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Resistance of polychaete species and trait patterns to simulated species loss in coastal lagoons

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ABSTRACT

The loss of species is known to have negative impacts on the integrity of ecosystems, but the details of this relationship are still far from being fully understood. This study investigates how the distribution patterns of polychaete species and their associated biological trait patterns in six Mediterranean coastal lagoons change under computationally simulated scenarios of random species loss. Species were progressively removed from the full polychaete assemblage and the similarity between the full assemblage and the reduced matrices of both species and trait patterns was calculated. The results indicate the magnitude of changes that might follow species loss in the real world, and allow consideration of the resistance of the system's functional capacity to loss of species, expressed through the species' biological traits as an approximation to functioning. Comparisons were made between the changes in the distribution of species and of traits, as well as between the six different lagoons. While the change of species and trait patterns was strongly correlated within most lagoons, different lagoons showed distinctly different patterns. In disturbed lagoons, the dominance of one or few species was the major driver for the observed patterns and the loss of these species caused extreme changes. Less disturbed lagoons were less susceptible to extreme changes and had a greater resistance towards species loss. Species richness appears to be less important for the ability of the lagoons to buffer changes, instead the initial composition of the assemblage and the identity of the lost species determine the response of the system and our ability to predict changes of the assemblage's functional potential.

1. Introduction

It is widely understood that biodiversity and ecosystem functioning are positively related, and that a loss of biodiversity usually has negative effects on ecosystem functioning (Hooper et al., 2005; Loreau et al., 2001; Naeem et al., 1995). A central question of recent ecological research is therefore how diversity – expressed as species richness – relates to the stability of the ecosystem, either concerning the ability to resist to (resistance) or to recover from (resilience) disturbances (Ives and Carpenter, 2007; Stachowitcz et al., 2007). Species-rich systems are generally considered more stable (Lawton and Brown, 1993; Loreau et al., 2001; McCann, 2000; Tilman et al., 1997a), since there is a greater probability that important functions are performed by multiple species, and functions of lost species can potentially be performed by the remaining species. This provides the system with a certain resistance towards loss of function, a concept known as the "insurance hypothesis" (Yachi and Loreau, 1999). However, there is

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evidence that species richness alone is not always enough to explain effects on ecosystem function. Individual species can have over-proportional effects on ecosystem processes, the so-called identity or composition effects (Stachowitcz et al., 2007). Consequently, ecosystem stability depends on a variety of factors, from species richness effects to the complementary or dominant properties ("sampling effect") of its species (Stachowitcz et al., 2007). The ability to predict the effects of species loss and to understand which of these factors are responsible for providing stability to the system is, therefore, of utmost importance to conserve ecosystem functioning (O'Connor and Crowe, 2005; Petchey, 2000).

In the last decades, a number of studies in the marine realm have started to investigate the details of the relationships of species richness, community composition and ecosystem functioning, either through experimental studies that provide data directly linked to ecosystem processes (e.g. Bracken et al., 2008; Bracken and Low, 2012; Bulling et al., 2008; O'Connor and Crowe, 2005; O'Gorman et al., 2011; for a review see Stachowitcz et al., 2007) or through approaches such as the Biological Traits Analysis (BTA). Biological Traits Analysis does not measure functioning directly, but uses species' biological traits as a proxy for certain ecosystem functions (Bremner et al., 2003; Norling et al., 2007; Violle et al., 2007). The approach is particularly suited to compare multivariate patterns of the structure of communities and those of their biological traits (e.g. Bremner, 2008; Bremner et al., 2006a, 2006b; Hewitt et al., 2008; Marchini et al., 2008; Törnroos and Bonsdorff, 2012; Törnroos et al., 2015).

This study uses Biological Traits Analysis (BTA) and combines it with a method to quantify structural redundancy in marine benthic species assemblages which was proposed by Clarke and Warwick (1998). Their method identified small subsets of species in a community that revealed the same multivariate patterns of biodiversity as the complete set of species. From a structural point of view, the species not included in this subset can be considered redundant, in the sense that they are not required to reproduce the community patterns derived from the full dataset. Clarke and Warwick's (1998) method is here applied to biological traits data in addition to the community structure data. Biological traits represent a different aspect of the ecosystem's properties which are much more closely related to ecosystem functioning than the identity of species (Reiss et al., 2009). Thus, the approach can identify species which are redundant concerning their biological properties and thus, potentially, concerning their role in the ecosystem. Clarke and Warwick's (1998) method is then taken a step further to explore the changes of the multivariate patterns of both species and their traits under simulations of random species loss. The resulting patterns indicate the magnitude of changes that might follow species loss and allow consideration of the stability (i.e. resistance) of the system's functional capacity to loss of species, expressed through the species' biological traits as an approximation to functioning.

The concept is tested by assessing the multivariate patterns of polychaete assemblages and their biological traits in six coastal lagoons in the Mediterranean and Black Sea. Coastal lagoons are functional ecotone ecosystems (Basset et al., 2013) with strong seasonal changes, often subjected to intensive anthropogenic use and pollution and eutrophication (e.g. Arvanitidis et al., 2005; Barnes, 1980, 1991). They often are characterised by reduced species diversity (e.g. Mouillot et al., 2005; Reizopoulou and Nicolaidou, 2004), making them an intriguing environment to study ecosystem processes. The lagoons studied here contain varying numbers of species (from 5 to 21) which allows assessing the importance of species richness versus species identity for the stability of structural and trait patterns. Systems with low species richness are furthermore considered ideal for examining the biodiversity-ecosystem functioning relationship since the roles of individual species can be studied (Vitousek and Hooper, 1993).

The analyses in this study are performed under three simplifying assumptions (see also Section 4.3 for a discussion on these limitations): a) that species loss is random, b) that the species pool of each lagoon is not altered by re-entry of species from the adjacent sea upon loss of species from the lagoon and c) that species interactions do not change upon removal of certain species, and abundant and rare species continue as such after random removal of other species. Furthermore, only the polychaetes fraction of the macrobenthos dataset was analysed. Since the main aim of the study was to investigate general relationships between the different aspects of the ecosystem, focusing on a rather well-studied taxon with plenty of available expertise to collect traits information minimises the bias due to gaps in information — a common problem in biological traits analysis (Tyler et al., 2011) and allows a better estimate of the reliability of the method. This study therefore presents a simplified approach to potential real-world changes. However, we do not attempt to determine absolute effects of the loss of biodiversity on ecosystem function in these specific lagoons, but investigate how and at what rate the "functional capacity" of the studied communities might be affected by the loss of species. Furthermore, the method makes it possible to identify species that contribute most or least to the observed patterns. Finally, by comparing the change of the multivariate patterns of different aspects of the ecosystem, it is then possible to determine to what extent structural redundancy can be used as a proxy for redundancy within the trait pool – and thus potentially different functions – of an assemblage.

2. Material and methods

2.1. Datasets

2.1.1. Species occurrence data/sampling information/environmental information

The biotic dataset contains occurrence data of 48 polychaete species from six coastal lagoons in the Eastern Mediterranean Sea: Grado Marano, Grado Valle di Pesca and Margherita di Savoia in Italy, Logarou and Agiasma in Greece, and Varna in Bulgaria (Fig. 1, Table 1). All lagoons are characterised by natural seasonal fluctuations of salinity, temperature and oxygen concentration, but the degree of these fluctuations as well as the nature and level of additional anthropogenic pressures differs in each of these lagoons. The lagoons of Grado Marano, Agiasma and Varna are exposed to high organic and nutrient loading as well as chemical pollution and physical disturbances through navigation (Basset et al., 2008). Grado Valle di Pesca and Logarou are, at least in part, used for fish farming. They are subjected, at least in part, to increased organic and nutrient loading. Margherita di Savoia is used for salt production and receives strong fluctuations of salinity (from 40 to over 80 psu) over the course of the year, depending on the control of seawater influx and evaporation. The surface area of the six lagoons ranges from >100 km^2 (Grado Marano) to <1 km^2 (Grado Valle di Pesca). Details on lagoonal characteristics and environmental parameters can be found elsewhere (Barbone et al., 2007; Basset et al., 2008; Reizopoulou et al., 2014; Sangiorgio et al., 2008; Sigala et al., 2012).

In each lagoon, four to five stations or station pairs were sampled along the most pronounced environmental gradient (salinity or pollution). Sampling took place once in autumn 2004 and once in spring 2005 (with the exception of Varna, for which only data for five stations from autumn are available). At each station and in each season, five replicate units were collected by means of a box corer. Polychaete abundances were subsequently averaged per sample for the purposes of this analysis. Details on the sampling procedure and laboratory analyses can be found in Sigala et al. (2012).

2.1.2. Trait data

For the purposes of this study, 32 biological traits were chosen initially, describing the environmental preferences as well as morphological, behavioural and life cycle characteristics of each species. By encompassing a wide spectrum of aspects, a fairly accurate picture of ecological functioning of the polychaete assemblages can be obtained (Bremner et al., 2006a). Each of the traits is divided into several