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# Functional diversity and redundancy of soft bottom communities in brackish waters areas: Local vs regional effects

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ABSTRACT

The present study aims to detect functional diversity as well as functional redundancy patterns of soft bottom benthic communities in relation to the prevailing environmental factors, across several brackish water areas. We further tested whether differences in spatial scale can account for the possible variability in functional trait distribution, as well as for the local community assembly processes driven by species functional traits. Our main results suggested that environmental variation induces a large amount of variability in functional trait distribution at local and regional scale, a result which underscores the importance of habitat and environmental variation in the functioning of soft sediments in brackish areas. Conversely to functional diversity, functional redundancy remained invariable in both local and regional scales, therefore acting as an insurance against the enhanced environmental variability and maintaining ecosystem processes and services. Our findings led us also to conclude that environmental factors control the distribution of certain functional traits thus acting as environmental filters, in both local and regional scales. On the other hand, dominant species interactions accounted for the reduced levels of functional divergence at the less confined brackish water areas. This finding supported the view that interactions among dominant species can potentially induce negative effects on the functionality of brackish water soft sediments. From all the above, it is reasonable to assume that community shaping and functioning of the examined brackish water areas are governed by both biotic interactions and environmental filters, which are acting simultaneously at varying degrees of influence.

## 1. Introduction

The concept of functional diversity has progressively attracted the interest of marine ecologists since it has been increasingly used in various types of marine as well as brackish water ecosystems. Contrary to species diversity, functional diversity deals with the distribution and the range of what organisms do in communities, therefore including complementarity and redundancy of co-occurring species (Petchey and Gaston, 2006; Schleuter et al., 2010). Unsurprisingly, several methods of measuring functional diversity have been proposed mainly based on species multiple ecological and morphological traits. In this sense, specific species traits are considered to be indicators of ecosystem functioning on the grounds that they are related directly or indirectly to ecosystem processes and functions. Those methods are including ordinations of traits in multivariate species space (e.g. Bremner, 2008; Bremner et al., 2003, 2006) or functional diversity indices that take into account species trait information (e.g. Mouchet et al., 2010; Podani and Schmera, 2006; Ricotta 2005; Schleuter et al., 2010; Villéger et al., 2008). Several authors have proposed that functional diversity can be divided into three major components, i.e., functional richness, functional divergence and functional evenness, and thus functional diversity indices can be categorized according to the component that they measure in the functional space (Mason et al., 2005; Mouchet et al., 2010).

Following Hewitt et al. (2008), the majority of the research effort in functional diversity patterns decoding in aquatic ecosystems has been mainly focused at the comparisons across different regions and along environmental gradients, at the assessment of anthropogenic impacts, at the relationships between species and functional diversity as well as at the relationships of ecosystem functions with stability and resilience. More recently, several research efforts have also attempted to use functional diversity of species assemblages in order to reveal species coexistence processes, as well as to identify which of the assembly rules has the strongest influence on community shaping (de Bello et al., 2009; Mason et al., 2008; Mouillot et al., 2007; Mouquet et al., 2002). In this sense, one of the main assembly rules is the niche filtering hypothesis which suggests that coexisting species are more similar to one another than would be expected by chance as a result of the environmental conditions (Zobel, 1997). On the contrary, limiting similarity hypothesis predicts that biotic interactions are also important and the most similar species are strongly competing, whereas the complementary species are coexisting in a stable way (MacArthur and Levins, 1967). The latter interactions are expected to increase functional diversity within a community on the

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grounds that they constrain the similarity among coexisting species traits (Hooper et al., 2005).

Given that the importance of different factors is changing at different spatial scales, there is growing evidence that habitat heterogeneity and environmental variation induce a large amount of variability in functional trait destitution (e.g. Bremner et al., 2003; Heino, 2005). Therefore, it is crucial to verify if the latter pattern persists at various types of aquatic ecosystems in order to support evidence to the generalization of such a hypothesis.

Brackish water areas include a variety of ecosystems such as lagoons, estuaries, semi-enclosed gulfs and saltmarshes. It is widely acknowledged that they are critical transition zones between land, freshwater habitats, and the sea since they provide essential ecosystem services, functions and processes (Levin et al., 2001). Brackish water areas are widely threatened by pressures arising from human activities, often affecting species diversity and ecosystem functionality (Basset et al., 2008) with potentially important socio-economic consequences (Costanza et al., 1997). Investigation of functional diversity patterns in coastal wetlands mainly includes areas such as lagoons (e.g. Basset et al., 2008; Mistri et al., 2001) or estuaries (e.g. Heino, 2005; Sanders et al., 2007). However, their functioning in relation to the environmental conditions is not yet well understood in both local and regional scales (de Bello et al., 2009; Mouillot et al., 2006). Hence, the identification of such relationships in various spatial scales is of great importance in order to optimize the effectiveness of the monitoring of these ecosystems, as well as to provide essential ecological input for conservation strategies and plans in the future.

In this manuscript we attempted to address functional diversity as well as functional redundancy patterns of benthic communities in relation to the prevailing environmental factors at local and regional scales in brackish water areas distributed across a semi-enclosed gulf. In addition, we aimed to detect whether differences in spatial scale can account for the possible variability in functional trait distribution, as well as for the community assembly processes driven by species functional traits.

## 2. Materials and methods

### 2.1. Study area–sampling design

The study area was Kalloni Gulf which can be considered as a shallow, productive, semi-enclosed Gulf that communicates with the northeast Aegean Sea through a narrow (0.7 km wide) inlet (Evagelopoulos and Koutsoubas, 2008). Kalloni Gulf has long been subjected to anthropogenic pressure mainly induced by agricultural as well as industrial development and urbanization. The study area involved four wetlands distributed along Kalloni Gulf coastline. These wetlands were Polihnitos (PB) and Kalloni saltworks (KB), Messa estuary (PB) and Parakoila marsh (PAB) (Fig. 1). According to their geographical location across Kalloni Gulf, sampling sites of Kalloni saltworks (KB) and Messa estuary (BB) were considered to be more confined areas, whereas sampling sites of Polihnitos saltworks (PB) and Parakoila marsh (PAB) were considered to be less confined areas in relation to their distance from the open Aegean Sea.

A single sampling was carried out in spring 2006 and involved both water column and sediment samples. Water column samples (three replicates at each site) were collected with a Ruttner type sampler from the surface water in the morning. Considering sediment sampling, three replicate benthic samples were taken at each sampling site by means of a Van Veen grab (0.1 $m^2$ sampling surface) in substrates consisting of sandy mud with no macrophytic vegetation cover. The depth of the sampling stations was 0.5 m in all cases. Samples were washed in the field through a 0.5 mm sieve, fixed in 10% formalin and stained with the addition of the Rose Bengal stain. Additional sediment samples were received from undisturbed surface sediment (top 2 cm) for organic carbon and grain size analyses.

Water column chl-a concentrations were estimated according to a technique proposed by Neveux and Panouse (1987). Sediment organic carbon concentration measurement involved the use of Walkey and Black (1934) method as modified by Jackson (1958) and described by Loring and Rantala (1992). Benthic invertebrates' sample treatment included sorting, identification at the lowest possible taxonomic level and enumeration (Holme and McIntyre, 1984).

### 2.2. Functional traits

The functional characteristics which were selected in the present study incorporated those functional traits (variables) that describe some of the major ecological functions with the strongest effect on energy flow in the ecosystem and are likely to be available for most of the species. Hence, we used those functional traits that are commonly met in the relative literature concerning benthic ecosystems (e.g. Bremner et al., 2003; Dimitriadis and Koutsoubas, 2011; Hewitt et al., 2008; Michaud et al., 2006; Norling et al., 2007; Pacheco et al., 2010; Papageorgiou et al., 2009; Sanders et al., 2007; Tillin et al., 2006). Those traits are known to act directly or indirectly as indicators of important processes in aquatic ecosystems such as nutrient fluxes across the sediment–water interface, bioturbation and irrigation, habitat modification, sediment transport and carbon recycling (Bremner, 2008; Giller et al., 2004; Hewitt et al., 2008). Seven major functional traits (variables) were incorporated in our study: two variables related to nutrients and space resources dynamics ('adult mobility' and 'living position'), three variables connected to trophic structure ('feeding type', 'feeding apparatus' and 'food type'), one variable reflecting habitat modification ('habitat modificators'), as well as one variable related to bioturbation ('bioturbation'). The selected functional traits were then divided into categories (modalities) so as to incorporate the range of the possible functional species attributes within each functional trait (Table 1). Species were assigned to each one of the thirty modalities (fuzzy coding was used in cases where species exhibited multiple traits within each variable — Chevenet et al., 1994) based on a variety of scientific literature, internet sources and expert consultancy (Table 2). Filling in missing data was based on information of congeneric species as it was proposed by Tillin et al. (2006) and Papageorgiou et al. (2009).

### 2.3. Functional diversity and redundancy

In the present study we calculated FDiv (Functional Divergence) index proposed by Mason et al. (2005) and modified by Lepš et al. (2006), for each one of the modalities whereas community functional diversity of multiple traits was calculated as the average of FDiv values deriving by single traits within each sampling site (Lepš et al., 2006) (Appendix 1). The latter index captures the functional divergence component of functional diversity facets and as such it is known to define how far high species abundances are from the center of gravity of the functional space (Villéger et al., 2008) (Further explanations in the terminology and calculation of functional diversity indices can be found in: Lepš et al., 2006; Villéger et al., 2008; Schleuter et al., 2010). Given that pronounced numerical dominance of few species is the typical community mode observed in transitional waters ecosystems (Reizopoulou and Nikolaidou, 2004), it is reasonable to believe that FDiv is an appropriate index for the measurement of functional diversity in such ecosystems. Rao's quadratic entropy index ($FD_Q$) was also used as a functional diversity measure (i.e., mean functional distance between two randomly selected individuals) (Botta-Dukát, 2005; Lavorel et al., 2008) in order to calculate functional redundancy as it is suggested and discussed by de Bello et al. (2007)(Appendix 2). According to the latter authors functional redundancy can be defined as the degree of community's saturation