNA[1], Luca MAZZOTTA[1], Gabriele MARINI[1], Mario CIOTTI[1], Ilaria ROSATI[3], Fabio VIGNES[1], Serena ARIMA[4] and Alberto BASSET[1]

[1] Department of Biological and Environmental Sciences and Technologies, University of Salento, Via Monteroni, Ecotekne, 73100 Lecce, Italy
[2] Region of Ionian Islands, Theotokou Ioanni, 71, 49100 Corfu, Greece
[3] Institute of Research on Terrestrial Ecosystems, National Research Council (IRET-CNR), 00185 Rome, Italy
[4] Department of Methods and Models for Economics, Territory and Finance, University of Rome, Via Del Castro Laurenziano 9, 00161 Rome, Italy

Corresponding author: gjoni.vojsava@unisalento.it

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Abstract

This study investigates the variation patterns of the functional structure of macroinvertebrate guilds in relation to the taxonomic one, across aquatic ecosystem types and along the salinity gradient, from freshwater to marine, as well as the resulting implications for guild organization and energy flows. Synoptic sampling was carried out on Corfu Island (Greece) using the leaf-pack technique at 30 aquatic ecosystems, including freshwater, lagoon, and marine sites, and the following were analyzed: i. taxonomic composition and population abundance; ii. trophic guild composition and relative abundance; and iii. body size spectra and size patterns. The following variation patterns across the three ecosystem types were observed: a. the trophic guild composition and body size spectra were more conservative than the taxonomic composition within and among ecosystem types; trophic guild and size spectra composition were more similar between river and lagoon ecosystem types than with marine ones; b. dominance as regards resource exploitation of large species over smaller ones was inferred at all sites; and, c. higher body size-specific density of individuals was consistently observed in lagoon rather than freshwater and marine ecosystems. The results support previous findings suggesting a common hierarchical organization of benthic macroinvertebrate guilds in aquatic ecosystems and show that higher energy density is transferred to benthic macroinvertebrates in lagoon ecosystem types compared to both freshwater and marine ones.

Keywords: Body size density relationship; freshwater and transitional water ecosystems; functional groups; community structure and energy flow.

Introduction

Plant detritus, both autochthonous and allochthonous, is a main source of energy in inland and coastal marine ecosystems. Allochthonous inputs from terrestrial ecosystems account for up to 95% of all energy inputs in freshwater systems (Likens, 1975; Benfield, 1997; Webster & Mayer, 1997) with well-known spatial and temporal patterns (Cummins *et al*., 1989; Merritt *et al.,* 1996). It also represents an important source of energy in coastal transitional and marine ecosystems, through riverine inputs.

Benthic macroinvertebrates play a key functional role in detritus decomposition (Boling *et al*., 1975) and the transfer of the energy embedded in plant detritus to the higher levels of aquatic food webs (Power & Dietrich, 2002). This benthic macroinvertebrate role has been studied extensively in freshwater ecosystems (Petersen & Cummins, 1974; Wallace & Webster, 1996; Palmer *et al*., 1997; Covich *et al*., 1999; Covich *et al.,* 2004) and more recently in lagoon (Sangiorgio *et al*., 2008; Quintino *et al.,* 2009) and marine ecosystems (Dimech *et al*., 2006).

Benthic macroinvertebrates involved in detritus processing have been described using both taxonomic and functional approaches (Fauchald & Jumars, 1979; Koutsoubas *et al*., 2000; Luczkovich *et al.,* 2002; Cummins *et al.,* 2005; Casagranda *et al*., 2006; Faulwetter *et al.,* 2014; Merritt *et al.,* 2017), including morpho-functional ones (Reizopoulou & Nicolaidou, 2007; Basset *et al.,* 2008a), dealing with body size distributions and size density relationships (Gjoni *et al*., 2017). Different guilds, namely, shredders/scrapers, gathering collectors, suspension filter feeders and predators have different functional roles in the processing of plant detritus (Cummins, 1974; Cummins *et al.,* 2005; Merritt *et al.,* 2017) and different size classes have different resource requirements and impacts on plant detritus processing (Rossi, 1985). However, the relative importance of these structural components of macroinvertebrate guilds, that is, taxonomic, tropho-functional and morpho-functional, on guild organization and the transfer of energy from dead organic matter is still partially addressed (Wallace & Webster, 1996; Covich *et al*., 2004), particularly considering the full gradient of aquatic ecosystems, from freshwater to marine ones.

In fact, relatively little is known about the comparative variation patterns of taxonomic, functional and morpho-functional structure of macroinvertebrate guilds on inland, transitional and marine aquatic ecosystems, and on overall macroinvertebrate guild organization, despite the fact that: 1. patterns of variation of taxonomic composition and diversity across salinity gradients, have been widely described (e.g. Guélorget & Perthuisot, 1983; Quintino *et al*., 2009; Whitfield *et al.,* 2012) and 2. many studies have already investigated the potential influence of both abiotic and biotic factors on temporal and the spatial variability of functional diversity, i.e. the diversity and range of functional traits of the biotic component at the scale of interest (Wright *et al*., 2006), in freshwater (Covich *et al*., 1999; Mermillod-Blondin & Rosenberg, 2006), transitional (Marchini *et al*., 2008; Sigala *et al*., 2012) and marine (Emmerson *et al*., 2001; Raffaelli *et al*., 2003; Norling *et al*., 2007; Pacheco *et al*., 2010) ecosystems.

This study focuses on the variation of functional diversity components and size-based community organization of the macroinvertebrate guilds in the North-Eastern Mediterranean Sea aquatic ecosystems, and aims to: i. describe the taxonomic composition, the body size and abundance of trophic guilds, as well as body size spectra within and among river, lagoon and marine ecosystem types and ii. address the size and energy density patterns across river, lagoon and marine ecosystem types and, in particular, the transfer of energy density to benthic macroinvertebrate guilds, using a cross-community approach.

The cross-community approach used in the study is based on the metabolic theory principles and analysis of size-abundance relationships (Brown *et al*., 2004; Woodward *et al*., 2005; White *et al*., 2007) used recently as an ecological tool linking biodi, versity and ecosystem functioning (Gjoni *et al.,* 2017; Gjoni & Basset, 2018) in the Mediterranean and Black sea lagoon ecosystems. Therefore, the cross-community approach could perhaps contribute to the debate on the role played by benthic biodiversity in regulating aquatic ecosystem processes (Giller *et al*., 2004).

Transitional water ecosystems, as ecotones among freshwater, marine and terrestrial ecosystems (Basset *et al*., 2013), are functional sinks for plant allochthonous detritus from all three neighbouring ecosystem realms (Macko *et al*., 1993) and are considered to have higher detritus-based energy density and higher spatial and temporal heterogeneity than at least freshwater and marine ecosystems (Cummins *et al.*, 1989; Guélorget & Perthuisot, 1983; Reizopoulou & Nicolaidou, 2004), although no direct comparisons have been performed to date. The hydrological connections of lagoon ecosystems with their freshwater and marine input ecosystems are also pathways of species dispersal and introduction of potential detritus colonizers (Palmer *et al*., 1996; Giller *et al*., 2004).

Material and Methods

Study area

The field experiment was carried out in three ecosystem types, river, lagoon and marine, at Corfu Island (Greece), North-Eastern Mediterranean Sea (Fig. 1), covering a wide salinity range. The aquatic ecosystems of the Corfu Island, which were selected as study sites for this study, and the component freshwater, transitional and marine ecosystems, had received very little attention as research and monitoring sites so far. Abiotic and biotic data have been collected from these ecosystems only occasionally and mainly for specific purposes. Systematic research studies are almost completely lacking and published data, even in national/regional journals, are extremely limited or completely unavailable.

The freshwater ecosystems considered in this study were the Fonissa, Messonghi and Potamos rivers. River Fonissa flows in the north-western part of Corfu and is the longest river on the island. The river has a permanent

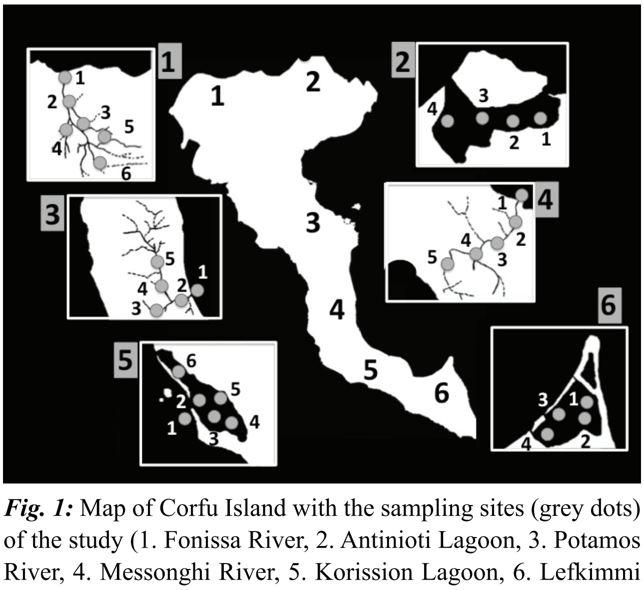

Fig. 1: Map of Corfu Island with the sampling sites (grey dots) of the study (1. Fonissa River, 2. Antinioti Lagoon, 3. Potamos River, 4. Messonghi River, 5. Korission Lagoon, 6. Lefkimmi Lagoon).

flow throughout the year but, due to the coastal dune system, the connection with the sea is narrow. River Messonghi is located in the south-eastern part of the island; it has an intermittent flow, with summer drought periods in the upstream tracts while the connection to the sea is permanently open and wide. River Potamos flows in the eastern part of the island; it has a permanent flow and a well-developed connection to the sea.

The lagoon ecosystems include Antinioti, Korission and Lefkimmi. Antinioti lagoon (2,0 km^2) is located in the north of the island. It is characterized by an inflow from a small stream and marine water exchange, due to the mouth connecting the lagoon to the sea; it is also characterized by a strong load of chemical pollutants, accumulating in the sediment (Botsou *et al*., 2015). Korission lagoon is located in the south-western part of the island and is included in the Natura 2000 network of protected areas (Diamantopoulou *et al*., 2008). Korission lagoon is characterized by limited freshwater input from a few small streams and limited exchange with marine water, due to the fact that it is a large lagoon (6.0 km^2) with only one outlet to the sea. Korission lagoon is the only lagoon considered in the study for which some biological data, i.e. phytoplankton biodiversity and functional diversity, is available in the literature (Roselli *et al*., 2013). Both the taxonomic and functional diversity of Korission phytoplankton guilds were found to be globally high and also higher than in other Mediterranean lagoons (Leonilde *et al.,* 2017). Finally, Lefkimmi lagoon (2.0km^2) is located in the south-eastern part of the island and has been used in the past as a salt pan. Currently, Lefkimmi lagoon is not connected to ny freshwater or marine environments, and water salinity is characterized by high seasonal variability, following the alternation of rainfall and drought periods. It ranges from being meso/polyhaline in the summer and oligo/mesohaline in the winter *sensu* Kjerfve (1994).

The marine ecosystem sampling sites were located close to the mouth of Antinioti lagoon (one sampling site) and Korission (one sampling site), as well as in the small deltas of rivers Potamos and Messonghi (two sampling sites each). The marine sampling sites were located at increasing distance from the mouth of the lagoon or the river delta in order to minimize transitional water influence. Nevertheless, some transitional water influence on the abiotic conditions of the coastal area was observed at a few sampling locations, depending on the tidal conditions (i.e. low tide) at which sampling campaigns has been carried out, in order to homogenize sampling procedures at different lagoons/river mouths and locations (Appendix Table 1).

This experimental study was performed in spring (April - May, 2014). Water salinity is a major niche filter for lagoon and marine ecosystems (Battaglia, 1959), affecting species colonization and distribution (Barron *et al.,* 2002; Ayadi *et al*., 2004; Evangelopoulos *et al*., 2008; Nielsen *et al.,* 2008; Reizopoulou *et al.,* 2014). In total, the study includes 30 sampling sites, eleven river, thirteen lagoon and six marine sites. At every site, 12 replicate reed leaf-packs were used as trophic traps.

The leaf-bag technique (Petersen & Cummins, 1974) was used to collect data for three different categories: i. taxonomic composition and population abundance of macroinvertebrate guilds, ii. individual body size of macroinvertebrate taxa; and iii. key physico-chemical characteristics of each sampling site. The term 'guild' defines the benthic macroinvertebrates according to their body size and functional traits, as well as their functional role in the processing of organic matter in the sediment of aquatic ecosystems (Root, 1967).

Field and laboratory procedure

The experimental fieldwork consisted in the follow-up of *Phragmites australis* leave decay, using the leaf-packs of 5 mm mesh size. Before their use, the leaves were cut into 8 cm long fragments excluding the basal and apical parts, and then were filled with 3.000 + 0.005 g of oven-dried leaves (60° C, 72 h). At the beginning of the experiment (day 0), the leaf-bags were placed at the sites, on the bottom, and replicates were collected over a 30-day period.

Each leaf-bag was sieved through a 0.5mm mesh size and the remaining material was preserved in jars containing 4% buffered formaldehyde in seawater and sorted at the laboratory under a stereomicroscope. Taxonomic identification was performed to the lowest possible resolution for most of the macroinvertebrate specimens; then they were counted and total length was measured to the nearest 0.01 mm using an image analysis device (Leica QWIN 3). Taxonomic identification of macroinvertebrate guilds in the river ecosystems compared to the other ecosystem types was limited.

Thus, to estimate the body size of the individuals, we used the length-mass relationship, which is the most widely used approach for estimating the ash free dry weight (i.e. AFDW). The use of length-mass relationships based on macroinvertebrates in transitional water ecosystems, is supported by Rosati *et al*. (2012), when gross estimates of population biomass is required. The length-mass relationship is faster and more precise than other tools and models used to estimate the biomass of aquatic invertebrates (Benke *et al.,* 1999). Length-mass relationships are described as $M = a L^b$, where M = body mass, L = body length; a = specific body mass, and b = regression slope.

Specific body mass (a) and regression slope (b) of each taxa has been already recorded on lagoon ecosystems in the Mediterranean Sea and Black Sea (Rosati *et al.,* 2012), as well as on freshwater ecosystems (Benke *et al.,* 1999). The data used were originally stored on the Transitional Water Data Platform (www.circlemednet.unisalento.it) and are available on the LifeWatch-ERIC infrastructure's Platform (www. servicecentrelifewatch.eu).

All taxa were then divided into functional feeding groups (hereafter referred to as trophic guilds), in accordance with their morpho-functional and behavioural food resource acquisition mechanisms. Predators are organisms that consume other organisms (i.e. engulf prey or tissue); suspension feeders are organisms that capture re-suspended material (i.e. planktonic organisms) from the water column. Gathering collectors are organisms that collect FPOM from interstices in sediment. Shredders and scrapers are organisms that consume both particles attached to rocks, wood and rooted plants, as well as plant material pieces, and are included in the same functional group for this study. The classification of the taxa into functional groups was based on Gjoni & Basset (2018), where each taxa were divided into functional feeding groups in accordance with their morph functional and behavioral mechanisms of food resource acquisition. The classification was mostly based on the systematic studies of freshwater macroinvertebrates (Cummins 1974; Merritt *et al.,* 1996; Cummins *et al.,* 2005), but were also drawn from a wide range of studies of estuarine and marine ecosystems (Fauchald & Jumars, 1979; Koutsoubas *et al.,* 2000; Luczkovich *et al.,* 2002; Casagranda *et al.,* 2006; Faulwetter *et al.,* 2014) and from global databases (Appendix Table 2).

Statistical Analysis

The Bray-Curtis dissimilarity index was used to compare dissimilarity of the taxonomic, functional and morpho-functional structure of benthic macroinvertebrates within and among the three ecosystem types, included in the study.

ANOVA analyses were used to compare average body size of the individuals, average abundance, and average species richness across the three ecosystem types, as well as across the ecosystems within every type. ANOVA analyses were also used to compare the average body size of the individuals and the average abundance among the four trophic functional guilds (i.e. gathering collector, suspension feeder, shredder/scraper and predator) across three ecosystem types (i.e. river, lagoon and marine). Moreover, Student's t-test was used to compare the two ecosystem types when necessary, due to the absence of a trophic guild in one of the ecosystem types.

Individual size distribution models (ISD; Reizopoulou & Nicolaidou, 2007) following geometric size classes (AFDW; class 1 = 0.1mg, class 2 =0.2–0.3mg, class 3 =0.4–0.7mg, class 4 = 0.8–1.5mg, class 5 =1.6–3.1mg, class 6 =3.2–6.3mg, class 7 =6.4–12.7mg, and class 8 >12.8mg) were fitted, showing the abundance of the individuals for each body size class.

Linear regression models were used to analyze size abundance relationship models (White *et al.*, 2007), with data aggregation at population and community levels: a. local size density relationship (LSDR) as the log-log scaling relationship of average body size and average abundance for each species/population per each site, and b. cross-community scaling relationships (CCSRs) as the log-log scaling relationships of average body size and overall population density of individuals at each site The significance of differences among both LSDR and CCSR scaling coefficients (slopes and intercepts) was estimated by ANCOVA (with body mass as a covariate), and by comparing 95% confidence intervals.

The residuals of the LSDRs and CCSRs, and the models were computed in order to evaluate size-specific guild density from the estimated value of the LSDRs and CCSRs, and the distribution of residuals was compared across the three ecosystem types (river, lagoon, marine) using one-way ANOVA. For this purpose, the different sampling locations were organized into water salinity clusters, according to the Venice system (Battaglia, 1959), and patterns of variation of the body size-specific guild and individual densities along the salinity gradient were addressed using linear regression models.

Results

The dataset considered for the study includes 16,020 individuals belonging to 9 classes, 6 phyla, and 59 lower taxa, 38% of which were classified at species level. 56% of all taxa belong to the river ecosystem type, 18% to the lagoon ecosystem type, and 26% to the marine ecosystem type. Thus, 9% of the taxa belong to both lagoon and marine ecosystems and 2% to both river and lagoon ecosystems. Considering macroinvertebrate functional trophic groups, 42% of the collected taxa belong to shredders/scrapers, 29% to predators, 20% to gathering collectors and 9% to suspension feeders.

Average individual body size (ANOVA $F_{2,\ 15792}$= 54.20, $P < 0.0001$) and average abundance (ANOVA $F_{2,\ 322}$= 66.32, $P < 0.0001$) were significantly different across ecosystems types, with lagoon ecosystems showing higher individual average abundance than the other ecosystem types, and the marine ecosystems higher average body size. The river ecosystems showed higher average species richness (Table 1).

The same analysis performed for each ecosystem type showed significant differences in average body size (ANOVA $F_{2,\ 2708}$ = 35.43, $P < 0.0001$) and average abundance (ANOVA $F_{2,\ 61}$ = 6.291, $P < 0.05$) among river ecosystems. Messonghi River showed higher individual abundance than the other riverine ecosystems and Potamos River higher average individual body size. Significant differences in average body size (ANOVA $F_{2,\ 12248}$ = 22.71, $P < 0.0001$) and average abundance (ANOVA $F_{2,\ 105}$ = 32.81, $P < 0.0001$) were observed among lagoon ecosystems, with larger individuals in Antinioti and Korission than in Lefkimmi lagoon, while higher average individual abundance was observed in the latter (Table 1). Average individual body size (ANOVA $F_{3,\ 829}$ = 6.383, $P < 0.001$) was the only descriptive characteristic of macroinvertebrates that was found to be significantly different among marine ecosystems, with Messonghi and Potamos marine ecosystems showing higher average individual body size than the other marine ecosystems (Table 1).

As regards the three approaches used to describe macroinvertebrate community structure, species composition was highly variable across ecosystem types and also among ecosystems within types. The dissimilarity analysis (Bray - Curtis dissimilarity index) showed significantly higher similarity among taxonomic composition, than

Table 1. Average water salinity (psu), average body size (mg, AFDW), average individual abundance (N site^{-1}), and global species number (N) within and across ecosystem types locations along the salinity gradient are reported. Standard errors (±) are also included.

Ecosystem Type	Average Salinity	Average Body size	Average Abundance	Species Number
River	**0.76 ± 0.05**	**0.96 ± 0.13**	**35.10 ± 2.84**	**60**
Fonissa	1.33 ± 0.01	0.69 ± 0.03	42.14 ± 7.41	27
Messonghi	1.50 ± 0.07	0.35 ± 0.03	79.29 ± 16.01	27
Potamos	0.87 ± 0.05	0.89 ± 0.09	24.27 ± 4.44	31
Lagoon	**15.44 ± 0.98**	**0.51 ± 0.03**	**113.44 ± 10.93**	**16**
Antinioti	15.43 ± 0.89	0.68 ± 0.12	76.90 ± 10.30	13
Korission	18.88 ± 0.95	0.25 ± 0.01	77.02 ± 8.54	8
Lefkimmi	11.29 ± 0.67	0.63 ± 0.09	248.17 ± 32.71	6
Marine	**32.18 ± 1.11**	**1.64 ± 0.52**	**26.64 ± 3.73**	**26**
Antinioti	21.50 ± 0.99	0.10 ± 0.04	7.50 ± 2.50	5
Korission	37.40± 1.23	0.09 ± 0.01	40.30 ± 10.05	9
Messonghi	34.63 ± 1.05	5.45 ± 1.13	14.00 ± 2.32	13
Potamos	32.68 ± 0.97	5.54 ± 1.46	12.94 ± 3.95	13

among tropho-functional composition and size spectra (t-Student tests, $P < 0,01$ for all comparisons; Fig. 2).

Considering the trophic functional guilds, the same analysis across the three ecosystem types, showed significantly different average body size (ANOVA $F_{2,\,194}$= 9.101, $P < 0.001$) and abundance (ANOVA $F_{2,\,194}$= 7.518, $P < 0.05$) for gathering collectors. However, gathering collectors showed higher values for both size and abundance in river ecosystem type. Scraper/shredders showed significantly different average body size (One-way ANOVA $F_{2,\,203}$= 6.829, $P < 0.001$) and abundance (One-way ANOVA $F_{2,\,203}$= 4.060, $P < 0.05$) among ecosystem types too, with the lagoon ecosystem type having higher values than the other types (Figure 3 and 4). Suspension feeders are absent in marine ecosystems but showed higher values for both body size (Student's t-test: $P < 0.01$) and abundance (Student's t-test: $P < 0.01$) in the river ecosystem type compared to the lagoon type. Finally, predators showed significantly different average body size (ANOVA $F_{2,\,186}$= 6.258, $P < 0.001$) and abundance (ANOVA $F_{2,\,186}$= 7.810, $P < 0.01$) across ecosystems types, with higher abundance in the lagoon type and higher body size in the marine type (Figs 3, 4).

The size distribution of individuals reveals a common pattern among the three ecosystem types, due to the left skewed distribution, with up to ~25% for river, ~35% for lagoon and 40% for marine ecosystem types, for the individuals in the smallest size class (Fig. 5A-C). Left skewed distributions were also observed at ecosystem level. In Messonghi river and Antinioti lagoon, 35% of the individuals belong to the smallest class, followed by Lefkimmi lagoon (45%). An even higher percentage of individuals belonging to the smallest size class, were observed in all four marine ecosystems (55-65%). Exceptions were observed in rivers Fonissa and Potamos, where 30% and 20% of the individuals, respectively, belong to the fourth class, and Korission lagoon where 45% of the individuals belong to the third class (Fig. 5C-N).

Size-density relationships showed common patterns: i. LSDR showed a significant scaling coefficient of -0.21 with an explained variance of 7% (Figure 6A) and ii. the variance explained by the CCSR model was 18.05% and the slope was -0.37 (Fig. 6B). The scaling relationships of the log-log LSDR and CCSR model were significant, with slopes consistently higher than the expected value (b= -0.75), according to the energy equivalence role (EER; Damuth 1981; 1987; 1991).

For both the LSDR and CCRS, the analysis of residuals from the lineal regressions showed significant differences in body size-specific densities among aquatic ecosystem types (Fig. 7A; One-way ANOVA $F_{2,\,27}$= 5.337, $P < 0.01$; and One-way ANOVA $F_{2,\,35}$= 2.333, $P < 0.01$, respectively). Both residual analyses showed higher values for lagoon ecosystem locations than for river and marine ones (Fig. 7A). A significant pattern of variation of body-size specific guild density (CCSR) was observed along the salinity level of each sampling site according to a quadratic relationship (Fig. 8), showing that water salinity influences the macroinvertebrate size-specific density of the three aquatic systems (Fig. 8).

Discussion

The description of the variation patterns of community structural and functional components across different ecosystem types is a main approach to investigating the generality of the underlying mechanisms and the relevance of the related driving forces. Here, we studied the comparative pattern of variation of structural com-

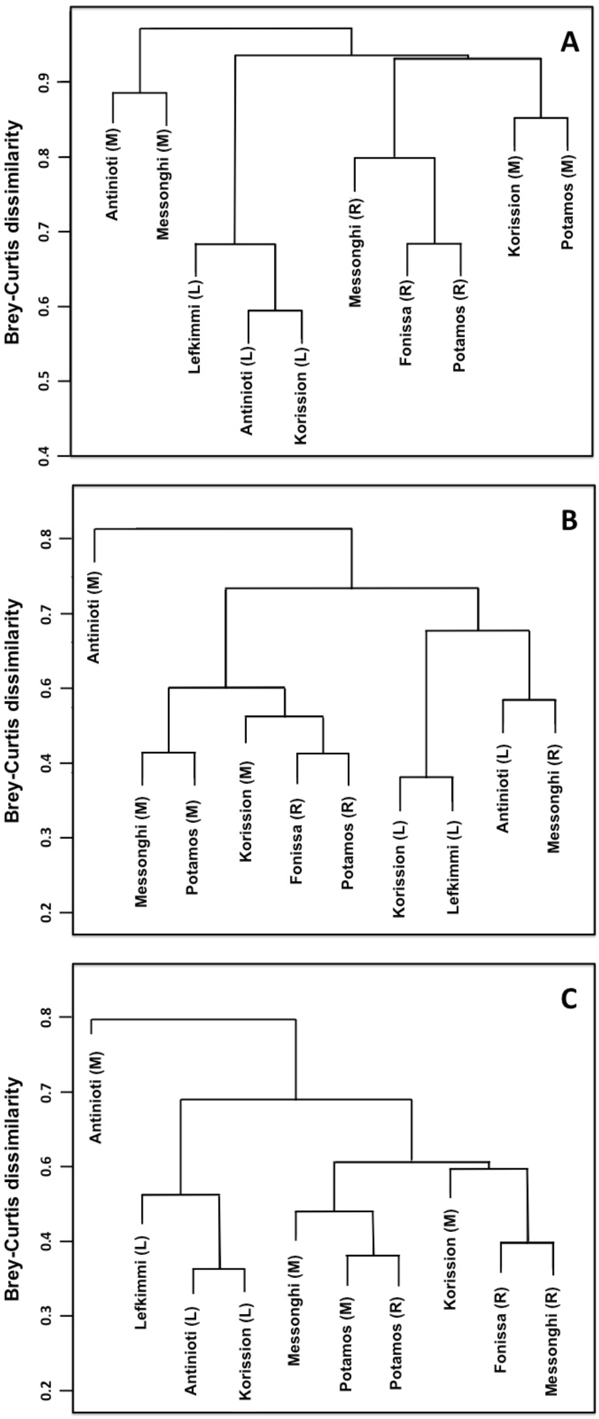

Fig. 2: Dissimilarity index of (Bray-Curtis distance on abundance matrix) on: A. taxonomic composition, B trophic guilds, and C. body size spectra, within and among the aquatic ecosystem types (R=river, L=lagoon, M=marine) included in the study.

ponents of benthic macroinvertebrate communities in the three aquatic ecosystem types of Corfu Island, in order to decode the underlying community organization mechanisms. The results of the study emphasize three main points:

The taxonomic composition of benthic macroinvertebrate guilds was clustered according to ecosystem type, showing that ecosystem type works as a niche filter for the taxa, more than for trophic guilds and body size spectra, which were more similar between river and lagoon ecosystem types than with marine ones;

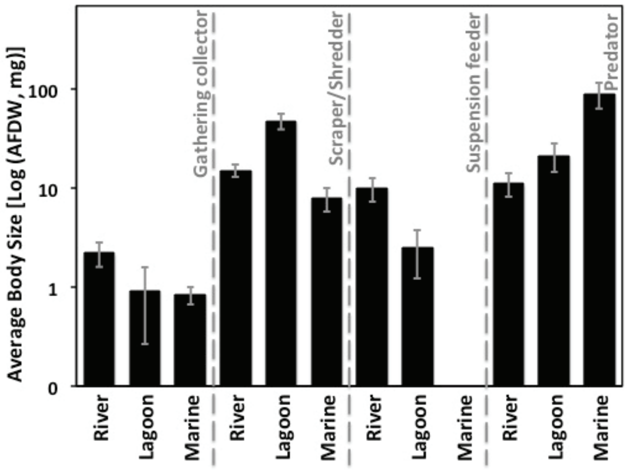

Fig. 3: Average individual body size across the three ecosystems types among the trophic functional guilds. Vertical bars represent 95% confidence intervals.

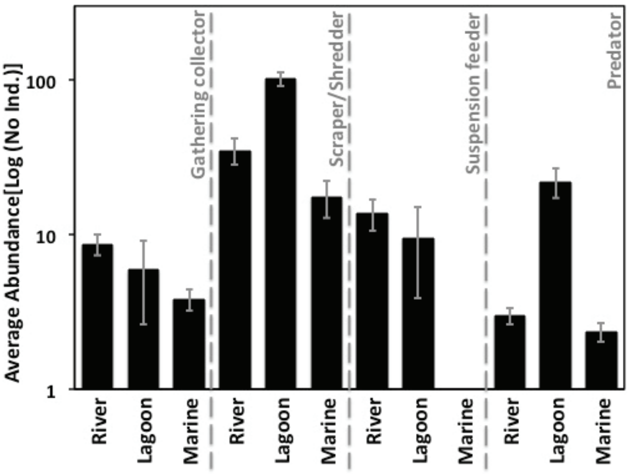

Fig. 4: Average abundance across the three ecosystems types among the trophic functional guilds. Vertical bars represent 95% confidence intervals.

The benthic macroinvertebrate guilds were characterized by the dominance of large species within and among ecosystem types and study site locations;

Community organization of benthic macroinvertebrate guilds across the salinity gradient was body size mediated, with lagoon ecosystems being characterized by higher energy density at the macroinvertebrate level compared to freshwater and marine ecosystem types.

The results of this study do not seem to depend on methodological bias associated with the data collection, data analysis, trophic guild classification and experimental design. First of all, the use of the leaf pack technique is a well-established method used to sample vagile benthic macroinvertebrates along salinity gradients (Quintino *et al.,* 2011; Sangiorgio *et al.,* 2014); in this respect, an underestimate of the density of low vagile or sessile species does not introduce a bias in data collection since this study focuses on macroinvertebrates involved in detritus

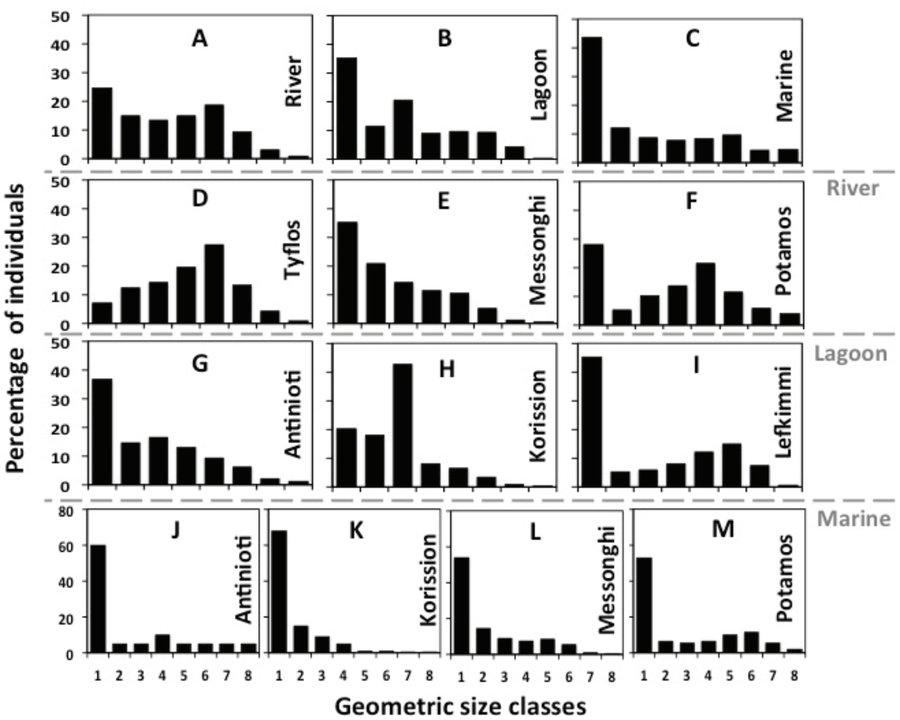

Fig. 5: Individual or index size distribution (ISD; *according* Reizopoulou and Nicolaidou, 2007) of the macroinvertebrate guilds across the three ecosystem types (A-C), within river ecosystem type (D-F), within lagoon ecosystem type (G-I), and within marine ecosystem type (J-N).

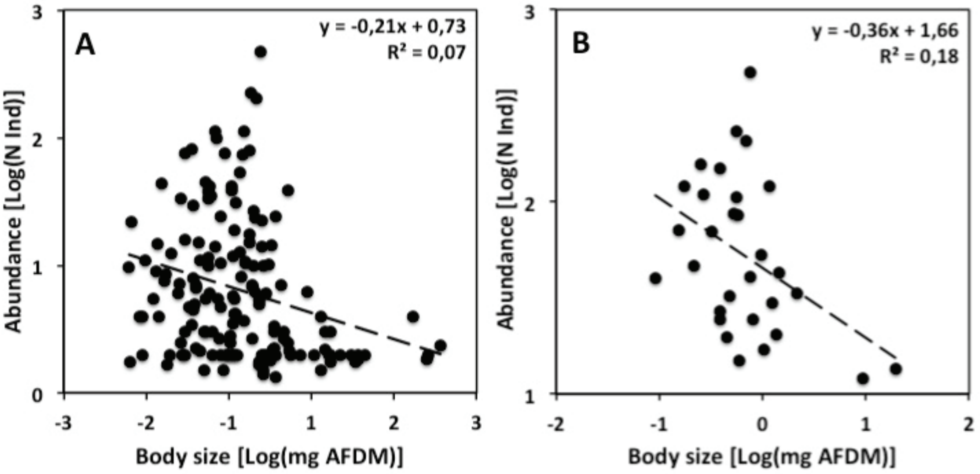

Fig. 6: Body size patters of the macroinvertebrate guilds in the study: A. Local size-density relationship at the population/species level of the sampling sites (slope 95% CI: −0.41, −0.07), and B. Cross-community scaling relationship at sampling site level (slope 95% CI: −0.67, −0.06).

processing within aquatic ecosystems, while most low vagile or sessile species rely primarily on fine particulate organic matter or prey on consumers that are larger than benthic macroinvertebrates.

The period during which the leaf packs were placed at the sampling sites is related to the fungal biomass of the leaf, since it was suggested that full microbial conditioning of leaves occurs after about three weeks of leave immersion in an aquatic ecosystem (Boling *et al*., 1975). During the first thirty days, macroinvertebrates are able to control the growth of microflora due to the fact that they feed mostly on the leaf surface and less by shredding leaves (Mancinelli *et al.,* 2009). The fungal biomass on leaves has also been described in salt and freshwater wetlands (Newell *et al.,* 1995; Kuehn *et al.,* 1998; Findlay *et al.,* 2002; Su *et al.,* 2007), as well as in temporally ponds (Bertoli *et al.,* 2016), with similar findings.

The leaf pack technique, has also been compared with the box corer method, and shown that it is able to sample arthropod species and particularly shredder and scraper species, while annelids are mainly sampled by the box corer method. Thus, the taxonomic and functional composition for both methods also varies in relation to water salinity (Sangiorgio *et al*., 2014).

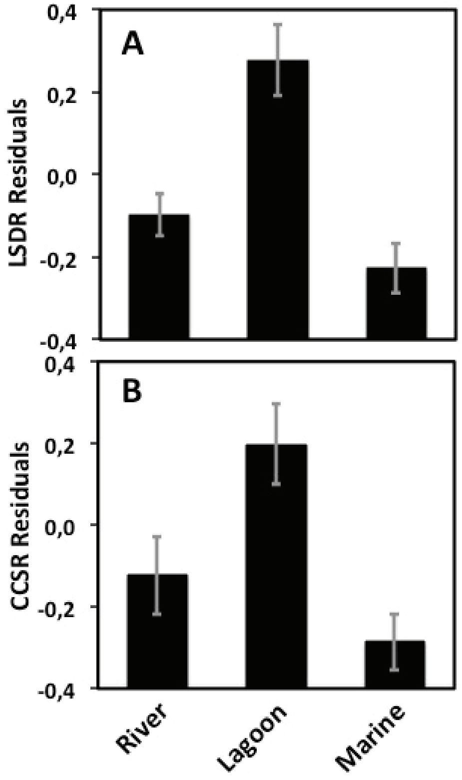

Fig. 7:Analysis of LSDR (A) and CCSR (B) residuals of the macroinvertebrate guilds at sampling site level of the three different ecosystem types.

In this study, water salinity was the main important driver of the heterogeneity of sampling sites; it was defined in the experimental design and achieved by selecting the sampling site positions according to the different freshwater and marine water inputs.

Finally, the lack of seasonality is unlikely to introduce significant bias in the analysis of the current study both because functional guilds and size patterns do not seem to reveal relevant seasonal variation patterns in benthic macroinvertebrates (Barbone *et al.*, 2012; Basset *et al.*, 2013; Gjoni *et al.,* 2017) and because the study focuses on a comparative analysis of the macroinvertebrate structural and functional components within and among aquatic ecosystem types.

The resolution used for taxonomic classification of the collected macroinvertebrate organisms did not introduce any bias in the data either, even though only 38% of the taxa were recognized at species level. In fact, the potential bias introduced did not affect the comparative analysis of macroinvertebrate guild dissimilarity within and across aquatic ecosystem types. Actually, since more than 95% of the collected individuals belonged to only 12 taxa, any potential bias in the dissimilarity analysis of taxonomic composition vs. trophic guilds and particularly size spectra classes was minimized or prevented. Moreover, the classification of the macroinvertebrates into functional groups is a source of uncertainty, due to the fact that classification of macroinvertebrate taxa into functional groups reflects an approximate approach followed by Gjoni & Basset (2018) with a reduced risk of misclassification of benthic macroinvertebrate taxa. The classification of the trophic behaviour of benthic macroinvertebrates in lagoon and marine ecosystems is uncertain because of the certain degree of omnivore, including also cannibalism, the changing feeding strategy during the life cycle and their multiple functional feeding 'roles' (Commito & Ambrose, 1985; Polis, 1994).

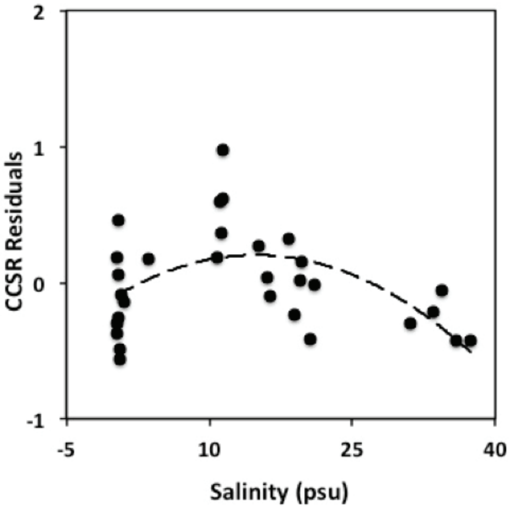

Fig. 8: Second-degree polynomial equation of the relationship between the CCSR residuals and the salinity level at each sampling site of the study ($y = -0.001x^2 + 0.042x - 0.108$; d.f. = 30; $R^2 = 0.299$; $P < 0.001$).

The description and analysis of ISD, LSRD and CCSR were carried out according to main literature references (Reizopoulou & Nicolaidou, 2007; White *et al.*, 2007; Basset *et al.*, 2008); therefore, the variation observed in both individual body size and individual abundance, as well as the observed variation of the size-density relationships cannot be due to methodological bias in model description and analysis. The body size independent specific densities with respect to the CCSR regression lines have already been used on macroinvertebrate guilds of lagoon ecosystems (Gjoni *et al.*, 2017; Gjoni & Basset 2018). Therefore, residuals of body size-specific individual density from the CCSR are likely to reflect the real conditions of aquatic ecosystems rather than stochastic biases. Consequently, CCSR model residuals are likely to be considered adequate estimates of the energy flow in aquatic ecosystems (Gjoni *et al.,* 2017).

The questions 'which species can occur in this ecosystem?' and 'which traits allow species to occur in this ecosystem' depict two approaches to defining the mechanisms underlying biodiversity organization and architecture (McGill *et al.*, 2006). Point (1) suggests that benthic macroinvertebrate guilds in the studied aquatic ecosystem types are hierarchically organized, with size structure representing the highest level in the hierarchy, with trophic guild composition and taxonomic nested within. First of all, the results and the proposed underlying hierarchical organization are supported by the lower dissimilarity observed for trophic guild composition and size spectra structure with respect to taxonomic composition, within and among ecosystem types across the salinity gradient. Taxonomic composition variation among freshwater, transitional water and marine ecosystems is described by the distribution of both macroinvertebrate orders and classes, and by the distribution of taxa at the more defined level of genera and species. The river ecosystem type was dominated in terms of individual abundance by insect species, the lagoon type by crustacea and the marine type by crustacea and polychaetes. *Asellus aquaticus*, Habrophlebia sp. and *Planorbis planorbis* were the most abundant in river ecosystem types, *Ecrobia ventrosa*, *Gammarus aequicauda* and *Idothea baltica* in lagoon types, and *Corophium volutator*, *Melita palmata* and Carcinus sp. were the most abundant and characteristic taxa of marine ecosystem types.

However, trophic guild composition and size spectra also showed a certain degree of variability among ecosystems (Fig. 2) since biological functional traits (i.e. feeding behaviour and body size, but also life cycle, physiological characteristics, etc.) reflect the adaptation of the species to the environment in which they live (Stearns, 1976). Benthic macroinvertebrate guilds live on or inside the sediment, as well as close to the surface or deeper, and their feeding function is an important factor of benthic community diversity (Taurusman, 2010; Uwadiae, 2010). They are classified into functional groups, or trophic guilds, which are based on morpho-functional traits and behavioural mechanisms and have implications for resource use and energy transfer (Wallace & Webster, 1996).

In this study, the suspension feeders (e.g. *Ephemerella sp.* and *Habrophlebia sp.*) and gathering collectors (e.g. *Chironomus plumosus* and *Chironomus salinarius*) are mostly insects and are both characterized by high dominance in river ecosystems. The scrapers/shredders were mostly crustaceans (e.g. *Corophium volutator, Gammarus aequicauda* and *Lekanesphaera hookeri*) and were abundant in lagoon ecosystems. Moreover, predators were mostly crustaceans (e.g. *Idotea baltica*), polychaetes (e.g. *Hediste diversicolor* and *Neanthes acuminate*) and also dominant in lagoon ecosystems, with their large-sized animals occurring in marine ecosystems. Some traits influence the functions of an organism that, in turn, affect ecosystem functioning, (McGill *et al.*, 2006).

Recently, a hierarchical organization of taxonomic, functional and morpho-functional approaches has been proposed for predicting functional diversity distribution, using benthic macroinvertebrates (Kaminsky *et al.*, 2018), fish (Riera *et al.,* 2018) and phytoplankton (Leonilde *et al.,* 2017) as model organisms. Therefore, our results extend these findings to benthic macroinvertebrates, as well. Moreover, the 'functional' and 'morpho-functional' approaches seem to be more complete with respect to the traditional approaches using taxonomic data, since they reflect the integration of the evolutionary and energetic responses of the species, in terms of colonization and growth, to the abiotic conditions occurring in ecosystems (Dolédec *et al.,* 1999).

Point (2), is mainly supported by the analysis of size-density relationships, which take into account both individual average body size and individual abundance, and allow to evaluate body size-specific individual density. In fact, both for population size-density relationships (i.e. LSDRs) and community size-density relationships (i.e. CCSR) the slope of the linear regression was higher, less negative, than the value b=-0.75 expected by the energetic equivalence rule (Damuth, 1981; 1991; Nee *et al*., 1991). Therefore, although a left skewness of the ISD was observed for most ecosystems and locations, the scaling of individual abundance with individual body size evidenced a dominance of large individuals and large taxa in all aquatic ecosystem types.

Body size patterns are based on the theoretical framework of the ecology of energetics, through the well-known allometric scaling of animals and plants, as well as microorganism traits (i.e. metabolic rate, home rage, population density etc.) with individual body size (Peters, 1983; Peters & Wassenberg, 1983; Glazier 2005; Woodward *et al*., 2005; White *et al*., 2007; Glazier *et al*., 2018). Body size pattern scaling with population density are expected to scale with an exponent of b = -3/4 (West *et al*., 1997; White *et al*., 2007). The body size-related energy constraints determine the slope, where deviation from the expected slopes expresses either small ($b < -3/4$) or large ($b > -3/4$) species dominance (Damuth, 1981; 1987; 1991). The body size patterns of the study are consistent with previous studies based on body size patterns of macroinvertebrates in Mediterranean and Black sea lagoons (Gjoni *et al*., 2017; Gjoni & Basset 2018), and show that benthic macroinvertebrate guilds are characterized by the dominance of large species. A dominance of large species is also consistent with evidence from spatially explicit individual modelling (Basset & De Angelis, 2007), which described a size-mediated coexistence mechanism with a competitive advantage for large species, and both experimental (Basset, 1997) and field (Basset *et al*. 2008b) studies on macroinvertebrate guilds. Moreover, deviations from the theoretical expectation were also observed in size patterns of macroinvertebrate guilds in both transitional (Basset *et al.,* 2008a) and freshwater (Basset *et al.,* 2004) ecosystems in the Mediterranean Sea. The CCSR model describes the community organization of macroinvertebrate guilds spatially and temporally limited in the three ecosystem types, while the LSDR model, as proxy, describes the co-occurring species population in the local guilds.

Studies on cross-community models are increasing, since they have been highlighted as a new ecological method for describing community organization and the underlying processes at spatiotemporal scales, thus deepening our understanding of the relationship between biodiversity and ecosystem functioning (Gjoni *et al*., 2017; Gjoni & Basset, 2018). Patterns of CCSRs have been also observed in amphibian and macroinvertebrate guilds in temporal ponds (Arim *et al*., 2011), bacteria, algae and protozoans (Long & Morin, 2005), land bird communities (Meehan *et al*., 2004), desert rodent communities (White *et al*., 2004) and marine phytoplankton communities (Li, 2002).

Regarding point (3), it is directly supported by the patterns of variation of the body size-specific densities among aquatic ecosystem types, showing higher densities for lagoon rather than both freshwater and marine ecosystems, as well as by the patterns of variation along the salinity levels considered. The CCSR approach has been already applied for comparative representation of the heterogeneity of energy allocation or flowing within ecosystem and among ecosystems. The analysis of the residual of size-density relationships at community level has been applied to describe the quantitative energy pathways of benthic macroinvertebrates in lagoon ecosystems (Gjoni *et al*., 2017). Here, we have followed the same analysis comparing the energy flow among the macroinvertebrate guilds across freshwater, lagoon and marine ecosystem type. Our findings showed that the lagoon ecosystems have a higher energy flow than the river and the marine ecosystems. This evidence is consistent with the higher organic matter inputs to lagoon ecosystems rather than to freshwater and marine ecosystems and with ecological status conditions allowing the transfer of energy from dead detritus to macroinvertebrate consumers. Lagoon ecosystems are characterized by high organic matter inputs, from freshwater and marine environments, derived from detritus decomposition (McLusky & Elliott, 2007) and high primary productivity that are dominated by depositional processes (Kjerfve, 1994). Primary production and organic matter input are the most important food resource for primary consumers in estuaries and lagoon ecosystems (Lindeman *et al.,* 1942; Moore, 1975; Newell *et al*., 1982).

Freshwater, lagoon and marine ecosystem types that are characterized by high spatial heterogeneity over space and time, combining trophic interactions, as well as behavioural and morphological characteristics of benthic communities with ecosystem properties, may predict functional diversity distribution. By emphasizing the overall importance of the cross-community approach as an ecological tool able to link biodiversity and ecosystem functioning, this study represents a step forward for low-diversity manipulative studies focused on changes in biodiversity and ecosystem functioning at local scale. Our empirical findings indicate that size-based and cross-community approaches may be used as ecological tools to describe and compare functional diversity distribution across ecosystem types.

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APPENDIX

Table 1. The list of the sampling sites in the study, along their physico-chemical characteristics: salinity (psu), temperature (°C) and pH (* = referred in a single measurement).

Ecosystem type	Name	Site	Salinity	Temperature	**pH**
			Average SD	Average SD	**Average SD**
River ecosystem type	Fonissa	1	0.57 ± 0.05	14.61 ± 1.62	7.34 ± 0.12
	Fonissa	2	0.56 ± 0.05	14.58 ± 1.39	7.37 ± 0.13
	Fonissa	3	0.49 ± 0.01	13.55 ± 1.04	7.31 ± 0.12
	Fonissa	4	0.29 ± 0.02	17.03 ± 2.82	7.30 ± 0.14
	Fonissa	5	0.33 ± 0.03	14.51 ± 0.44	7.31 ± 0.03
	Fonissa	6	0.29 ± 0.01	13.22 ± 0.03	7.29 ± 0.09
	Messonghi	1	3.60 ± 1.42	17.07 ± 1.32	7.09 ± 0.09
	Messonghi	2	0.46 ± 0.04	16.17 ± 0.29	7.37 ± 0.06
	Messonghi	3	0.44 ± 0.03	15.90 ± 0.70	7.38 ± 0.05
	Potamos	1	1.00 ± 0.01	15.10 ± 3.40	7.16 ± 0.07
	Potamos	2	0.74 ± 0.01	13.53 ± 3.53	7.11 ± 0.01
Lagoon ecosystem type	Antinioti	1	10.78*	15.28 ± 2.39	6.89 ± 0.33
	Antinioti	2	15.14*	18.53 ± 3.47	6.69 ± 0.53
	Antinioti	3	16.10*	18.40 ± 2.01	6.15 ± 1.08
	Antinioti	4	19.70*	18.51 ± 2.02	7.01 ± 0.22
	Korission	1	20.57 ± 0.64	19.67 ± 0.01	7.24 ± 0.10
	Korission	2	19.48 ± 0.16	19.38 ± 0.55	7.35 ± 0.05
	Korission	3	19.00 ± 0.61	19.07 ± 0.01	7.34 ± 0.06
	Korission	4	18.37 ± 0.97	18.77 ± 0.14	7.26 ± 0.05
	Korission	5	16.43 ± 0.63	18.74 ± 0.13	7.44 ± 0.06
	Lefkimmi	1	11.28*	21.04 ± 0.45	7.02 ± 0.41
	Lefkimmi	2	11.35*	21.68 ± 0.01	6.60 ± 0.78
	Lefkimmi	3	11.38*	22.18 ± 0.15	6.70 ± 0.66
	Lefkimmi	4	11.15*	22.96 ± 0.45	6.62 ± 0.77
Marine ecosystem type	Antinioti	1	21.05*	18.40 ± 3.36	.27 ± 0.02
	Korission	1	37.40 ± 0.01	18.45 ± 1.81	7.24 ± 0.01
	Messonghi	1	35.87 ± 0.72	18.66 ± 0.39	7.17 ± 0.02
	Messonghi	2	33.43 ± 1.33	17.49 ± 0.84	7.22 ± 0.03
	Potamos	1	31.04 ± 2.82	20.47 ± 2.14	7.03 ± 0.05
	Potamos	2	34.32 ± 2.05	19.93 ± 2.03	7.16 ± 0.0

Table 2. Checklist of taxa collected where for each taxa is reported the trophic guild, the ecosystem type and the specific location from which the individuals of the taxa have been collected.

Scientific name	Class	Ecosystem Type	Ecosystem Name	Trophic Guild
Abra segmentum	Mollusca	Lagoon	Lefkimmi	Suspension feeder
Aedes sp.	Insecta	River	Messonghi, Potamos	Shredder/scraper
Agapus sp.	Insecta	River	Potamos	Predator
Ancylus fluviatilis	Mollusca	River	Messonghi, Potamos	Shredder/scraper
Asellus (Asellus) aquaticus.	Crustacea	River	Messonghi, Potamos	Shredder/scraper
Atherix sp.	Insecta	River	Fonissa	Gathering collector
Atrichops sp.	Insecta	River	Fonissa	Predator
Baetidae	Insecta	River	Fonissa	Gathering collector
Bithyniidae	Mollusca	River	Messonghi, Potamos	Shredder/scraper
Carcinus aestuarii	Crustacea	Marine	Messonghi	Predator
Carcinus sp.	Crustacea	Marine	Potamos	Predator
Cardiidae	Mollusca	Lagoon	Korission, Lefkimmi	Suspension feeder
Chironomus plumosus	Insecta	River	Messonghi, Potamos, Fonissa	Gathering collector
Chironomus salinarius	Insecta	Lagoon, Marine	Antinioti, Korission, Lefkimmi	Gathering collector
Chironomus sp.	Insecta	River	Messonghi	Gathering collector
Coenagrion sp.	Insecta	River	Fonissa, Messonghi	Predator
Cordulegaster sp.	Insecta	River	Messonghi	Predator
Corophium volutator.	Crustacea	Marine	Korission, Potamos	Shredder/scraper
Corophium sp.	Crustacea	Lagoon	Antinioti, Korission	Shredder/scraper
Dytiscus sp.	Insecta	River	Potamos	Predator
Dytiscidae	Insecta	River	Messonghi	Predator
Ecrobia ventrosa	Mollusca	River, Lagoon	Antinioti, Korission, Lefkimmi, Fonissa, Potamos	Shredder/scraper
Ephemerella sp.	Insecta	River	Fonissa	Suspension feeder
Erpobdellidae	Annelida	River	Messonghi	Gathering collector
Gammarus aequicauda	Crustacea	Lagoon, Marine	Antinioti, Korission, Lefkimmi, Messonghi, Potamos	Shredder/scraper
Gammarus sp.	Crustacea	River	Fonissa, Messonghi, Potamos	Shredder/scraper
Gibbula sp.	Mollusca	Marine	Messonghi	Shredder/scraper
Gyrinidae	Insecta	River	Fonissa, Messonghi	Predator
Habrophlebia sp.	Insecta	River	Fonissa, Messonghi, Potamos	Suspension feeder
Haliplidae	Insecta	River	Messonghi	Shredder/scraper
Hediste diversicolor	Annelida	Lagoon, Marine	Antinioti, Messonghi, Potamos	Predator
Helobdella sp.	Annelida	River	Messonghi	Gathering collector
Hydrachnidia	Arachnida	River	Fonissa	Shredder/scraper
Idotea balthica	Crustacea	Lagoon, Marine	Antinioti, Korission	Predator
Ischnura sp.	Insecta	River	Fonissa	Predator
Jaera (Jaera) nordmanni	Crustacea	Marine	Potamos	Shredder/scraper
Lekanesphaera hookeri	Crustacea	Lagoon, Marine	Antinioti, Korission, Messonghi	Shredder/scraper
Lestes sp.	Insecta	River	Fonissa, Potamos	Predator
Malacoceros girardi	Annelida	Marine	Potamos	Gathering collector
Melita palmata	Crustacea	Lagoon, Marine	Antinioti, Korission, Fonissa, Messonghi, Potamos	Shredder/scraper
Microdeutopus gryllotalpa	Crustacea	Marine	Potamos	Shredder/scraper
Microdeutopus sp.	Crustacea	Marine	Potamos	Shredder/scraper
Neanthes acuminate	Annelida	Lagoon, Marine	Antinioti, Messonghi, Potamos	Predator
Oligochaeta	Annelida	River	Potamos	Gathering collector
Pachygrapsus marmoratus	Crustacea	Marine	Antinioti	Predator
Physella acuta	Mollusca	River	Fonissa, Potamos	Shredder/scraper
Pirenella sp.	Mollusca	Marine	Messonghi	Shredder/scraper
Pirenella conica	Mollusca	Marine	Potamos	Shredder/scraper
Planorbis planorbis	Mollusca	River	Fonissa, Messonghi, Potamos	Shredder/scraper
Psychodidae	Insecta	River	Potamos	Shredder/scraper
Rhithrogena sp.	Insecta	River	Potamos	Filtering collector
Simuliidae	Insecta	River	Messonghi	Filtering collector
Statiomys sp.	Insecta	River	Potamos	Gathering collector
Stratiomyidae	Insecta	River	Potamos	Gathering collector
Tanypodinae	Insecta	River	Fonissa, Messonghi, Potamos	Gathering collector
Tipula maxima	Insecta	River	Potamos	Predator
Trichoptera	Insecta	River	Fonissa	Filtering collector
Tricolia sp.	Mollusca	Marine	Messonghi	Shredder/scraper
Upogebia pusilla	Crustacea	Marine	Potamos	Predator