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Functional composition, but not richness, affected the performance of sessile suspension-feeding assemblages

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ABSTRACT

The efficiency by which communities capture limiting resources may be related to the number of species or functional types competing therein. This is because species use different resources (i.e. complementarity effect) or because species-rich communities include species with extreme functional traits (positive selection effect). We conducted two manipulative studies to separate the effects of functional richness and functional identity on the feeding efficiency (i.e. filtration rate) of suspension-feeding invertebrates growing on vertical surfaces. In addition, one experiment tested whether the density of organisms influences the effect of functional diversity. Monocultures and complete mixtures of functional types were fed with a solution of microalgae of different sizes (6 μm–40 μm). Experiments conducted at two locations, Helgoland and Plymouth, showed that functional identity had far larger effects on filtration rate than richness. Mixtures did not outperform the average monoculture or the best-performing monoculture and this pattern was independent on density. The high efficiency of one of the functional types in consuming most microalgae could have minimised the resource complementarity. The loss or gain of particular species may therefore have a stronger impact on the functioning of epibenthic communities than richness per se.

1. Introduction

Present rates of species invasion and extinction (Thomas et al., 2004; Byrnes et al., 2007) have stimulated research linking biodiversity and ecosystem functioning (hereafter BEF), because of the potential loss of ecosystem ‘goods and services’ (Chapin et al., 2000). A substantial number of theoretical and empirical studies suggest that taxonomic and functional diversity are linked to the performance of ecosystems (Hooper et al., 2005; Stachowicz et al., 2007). However, to gain a mechanistic understanding of BEF relationships requires us to accurately distinguish changes in ecosystem processes due to the number of species (richness effect) from changes attributable to the usually stronger effect of species identity or composition (Schwartz et al., 2000).

Energy transfer in an ecosystem underlies services such as food production and nutrient cycling (Christensen et al., 1996). In coastal ecosystems, assemblages of sessile suspension-feeding invertebrates mediate the coupling and energy transfer between two major habitats—the water column and the benthos (Gili and Coma, 1998). Suspension feeders can directly control pelagic primary production by capturing large amounts of plankton, and indirectly regulate secondary production in coastal trophic webs by supporting populations of mobile predators (Navarrete et al., 2005; Nielsen and Maar, 2007). Assemblages of sessile suspension feeders provide therefore an opportunity to examine the functional consequences of biodiversity change.

Positive richness effects on ecosystem properties can result from resource complementarity or facilitation (complementarity effect; Tilman et al., 1997; Loreau, 2000). This theory was developed from observations on terrestrial plant communities, but it may also apply to aquatic ecosystems (Bruno et al., 2005; Griffin et al., 2008). For example, suspension feeders able to partition a resource on the basis of particle size can form complex assemblages made up of numerous species (Lesser et al., 1994): species feeding on smaller particles can coexist in the same community with other species feeding on larger prey. At the same time, higher diversity results in higher spatial complexity, which alters patterns in near-bottom currents and increases particle capture of individuals; this allows a species-rich assemblage to capture more food than any of its constituent species grown alone (Cardinale et al., 2002). These observations suggest that resource complementarity and facilitation may occur within suspension-feeding assemblages; however, few experiments have been

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designed to test the role of these processes in linking suspension feeder diversity and energy transfer (e.g. Cardinale and Palmer, 2002; Cardinale et al., 2002).

On the other hand, richness effects can result from the increased probability that species-rich communities include species with extreme functional values (sampling effect or positive selection effect; Huston, 1997; Loreau et al., 2001). This mechanism is based on the assumption that competitive ability and functional impact of species are positively correlated; thereby the performance of a mixture of species is explained by that of the best-performing species in monoculture (Tilman et al., 1997). However, when competitive abilities and functional impact are weakly or negatively correlated, negative selection effects can offset the resource partitioning and dampen, or even reverse, a positive BEF relationship (Bruno et al., 2006; Jiang et al., 2008).

Most BEF experiments suggest that sampling effects are the major mechanisms explaining richness effects (Cardinale et al., 2006; Stachowicz et al., 2007). Recent evidence suggests, however, that complementarity operates in natural communities, and also that its expression is influenced by other factors (Cardinale et al., 2007; Griffin et al., 2008). The density of organisms within assemblages influences the strength of intraspecific and interspecific competition, which in turn can affect the relationship between species richness and ecosystem properties (Cardinale et al., 2004; Weis et al., 2007). Despite recognition of its importance, empirical tests of the potential role of density in mediating the richness effects are still rare (but see Griffin et al., 2008).

While BEF research has largely focused at the species level (Hendriks and Duarte, 2008), grouping species into functional types allows for a more tractable study of complex systems: patterns are more consistent because the variability among functionally similar species is averaged out (Hooper et al., 2005). Here we present the results of field manipulative studies in which we tested the hypotheses that (1) the number of functional types increases the feeding rate of assemblages of suspension-feeding invertebrates, (2) these effects are influenced by the density of the assemblage, and (3) suspension feeders show different preferences for food particles of different size. In order to accurately test these hypotheses, we separated the effects of functional richness from the effects of functional identity. We used field-grown epibiota, grouped together according to functional traits related to their abilities to deplete limiting resources. A mixture of differently sized microalgae was used as food in order to allow for resource complementarity on the basis of size-specific filtration rates. Selective feeding in terms of particle size has been shown in barnacles (Crisp, 1964), bryozoans (Pascoe et al., 2007), ascidians (Petersen, 2007), and mussels (Rouillon and Navarro, 2003). In addition, we sought to maximise the ecological relevance of this work by replicating the experiment at two locations in north-eastern Atlantic coasts.

2. Methods

2.1. Experimental design

The experiments were conducted at Helgoland Island, south-eastern North Sea and at Plymouth, in the western English Channel. The original design encompassed the replication of identical experiments at both locations. Settlement patterns, however, were different between locations, as the abundance and diversity of settlers were larger at Helgoland than at Plymouth. Therefore, we did not conduct identically replicated experiments but we used the data from both locations to address different but complementary hypotheses. The data from Helgoland were used to test hypothesis 1 (the number of functional types increases the feeding rate of assemblages of suspension-feeding invertebrates) and hypothesis 2 (density influences the effect of functional richness). The data from Plymouth were used to test hypotheses 1 (see above) and 3 (suspension feeders show different preferences for food particles of different size).

Experiments included three functional types in monoculture and a complete mixture containing all functional types. Each treatment was replicated five times at Helgoland and three times at Plymouth. At Helgoland, all treatments were crossed with the factor density (either high or low) to test for density-dependent diversity effects on filtration rates. Our experimental design, in which overall density was kept constant across the diversity treatments (i.e. a replacement design), allowed a clear partitioning of the effects of functional richness and identity and detection of non-transgressive and transgressive overyielding (Loreau, 1998; Bruno et al., 2006). Non-transgressive overyielding occurs when the mixture performance exceeds that of the average of its component species in monocultures; transgressive overyielding occurs when the mixture performance exceeds that of the best-performing monoculture (Fridley, 2001).

Species were selected in accordance with natural patterns in the distribution and abundance of epibiota on vertical surfaces at both locations. Barnacles, bryozoans, ascidians, and mussels characterise these assemblages (Anger, 1978). We defined the functional types on the basis of morphological differences that may lead to resource partitioning in terms of particle size (Table 1). For example, barnacles use thoracic appendages (the cirri) to catch and handle food; a variety of setae present in the cirri allow barnacles to catch plankton across a large size range from flagellates to small crustaceans (Chan et al., 2008). Ascidians use ciliary pumps to drive water through a mucus-net that retains the suspended food particles. Bryozoans use lateral cilia to drive the water toward a filter formed by a band of stiff cilia. Mussels use gill filaments with lateral cirri that beat against the current (reviewed by Riisgård and Larsen, 2000).

We also considered the individual size as a functional trait, because the morphology of the organisms influences the physical habitat they occupy and may influence flow patterns and delivery of food. For example, in assemblages dominated by small and opportunistic

Table 1

Species of suspension-feeding invertebrates grouped as functional types according to modularity, size of individuals, and feeding mode (A).

A

Functional type	Species	Modularity	Size of individuals	Feeding mode[a]
Barnacles	*Elminius modestus*, *Balanus crenatus*	Solitary	<10 mm	Cirri beat
Colonials	Colonial ascidians: *Botryllus schlosseri*, *Diplosoma* sp.	Colonials	<10 mm	Cilia pump water into a mucus-net
	Bryozoans: *Cryptosula pallasiana*	Colonials	<10 mm	Ciliary sieving
Mussels	*Mytilus edulis*	Solitary	>10 mm	Gill filaments with lateral cilia

B

	Helgoland (Chlorophyll-*a* concentration [μg l^{-1}])			Plymouth (cell concentration [cells ml^{-1}])		
	t_0	t_1	%-removed	t_0	T_1	%-removed
Barnacles	1.41	0.92	35	14,189	10,455	26
Colonials	1.36	0.54	61	13,311	3150	76
Mussels	1.43	0.00	100	14,914	547	96
Mixture	1.43	0.49	65	13,113	729	94
Open space	1.49	0.98	34	NI	NI	NI
Controls	1.37	1.09	20	14,309	12,591	12

Average concentration of phytoplankton initially (t_0) and 1 h after (t_1) the filtration rate assays (B). The percent from initial phytoplankton concentration consumed in one h by each functional type and mixtures is given (%-removed). Open space corresponds to tiles covered by encrusting algae. Controls were used to quantify the changes in microalgal concentration that cannot be explained by filtration activity (e.g. cell precipitation or cell damage). *NI*: not investigated.

[a] Source: Riisgård and Larsen (2000).