CHAPTER 13

Reality check: issues of scale and abstraction in biodiversity research, and potential solutions

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13.1 Introduction

Over the past few decades, there has been extensive research into the relationship between biodiversity and the functioning of ecosystems—BEF research. Much of it has been done in terrestrial systems, and many of the seminal papers were terrestrially focused (e.g. Walker, 1992; Naeem *et al.* 1994; Tilman *et al.* 1996; Hector *et al.* 1999). This dominance and the tendency for terrestrial ecologists to ignore aquatic literature have both been documented (e.g. Raffaelli *et al.* 2005; Menge *et al.* 2009). However, BEF research in marine systems has proliferated in recent years (Stachowicz *et al.* 2007). There is a clear need to bridge the gap between terrestrial and marine ecologists, and to foster greater exchange of concepts, approaches and technology (Menge *et al.* 2009). Marine systems have a number of advantages for BEF research and are now yielding some influential findings (e.g. Stachowicz *et al.* 1999; Duffy *et al.* 2003; Solan *et al.* 2004; Bracken *et al.* 2008). Based on evidence to date, there appear to be some differences between BEF relationships in marine and terrestrial systems (Stachowicz *et al.* 2007). However, these comparisons may be hampered by differences in the approaches taken to terrestrial and marine BEF research (Stachowicz *et al.* 2008a). Recent re-analyses of two large meta-datasets of BEF studies did not identify an overall tendency for biodiversity effects to vary among ecosystems, and the findings suggested that similar mechanistic processes may underpin BEF relationships in terrestrial and aquatic systems (Schmid *et al.* 2009).

It is important to recognize that BEF research can be primarily motivated by different overall objectives: (a) pure ecological research, to understand something about how the natural world works, and (b) to generate results applicable to real-world management problems. Of course this distinction is not by any means exclusive, but it can influence decisions about approaches to research because each of these objectives has different requirements and constraints. Much of the research undertaken to date has been justified by the need to understand the consequences of changing biodiversity because of potential links between biodiversity loss, and the loss of ecosystem goods and services provided by organisms in intact ecosystems. However, much of it is more correctly classified as pure ecological research, based on abstracted systems (Duffy 2009). Particularly in marine systems, the majority of published studies have been undertaken in laboratory mesocosms (Figure 13.1), which potentially limits their applicability to real-world biodiversity declines. In pure ecological terms, a considerable degree of progress has been made, and some widely accepted generalities are emerging (Hooper *et al.* 2005; Stachowicz *et al.* 2007). However, the extent to which these findings can be applied to specific management or conservation issues is less clear (Srivastava and Vellend 2005).

In this chapter, we examine the nature of BEF research to date in marine systems, and specifically contrast it with that done in terrestrial systems. We then discuss limitations of our current knowledge, attributable in part to the approaches taken, before

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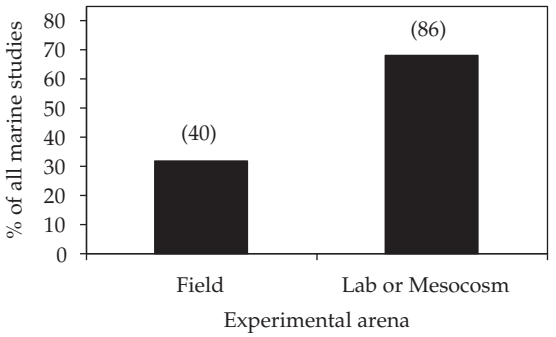

Figure 13.1 Experimental arenas of all marine BEF studies, including those evaluating both consumer and primary producer diversity. Data are based on papers summarized in Stachowicz *et al.* (2007). Relatively few studies (32%) have been conducted in the field; most (68%) have been done in the lab or in mesocosms. Parenthetical numbers over bars indicate the number of studies.

considering the relative merits of different approaches towards different objectives and making some suggestions for future research.

13.2 At which spatial and temporal scales have most biodiversity–ecosystem function (BEF) studies been conducted to date?

Two contemporary recent reviews, one summarizing BEF studies in marine systems (Stachowicz *et al.* 2007) and one meta-analysing the effects of producer diversity on biomass production in terrestrial systems (Cardinale *et al.* 2007) allowed us to assess, compare, and contrast the spatial and temporal scales of BEF research. We added data on duration and area to the Supplementary Material on marine study characteristics in the Stachowicz *et al.* (2007) review and accessed the online material accompanying the Cardinale *et al.* (2007) analysis for information on duration, area, and effects in terrestrial studies (Table 13.1). Note that for the sake of comparison, a particular paper could contain more than one study if results of multiple experiments were reported.

On average, marine BEF studies ($N = 122$) have been run for 90 ± 14 (mean ±s.e.m.) days, and the average experimental arena is 0.29 ± 0.05 m^2. Most marine studies (69%) have been conducted in laboratory or mesocosm arenas (Figure 13.1). These patterns contrast sharply with the durations and spatial scales of terrestrial producer BEF studies ($N = 108$), where the average experiment has been run for 897 ± 75 days and the average experimental arena is 11 ± 2 m^2. The vast majority of terrestrial studies (89%) were conducted in the field. However, the Stachowicz *et al.* (2007) review includes studies evaluating not only the effects of producer diversity on plant community responses—e.g. biomass accumulation, resistance, recovery, or nutrient uptake; see Allison 2004; Bruno *et al.* 2005; Bracken and Stachowicz 2006 for examples—but also effects of infaunal invertebrates on sediment characteristics—e.g. Emmerson *et al.* 2001; Waldbusser *et al.* 2004),

Table 13.1 Attributes of marine and terrestrial BEF studies.

		Values (means ± standard errors)			
Attribute	**Units**	**All marine studies**	**Marine producers**	**All terrestrial producers**	**Red. terrestrial producers†**
Sample size	*N*	122	33	108	33
Area	m^2	0.3 ± 0.1	0.8 ± 0.2	11.0 ± 2.2	3.0 ± 0.7
Duration	days	90 ± 14	158 ± 44	897 ± 75	552 ± 76
Expt. arena					
Field	%	32	65	89	85
Lab/mesocosm	%	68	35	11	15
Overyielding					
Non-transgr.	%	71	61	79	77
Transgressive	%	25	0	23	10

†'Reduced' terrestrial producer experiments are the earliest $N = 33$ studies reported in the Cardinale et al. (2007) database.

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effects of producer or consumer diversity on invasibility (e.g. Stachowicz *et al.* 2002; Arenas *et al.* 2006), and effects of diversity at one trophic level on processes at other trophic levels (e.g. Duffy *et al.* 2003; O'Connor and Crowe 2005). In explicitly and statistically comparing marine and terrestrial studies, we therefore limited the marine database to only those studies ($N = 33$) that described effects of producer diversity on algal community responses.

Interestingly, the field–lab difference between marine and terrestrial studies narrowed greatly when only producers were considered. Whereas the majority of marine BEF studies have been conducted in lab and mesocosm settings (Figure 13.1), the majority of marine *producer* BEF studies (65%) have been conducted in the field (Figure 13.2a), and the overall pattern is not strikingly different from that in terrestrial systems. What is striking is the difference between the spatial and temporal scales over which marine and terrestrial experiments have been run (Figure 13.2b). Both the average duration (nearly 900 days) and area (11 m^2) of terrestrial experiments are dramatically different from those in marine producer experiments, where the average duration is 158 ± 44 days and the average experimental arena measures only 0.8 ± 0.2 m^2.

There have been substantially more terrestrial producer BEF studies ($N = 108$) than marine producer studies ($N = 33$), which is due, in part, to a longer history of BEF experiments in terrestrial systems. The earliest experimental results reported in Cardinale *et al.* (2007) were published in 1985, whereas the earliest experiment reported in Stachowicz *et al.* (2007) was published in 1999, over a decade later. The longer time over which terrestrial producer BEF experiments have been evaluated could explain the longer duration of terrestrial studies, so we selected the $N = 33$ earliest terrestrial studies (published from 1985 to 2003) to balance sample sizes in marine and terrestrial systems. This reduced the average duration of terrestrial studies to 552 ± 76 days and the average experimental arena to 3.0 ± 0.7 m^2. Thus, balancing the number of studies and correcting for time partially, but not completely, compensated for differences in the duration ($t = 4.5$, $df = 64$, $P < 0.001$) and area ($t = 3.0$, $df = 64$, $P = 0.004$) of terrestrial versus marine producer BEF experiments. Similarly, the percentage of terrestrial studies conducted in the field declined slightly, to 85%, but that is still higher than the 65% of marine producer BEF studies conducted in the field ($\chi^2 = 10.7$, $P = 0.001$).

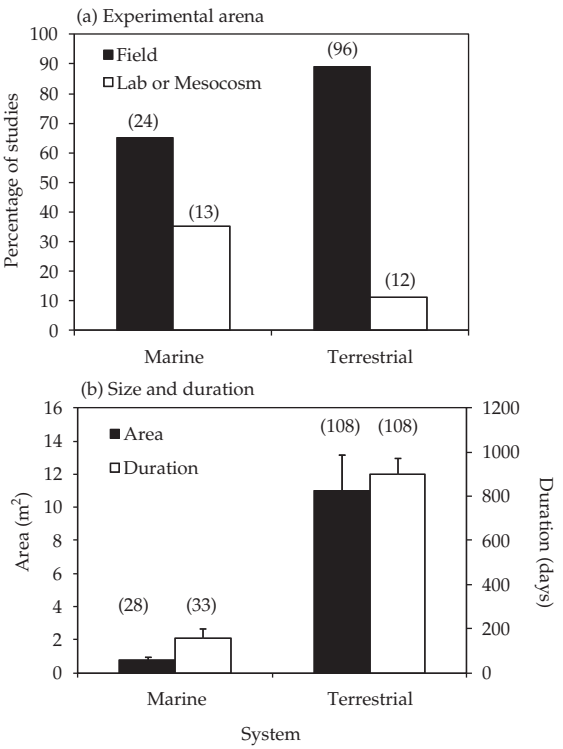

Figure 13.2 Characteristics of experiments evaluating the effects of primary producer diversity on plant community responses in marine and terrestrial systems. (a) Whereas overall patterns were similar—more studies were conducted in the field than in the lab in both systems—a relatively higher percentage of marine studies were conducted in lab and mesocosm arenas, whereas a higher percentage of terrestrial studies were conducted in the field($\chi^2 = 11.1$, $P < 0.001$). (b) Both the area ($t = 2.6$, df = 139, $P < 0.001$) and the duration ($t = 5.3$, df = 139, $P < 0.001$) of studies were higher in terrestrial systems. Parenthetical numbers over bars indicate the number of studies.

13.3 What important ecological processes or patterns may be lost in abstracting BEF experimental systems from natural ecosystems?

The legitimacy of all BEF research rests upon establishing a robust body of findings based on rigorous

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and realistic research (Naeem 2008). Therefore, comparison of different approaches and critical evaluation of their relative shortcomings and merits are essential. Although inferences from laboratory studies can be similar to those from comparable experiments done in the field, they can also differ in important respects (Carpenter 1996; Romanuk *et al.* 2009; Boyer *et al.* 2009). The magnitudes of effect sizes have also been shown to be inaccurately estimated by laboratory studies (Farrell and Crowe 2007), and a number of authors have argued that the domination of mesocosm studies in marine BEF research may have led to underestimation of the prevalence of diversity effects in marine systems (e.g. Stachowicz *et al.* 2008a; Duffy 2009). It is widely accepted that it is inappropriate to translate findings from laboratory or mesocosm studies directly into real-world applications, yet we face the challenge of designing more realistic empirical tests. Several innovative mesocosm-based studies have yielded insights into the mechanisms by which diversity may affect important patterns and processes (e.g. France and Duffy 2006; Cardinale 2011); however, scaling up from these experiments remains an issue. Here, we examine some of the specific deficiencies in our understanding of BEF relationships that may be arising from an overemphasis on lab- or mesocosm-based research.

The loss of natural patterns of dispersal is of particular concern. Mesocosm-based studies have shown that connectivity among habitat patches can modify the effect of species diversity on ecosystem properties (e.g. Matthiessen *et al.* 2007). A key advantage of most field experiments, including those in 'natural microcosms'—small, contained habitats that are naturally populated by minute organisms—is that they encompass movements of organisms between patches of varying degrees of suitability and connection—i.e. meta-community processes (Srivastava *et al.* 2004). Although the advantages of using natural microcosms for BEF studies have been identified (Srivastava *et al.* 2004), their potential remains underdeveloped. A drawback in their realistic interpretation, however, often revolves around the scale of the plots involved. Exchange of individuals between small patches on a shore—the scale at which most field experiments are conducted—is a very different process from movements between whole shores or areas of coast—the scale at which local extinctions occur and at which managers are obliged to take action. The way that dispersal mediates the effects of biodiversity on ecosystem functioning and stability has only recently been investigated, and there remains a need to test experimentally how scales of resource heterogeneity and dispersal interact (Gonzalez *et al.* 2009). Similarly, ecosystem processes at small scales—in rock pools, for example—are likely to be quite different from those at larger scales and contingent on different limiting factors.

The expression of natural behavioural patterns is clearly compromised by confined laboratory settings—e.g. Thompson *et al.* 1998; Romanuk *et al.* 2009; Griffin *et al.* 2009). Impaired expression of natural behavioural patterns is more problematic in experiments involving consumers. Many species, especially intertidal animals, change their behaviour rapidly in response to variable environmental conditions (Chapman 2000). Thus, many of the problems related to highly controlled BEF experiments are even more challenging when multiple trophic levels are included (see below). In the field, intertidal grazers often reduce their foraging activity or shift foraging efforts to different habitats or times to avoid predators (Trussell *et al.* 2003). Such trait-dependent interactions may not be expressed or may be enhanced in the confines of an experimental system, particularly when predators are held in containers smaller than their normal territorial habitat, as is often the case. When considering questions that cannot be addressed easily in the field, it is therefore essential that such studies be accompanied by field tests of related hypotheses, so that differences between field-based behaviour and laboratory-based behaviour can be measured, and the relevance of the laboratory studies sensibly evaluated (Chapman 2000). Studies that compare the results of field- and mesocosm-based studies are rare but the few that exist have shown interesting and contrasting results (e.g., Stachowicz *et al*. 2008a; Boyer *et al*. 2009; O'Connor and Bruno 2009).

Several theories predict that effects of species richness should be stronger in heterogenous environments or landscapes (Tilman *et al.* 1997;

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Cardinale *et al.* 2000; Loreau *et al.* 2003). Mathematical modelling (Cardinale *et al.* 2004), meta-analysis (Cardinale *et al.* 2007), and, more recently, direct experimental manipulations (Stachowicz *et al.* 2008a; Stachowicz *et al.* 2008b) have shown that the effect of diversity can increase with increasing experimental duration, and that increasing spatial scale should increase the strength of diversity effects due to the inclusion of a greater diversity of habitat patch types. Stachowicz *et al.* (2008a) emphasize the importance of structural heterogeneity, with a specific example that substrata used to 'cultivate' algae in assembly experiments may prevent natural recruitment or clonal spread and limit mechanisms to growth of individual ramets. The authors go further and suggest that by running analogous experimental manipulations in mesocosms and in the field over longer durations, it is possible to identify potential mechanisms that drive diversity effects. They argue that if mechanisms based on growth of adult thalli—such as complementarity of resource use—drive diversity effects, then we should expect to see similar responses from both types of experiments. If mechanisms that are more likely to operate in longer term studies and in systems open to processes such as recruitment—e.g. microhabitat differentiation, temporal complementarity, or facilitation—link diversity and function, then we would expect long-term field experiments to show strong diversity effects, and short-term mesocosm experiments to have weak or no effects. Stachowicz *et al.* (2008a) contend that short mesocosm experiments can only detect a subset of potential mechanisms, and conclude that the lack of species diversity effects reported to date should be interpreted with caution. They agree with others that call for longer experiments to test accurately for diversity effects (e.g. Cardinale *et al.* 2007).

Griffin *et al.* (2009) tested explicitly whether spatial heterogeneity of the physical environment can mediate effects of species diversity on ecosystem processes. They manipulated the diversity of intertidal molluscan grazers and the spatial heterogeneity of the substrata they grazed and measured algal consumption. They showed that on homogeneous substrata species identity had a strong effect, with the identity of best performing species dependent on the substratum. Heterogeneous substrata, containing suitable grazing conditions for all species, allowed the expression of spatial complementarity of resource use and thus enhanced total algal consumption, showing that spatial heterogeneity increases the importance of species richness for an ecosystem process.

As experimental systems become more complex and incorporate more environmental variability, the mechanisms by which species diversity stabilizes communities may also change because environmental control over populations may fluctuate (Ives and Carpenter 2007). Studies in a homogeneous lab environment may, therefore, be more likely to detect biotic interactions that may be far less significant under more natural conditions where abiotic or physical processes may dominate, and thus would not be detected in field experiments. Romanuk *et al.* (2009) tested for a relationship between species richness and community variability using similar communities in controlled laboratory microcosms, artificially constructed rock pools, and naturally occurring rock pools. The relationship was clear in laboratory microcosms, weaker in artificial rock pools, and absent in natural rock pools. The authors concluded that the effects of diversity may be difficult to detect in natural systems. It is also possible, however, that these effects are not as important as other abiotic or physical factors.

Mesocosm experiments, by their nature, limit temporal environmental heterogeneity and thereby reduce the need for multiple species capable of performing functional roles under different circumstances. Outbreaks of predators, storms, and other extreme events—heat waves, ice scour, etc.—can favour some species over others, such that diverse systems can continue to function effectively when depauperate systems may not. Homogeneous lab conditions are likely to favour one species, such that its monoculture is more likely to outperform mixtures than would be the case in a more variable natural environment. The lack of natural temporal variation in environmental conditions, coupled with the selection of convenient abundant taxa, also leads to underestimation of the importance of rare or temporarily redundant taxa, which may become

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abundant and/or influential under different environmental circumstances. This is a key omission, given that the majority of biodiversity in most ecosystems comprises rare taxa (de Aguiar *et al.* 2009). Many BEF experiments to date lack the temporal and spatial heterogeneity within replicates that may be key to species coexistence and enhance the likelihood that complementarity effects among species will be expressed (Stachowicz *et al.* 2007).

It may not be possible to accurately mimic multitrophic communities, including natural predator–prey interactions, using small-scale, short-term lab experiments. Moreover, the logistics involved in manipulating predator species diversity in the field are extremely difficult. This presents us with one the greatest challenges in BEF research because incorporating multitrophic-level effects into BEF theory, and increasing experimental realism have been identified as being among the next frontiers in BEF research (Srivastava and Vellend 2005; Stachowicz *et al.* 2007; Schmitz 2007; Bruno and Cardinale 2008; Duffy 2009). Paine (2002) suggested that the failure to incorporate consumers into BEF research has led to overly simplistic conclusions. In the quest to understand BEF relationships involving more realistic assemblages, it is important to consider appropriate densities of all species in experimental units. Many of the problems of extending model systems to incorporate multiple trophic levels are related to the problems associated with extending spatial and temporal scale (Bulling *et al.* 2006). The decision to include all species at similar densities or to create an assemblage that is representative of ambient densities in nature may affect the likelihood of identifying an effect, and should be based on the exact hypothesis being tested. For example, Bruno and O'Connor (2005) created tritrophic assemblages in mesocosms to test for effects of predator diversity. A similar biomass of each species of algae was added to each mesocosm at the start of the experiment, and a community-level trophic cascade effect was detected where the absence of carnivorous fish resulted in higher grazer abundance and lower algal biomass (Bruno and O'Connor 2005). O'Connor and Bruno (2007) used a similar experimental set-up but added algal species at different biomasses representative of each species' natural abundances based on surveys at local field sites. In this experiment, the absence of fish also resulted in an increase in grazer abundance, but this did not lead to a reduction in total algal biomass. Instead, a shift in algal assemblage structure occurred, whereby red algae that were initially present in low proportions increased as the biomass of the initially dominant brown algae decreased (see also Jenkins *et al*. 1999; Benedetti-Cecchi *et al.* 2001). The more varied components of the initial algal assemblage in this experiment appear to have led to a different response of total algal mass, driven by varied responses of different algal taxa within the assemblage.

While it is clear that predator richness can influence the strength of trophic cascades by modifying indirect interactions, the traits of predators and their prey that influence the direction of these effects are not well understood (Schmitz 2007). Mixed results have been reported from the various experiments that have manipulated predator richness to date, most of which have been performed in featureless containers or homogenous landscapes (Bruno and Cardinale 2008, but see O'Connor *et al.* 2008).

Several authors have recently recommended that future studies should include biological and environmental contingencies that are likely to affect predator–prey interactions, and should explicitly test for effects of different spatial arrangements of habitats (e.g. Dyson *et al.* 2007; Griffin *et al.* 2009).

13.4 Does the reduced temporal/spatial scale or compromised ecological realism of marine BEF studies affect our ability to extrapolate results to other systems?

It is clear from our data and discussions above that the results of marine BEF studies, which have been largely conducted in laboratory or mesocosm arenas, in relatively small experimental units, and for short durations, may differ dramatically from those in other systems. What evidence exists to suggest that the functional consequences of marine biodiversity change are fundamentally different than those in terrestrial systems? Here, we turn again to data summarized in Stachowicz *et al.* (2007) and

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Cardinale *et al*. (2007), and evaluate the frequency of mechanisms identified as links between biodiversity and ecosystem functioning.

A fundamental difference between marine and terrestrial results has been the relatively common finding that increases in terrestrial producer diversity result in *transgressive overyielding*, which occurs when a diverse assemblage performs better than the most effective component species by itself. This is the most conservative test for strong effects of changing biodiversity, and until recently, it had never been shown for marine producers (Figure 13.3). *Non-transgressive overyielding*, which occurs when a diverse assemblage performs better than the average of the component species, was a common finding in marine producer experiments; 61% of marine studies showed richness effects, compared to 79% of terrestrial studies. When we selected the 33 'earliest' terrestrial experiments to balance sample sizes and correct for duration effects, we still found slight differences in the percentage of non-transgressive overyielding effects in terrestrial (corrected to 77%) and marine studies ($\chi^2 = 5.9$, $P = 0.014$), but more significant differences in the percentage of experiments in terrestrial (corrected to 10%) and marine (0%) experiments exhibiting transgressive overyielding effects ($\chi^2 = 10.5$, $P = 0.001$). Note that limiting the potential duration of terrestrial producer experiments to balance the number of studies in marine and terrestrial systems more than halved (i.e. from 23% to 10%), the percentage of terrestrial studies exhibiting transgressive overyielding.

Why was transgressive overyielding—used synonymously with complementarity by many authors—so much more common in terrestrial systems? Two possibilities are suggested by the differences in the design of marine versus terrestrial experiments (Figure 13.2), and it seems likely that both play a role. Experimental duration has been linked to complementarity in both marine and terrestrial experiments (Cardinale *et al.* 2007; Fargione *et al.* 2007; Stachowicz *et al.* 2008a; Stachowicz *et al.* 2008b). All four of these studies demonstrate that as experimental duration increases, the importance of complementarity and

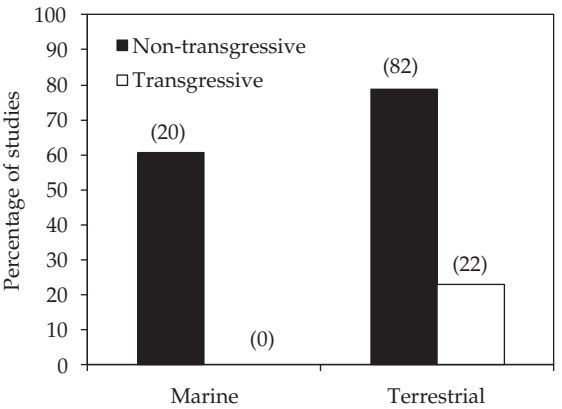

Figure 13.3 Overyielding in marine and terrestrial experiments evaluating the effects of primary producer diversity on plant community responses. Both transgressive and non-transgressive overyielding were more common in terrestrial systems ($\chi^2 = 5.1$, $P = 0.023$). In fact, Stachowicz *et al.* (2007) included no studies demonstrating transgressive overyielding in marine producer communities. Parenthetical numbers over bars indicate the number of studies.

richness effects increases, and the importance of selection and species identity effects declines. In the Cardinale *et al*. (2007) database, for example, the mean duration of experiments that demonstrated transgressive overyielding was 1592 days—over 4 years!—whereas the mean duration of experiments that showed non-transgressive overyielding was 665 days. In the one long-term marine study that has explicitly looked at how diversity effects on producer biomass change with time (Stachowicz *et al.* 2008b), the authors found that transgressive overyielding did not become apparent until the experiment had run for nine months, and the relative importance of diversity effects only consistently exceeded that of species identity effects after two years.

The area of the experimental arena also seems to be an important predictor of the potential for strong biodiversity effects. In the Cardinale *et al*. (2007) database, the experimental plots of terrestrial studies that demonstrated transgressive overyielding were considerably larger (31.9 ± 8.1 m^2) than those that did not (5.1 ± 1.5 m^2). The lack of transgressive overyielding in marine producer experiments precludes an identical comparison in marine systems, but marine experiments showing non-transgressive

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overyielding tended to be larger (1.0 ± 0.3 m^2) than those that did not (0.4 ± 0.1 m^2). In marine producer experiments, the effect of area, in and of itself, is difficult to separate from the effect of experimental arena—smaller experiments are usually conducted in lab or mesocosm settings—but the striking differences from terrestrial systems suggest that larger experiments are more likely to show strong effects of diversity.

It has been argued that complementarity effects are relatively rare, and identity effects—the key roles of particular species—are more important, in marine systems (see Crowe 2005; Gamfeldt and Bracken 2009). However, the comparisons we present above, as well as data in Cardinale *et al.* (2007) and Stachowicz *et al.* (2008a,b) suggest that most experiments evaluating the functional consequences of changes in marine producer diversity have not been big enough or long enough to detect some important mechanisms linking diversity and function.

Our discussion, thus far, has focused largely on producer diversity, as that is the common currency of the Stachowicz *et al.* (2007) and Cardinale *et al.* (2007) reviews. However, when the marine dataset was evaluated as a whole, transgressive overyielding became much more prevalent—it was found in 25% of all marine experiments—than in our analysis of producer experiments, despite the smaller area and shorter duration of experiments looking at sediment processes, invasibility, and trophic effects. Are primary producers anomalous in their requirements for space and time? The lack of a comparable dataset in terrestrial systems—where manipulations of consumer diversity are less common—makes it difficult to explicitly evaluate this possibility, but it seems likely that the benefits of conducting longer, larger experiments in the field would extend beyond primary producers. Some mechanisms linking diversity and function, such as seasonal complementarity in abundance or reproduction, will only become manifest over longer timescales, and larger experimental plots allow for more microhabitat heterogeneity, enhancing the potential for spatial complementarity (Stachowicz *et al.* 2008b).

13.5 Relative merits of different approaches to overcoming limitations of BEF studies

13.5.1 Empirical research to elucidate ecological concepts

Testing theoretical models of BEF relationships and characterizing their mechanistic underpinning requires complex experiments. Benedetti Cecchi (2004), for example, proposed a framework with an effective minimum of 16 treatments, and many more are required for experiments incorporating additional factors beyond diversity, density, and identity—e.g. environmental context, realistic versus random extinction, multitrophic effects, species versus functional group diversity. Each treatment must be replicated, and experiments with > 100 manipulated units may be needed to test complex models (e.g. Gamfeldt *et al.* 2005; Douglass *et al.* 2008; Nicol and Crowe, unpublished data). Designing experiments and selecting the combinations of species within treatments to examine BEF relationships requires that researchers make a series of decisions about how best to reduce the enormous numbers of possible species combinations to something manageable while not compromising realism, for example by mixing species that would not co-occur in nature (Srivastava *et al.* 2004; Naeem 2008). Tractable systems involving species that can be conveniently manipulated and functions that can be easily measured are required to run such experiments and statistical power is maximized if uncontrolled environmental variation is kept to a minimum.

It could be argued, therefore, that direct tests of theory are most easily achieved with laboratory or mesocosm experiments (Bulling *et al.* 2006), and that is certainly reflected in the decisions of many marine researchers to date (see above). Such experiments must inevitably focus on comparatively small organisms that are easily found in large numbers and can be conveniently kept in aquaria. Lab and mesocosm experiments can be well replicated and closely controlled, and offer a good opportunity to establish patterns and mechanisms that may arise in nature. Their main drawback is, of course, their artificiality, which potentially makes them irrelevant to the natural world (Carpenter 1996).

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More realistic tests can be undertaken in manipulative field experiments, although procedural artifacts can certainly arise and careful design is necessary (e.g. Underwood, 1997; Benedetti-Cecchi 2004; Benedetti-Cecchi 2006). Field experiments are perhaps logistically more challenging and are certainly less controlled than lab experiments. The lack of control is, however, their greatest strength; they are able to test whether factors found to be important in the lab remain so against a background of natural variation. If, in a carefully designed field experiment, residual variation outweighs diversity effects, then diversity is a less important factor than other, uncontrolled factors in the system. In fact, such variation often drives diversity effects as different species perform optimally under different conditions. An important distinction has been drawn between Synthetic Assemblage Experiments (SAEs), in which comparatively small numbers of taxa are brought together artificially, and Removal Experiments (REs), in which taxa are removed from plots which initially contain complete natural assemblages (Diaz *et al.* 2003). SAEs offer a high degree of control, but may include combinations of species that do not occur in nature, which may severely impair their capacity to detect diversity effects (Bracken *et al.* 2008). REs can only be done in the field and benefit from involving assemblages that have developed naturally over time and have been structured by real interactions (Diaz *et al.* 2003). It is also worth distinguishing between experiments manipulating arbitrarily defined patches of habitat and those in which experimental units can more defensibly be defined as delimited ecosystems, such as rock pools, lagoons, or lakes, which again offer a higher degree of realism (Srivastava *et al.* 2004).

A compromise when field experimentation is not possible may be to use outdoor mesocosms that mimic a relatively open system, and should employ a through-flow raw seawater system that at least enables recruitment of ephemeral species during the experiment (e.g. O'Connor and Bruno 2007). The effect of propagule supply regulating marine benthic systems has recently been investigated (Lee and Bruno 2009), highlighting the importance of creating 'open systems' in BEF mesocosm studies. Experiments must, however, be carried out over longer timescales to enhance our understanding of whether remaining species can numerically or behaviourally compensate for the loss of superficially similar species to assess the degree to which species are ecologically redundant (Stachowicz *et al.* 2007), and this can only be done accurately with field-based manipulations.

Scale is perhaps the biggest issue in extrapolating findings from complex manipulative experiments to real ecosystems (Symstad *et al.* 2003). There is a trade-off between spatial and temporal scale, and the degree of complexity and replication of studies (Raffaelli 2006). Experiments with large plot sizes tend to be poorly replicated or completely unreplicated (Raffaelli 2006). While we recognize the need for simpler experiments done at larger scales to bridge the gap between theory and practice, and to encompass whole ecosystems at scales relevant to management, unreplicated or pseudoreplicated comparisons between areas of differing diversity or condition—e.g. a marine protected area vs. a comparable area open to fishing—cannot be logically interpreted and should be avoided. We agree with Rafaelli (2006) that scales of experiments should be defined by features of the system, such as home ranges of organisms or generation times of their populations, rather than practical considerations, as is more commonly the case. If population processes are to be incorporated, using microbes as a model system offers one of the few opportunities for complex experiments over multi-generational time frames (e.g. Petchey *et al.* 2002). However, microbial microcosm experiments have been criticized for potentially low generality to larger fauna and flora, relying on oversimplified communities and the use of inappropriate scales to test theories based on the mechanisms driving ecosystem processes (Carpenter 1996; Srivastava *et al.* 2004; Jessup *et al.* 2004).

13.5.2 Empirical research for direct application to management/conservation

Research for direct application to specific management challenges requires a lesser degree of generality, but a greater degree of realism (Naeem, 2008). It is more likely to be focused on a particular

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ecosystem with particular species and stressors. Managers need to understand the potential consequences of a range of conservation strategies. Work with direct relevance to management often needs to be done at larger scales than work intended to explore nature for its own sake (see Chapter 11, this volume). Local extinctions and the actions of stressors tend to occur at the scale of whole shorelines or stretches of coast, and to span a number of years either in terms of the application of the stress—e.g. chronic sewage pollution or harvesting—or recovery—e.g. from an acute event such as an oil spill. It is not clear whether findings from small-scale studies can be scaled up, and doing so is likely to be misleading (Symstad *et al.* 2003; Cardinale *et al.* 2004; Srivastava *et al.* 2004; Bulling *et al.* 2006). For example, Byrnes and Stachowicz (2009) recently showed that the effects of changes in consumer species richness may manifest over longer time scales than permitted in short term lab-based studies.

It is rare that research projects receive funding to address processes over these time scales (but see Symstad *et al.* 2003), and, in many cases, it is logistically unfeasible and/or ethically indefensible to undertake experimental manipulations at large spatial scales. It is therefore necessary to adopt a more mensurative approach to characterizing patterns of impact. Peters (1991) argued eloquently that mechanistic understanding is not a prerequisite for management action; observed relationships between particular stressors and measured responses provide a valid basis for prediction. Evidence of real world benefits of biodiversity may be based on such predictive relationships (e.g. see Klein *et al.* 2003; Tylianakis *et al.* 2008, reviewed by Duffy 2009). The mechanistic understanding of cause and effect provided by experimental manipulations can greatly improve prediction, however. In this context, it is necessary to take advantage of opportunities presented by planned impacts or management interventions to design rudimentary large-scale experiments incorporating sampling at impacted sites and at carefully selected controls (e.g. Castilla and Fernandez 1998; Salomon *et al.* 2008; and see Walters 1986; Underwood 1995; Levin *et al.* 2009). Such experiments will rarely, if ever, be able to test complex BEF models, but they can be valuable in assessing the impact of changing abundance of particular components of diversity. A few other opportunities are available. For example, Zedler *et al.* (2001) tested BEF hypotheses as a component of research into large-scale habitat restoration, an application for which SAEs are explicitly required. In their experiments, it was possible to use complex designs, replicated in comparatively large-scale plots, and to generate findings of direct relevance to management.

The information and mechanistic understanding gained from decades of pure research must also be made available to managers in a synthesized and accessible form ('decision support tools', Nobre and Ferreira 2009). Ideally, managers would have access to accurate models of the ecosystems for which they are responsible, which they could use to simulate disturbances or changes to management (e.g. reductions in fishing pressure or increases in nutrient input) and evaluate the consequences for the functioning of the system, its 'ecological quality' or 'conservation status', and its capacity to provide ecosystem goods and services to society. They could use such models to inform decisions about which combinations of activities to allow in a system, taking account of the modifying influence of forecast changes in climate. Such models would require a high degree of mechanistic understanding of specific ecosystems. We do not currently have a sufficient understanding to develop effective models for any but a few impacts on any but a few, comprehensively studied systems. Nevertheless, initial models could be constructed for a larger number of systems, and sensitivity analyses could help to identify priority areas for empirical research into key mechanistic links. The findings of such research could then be incorporated into the models such that theoretical and empirical research agendas are directly interlinked.

On a more immediately accessible level, existing empirical knowledge of the functional traits of the component taxa in systems can be used to help environmental managers predict ecosystem consequences of changes to the biota in a system by using tools such as Biololgical Traits Analysis (Frid *et al.* 2008). Biological Traits Analysis characterizes all relevant traits in all taxa present, and expresses

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these as a matrix of functionality in which values assigned for particular taxa are weighted by their abundance. Such matrices can be analysed using exactly the same methods as multivariate matrices of species' abundances or biomass, and are sensitive to functionally relevant changes in assemblage structure (Bremner *et al.* 2003). Biological traits composition has been shown to be responsive to human impacts (Bremner *et al.* 2003), permitting a degree of simulation/prediction of functional consequences of particular impacts (Frid *et al.* 2008).

13.6 Conclusions

There is a clear case for a combined approach to the empirical side of BEF research (Bulling *et al.* 2006; Naeem 2008). Laboratory experiments are of value because of the possibility to control the environment very precisely, measure a range of ecosystem functions quite easily, and replicate the sorts of complex designs necessary to disentangle richness, identity, and density effects. They give an idea of the sorts of BEF relationships that *may* occur in nature, but need to be supplemented by field-based experiments of some kind. Field-based studies of longer duration are more likely to reveal natural mechanisms by which biodiversity can affect the functioning of ecosystems (Stachowicz *et al.*, 2008a). A key point is to test whether potential effects observed in laboratories are actually significant against a background of natural variability, and with the possibility of dispersal into and out of the systems. To generate findings at the scales required by managers, larger, more opportunistic experiments that take advantage of perturbations or management interventions—e.g. fisheries or protected areas—must be done by sampling diversity and measuring functioning in those areas and making comparisons with carefully selected controls. It could be argued that if BEF researchers wish to make their work more directly relevant to society, their research should be driven by a focus on key ecosystem services and designed accordingly (Raffaelli 2006), rather than focusing on key theoretical questions and selecting the most tractable systems and response variables.

Arguably, the distinction we make between 'pure' and 'applied' research is arbitrary. Certainly, so-called 'pure' research should also aim to be as realistic as possible and develop meaningful insight into the functioning of real ecosystems, whereas applied research has no less a requirement for logical rigour (Underwood 1995). Whatever approach is taken, careful design and interpretation are essential (Huston 1997; Allison 1999; Benedetti-Cecchi 2004). This relies to a great extent on a clear statement of hypotheses at the outset, and due consideration of the ultimate rationale for the work.

In both marine and terrestrial BEF research, the need to work with tractable systems, either in the lab or the field, has inevitably led to a bias towards particular habitats and systems—e.g. intertidal and shallow subtidal benthic habitats as opposed to pelagic or deeper subtidal systems; see Chapter 9—which may lead to misleading generalizations. It is important, as we expand BEF research into more systems, that we use comparable designs to avoid comparisons confounded by the problems associated with scale and length of experiment highlighted above.

In this chapter, we have focused predominantly on experimental manipulations of organismal diversity. In closing, we wish to join other authors (e.g. Srivastava and Vellend 2005; Raffaelli 2006; Naeem 2006; Naeem 2008) in emphasizing that such experiments must fit within a broader framework if BEF research is to deliver genuine ecological insight and practical tools for environmental management. Other chapters in this volume emphasize the role of observational studies and modelling approaches, the importance of considering diversity at genetic and habitat levels, and the importance of linking research with societal needs. We fully agree with Naeem's (2008) assertion that pluralistic, synthetic approaches should be the dominant trend in BEF research as it seeks to provide real-world applications to the widespread problem of biodiversity loss.

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References

Allison, G. (2004) The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs*, **74**, 117–34.

Allison, G. W. (1999) The implications of experimental design for biodiversity manipulations. *American Naturalist* **153**, 26–45.

Arenas, F., Sanchez, I., Hawkins, S. J. *et al.* (2006) The invasibility of marine algal assemblages: Role of functional diversity and identity. *Ecology*, **87**, 2851–61.

Benedetti-Cecchi, L. (2004) Increasing accuracy of causal inference in experimental analyses of biodiversity. *Functional Ecology*, **18**, 761–68.

Benedetti-Cecchi, L. (2006) Understanding the consequences of changing biodiversity on rocky shores: How much have we learned from past experiments? *Journal of Experimental Marine Biology and Ecology*, **338**, 193–204.

Benedetti-Cecchi, L., Pannacciuli, F., Bulleri, F. *et al.* (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology Progress Series* **214**, 137–50.

Boyer, K. E., Kertesz, J. S. and Bruno, J. F. (2009) Biodiversity effects on productivity and stability of marine macroalgal communities: the role of environmental context. *Oikos*, **118**, 1062–72.

Bracken, M. E. S., Friberg, S. E., Gonzalez-Dorantes, C. A. *et al.* (2008) Functional consequences of realistic biodiversity changes in a marine ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 924–28.

Bracken, M. E. S. and Stachowicz, J. J. (2006) Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology*, **87**, 2397–403.

Bremner, J., Rogers, S. I. and Frid, C. L. J. (2003) Assessing functional diversity in marine benthic ecosystems: A comparison of approaches. *Marine Ecology-Progress Series*, **254**, 11–25.

Bruno, J. F., Boyer, K. E., Duffy, J. E. *et al.* (2005) Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecology Letters*, **8**, 1165–74.

Bruno, J. F. and Cardinale, B. J. (2008) Cascading effects of predator richness. *Frontiers in Ecology and the Environment*, **6**, 539–46.

Bruno, J. F. and O'Connor, M. I. (2005) Cascading effects of predator diversity and omnivory in a marine food web. *Ecology Letters*, **8**, 1048–56.

Bulling, M. T., White, P. C. L., Raffaelli, D. G. *et al.* (2006) Using model systems to address the biodiversity-ecosystem functioning process. *Marine Ecology-Progress Series*, **311**, 295–309.

Byrnes, J. and Stachowicz, J. J. (2009) Short and long term consequences of increases in exotic species richness on water filtration by marine invertebrates. *Ecology Letters*, **12**, 830–41.

Cardinale, B. J. (2011) Biodiversity improves water quality through niche partitioning. *Nature*, **472**, 86–9.

Cardinale, B. J., Ives, A. R. and Inchausti, P. (2004) Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos*, **104**, 437–50.

Cardinale, B. J., Nelson, K. and Palmer, M. A. (2000) Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, **91**, 175–83.

Cardinale, B. J., Wright, J. P., Cadotte, M. W. *et al.* (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18123–8.

Carpenter, S. R. (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology*, **77**, 677–80.

Castilla, J. C. and Fernandez, M. (1998) Small-scale benthic fisheries in Chile: On co-management and sustainable use of benthic invertebrates. *Ecological Applications*, **8**, S124–S132.

Chapman, M. G. (2000) Poor design of behavioural experiments gets poor results: examples from intertidal habitats. *Journal of Experimental Marine Biology and Ecology*, **250**, 77–95.

Crowe, T. P. (2005) What do species do in intertidal systems? In: Wilson, J. G. (Ed.) *The Intertidal Ecosystem: The Value of Ireland's Shores.* Dublin, Royal Irish Academy, pp. 115–33.

De Aguiar, M. A. M., Baranger, M., Baptestini, E. M. *et al.* (2009) Global patterns of speciation and diversity. *Nature*, **460**, 384-U98.

Diaz, S., Symstad, A. J., Chapin, F. S. *et al.* (2003) Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution*, **18**, 140–6.

Douglass, J. G., Duffy, J. E. and Bruno, J. F. (2008) Herbivore and predator diversity interactively affect ecosystem properties in an experimental marine community. *Ecology Letters*, **11**, 598–608.

OUP CORRECTED PROOF – FINAL, 06/21/12, SPi

Duffy, J. E. (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, **7**(8), 437–444.

Duffy, J. E., Richardson, J. P. and Canuel, E. A. (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, **6**, 637–45.

Dyson, K. E., Bulling, M. T., Solan, M. *et al.* (2007) Influence of macrofaunal assemblages and environmental heterogeneity on microphytobenthic production in experimental systems. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 2547–54.

Emmerson, M. C., Solan, M., Emes, C. *et al.* (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature*, **411**, 73–7.

Fargione, J., Tilman, D., Dybzinski, R. *et al.* (2007) From selection to complementarity: Shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 871–76.

Farrell, E. D. and Crowe, T. P. (2007) The use of byssus threads by Mytilus edulis as an active defence against Nucella lapillus. *Journal of the Marine Biological Association of the United Kingdom*, **87**, 559–64.

France, K. and Duffy, J. E. (2006) Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, **441**, 1139–43.

Frid, C. L. J., Paramor, O. A. L., Brockington, S. *et al.* (2008) Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia*, **606**, 69–79.

Gamfeldt, L. and Bracken, M. E. S. (2009) The role of biodiversity for the functioning of rocky reef communities. In: Wahl, M. (ed), *Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change*. Heidelberg, Springer-Verlag, pp. 361–73.

Gamfeldt, L., Hillebrand, H. and Jonsson, P. R. (2005) Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecology Letters*, **8**, 696–703.

Gonzalez, A., Mouquet, N. and Loreau, M. (2009) Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In: Naeem, S., Bunker, D. E., Hector, A. *et al.* (eds), *Biodiversity, Ecosystem Functioning, and Human Wellbeing: an ecological perspective.* Oxford, Oxford University Press, pp. 134–46.

Griffin, J. N., Jenkins, S. R., Gamfeldt, L. *et al.* (2009) Spatial heterogeneity increases the importance of species richness for an ecosystem process. *Oikos*, **118**, 1335–42.

Hector, A., Schmid, B., Beierkuhnlein, C. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123–7.

Hooper, D. U., Chapin, F. S., Ewel, J. J. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Huston, M. A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–60.

Ives, A. R. and Carpenter, S. R. (2007) Stability and diversity of ecosystems. *Science*, **317**, 58–62.

Jenkins, S. R., Hawkins, S. J., and Norton, T. A. (1999) Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology* **233**, 41–63.

Jessup, C. M., Kassen, R., Forde, S. E., Kerr *et al.* (2004) Big questions, small worlds: microbial model systems in ecology. *Trends in Ecology and Evolution*, **19**, 189–97.

Klein, A. M., Steffan-Dewenter, I. and Tscharntke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 955–61.

Lee, S. C. and Bruno, J. F. (2009) Propagule supply controls grazer community structure and primary production in a benthic marine ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 7052–7.

Levin, P. S., Kaplan, I., Grober-Dunsmore, R. *et al.* (2009) A framework for assessing the biodiversity and fishery aspects of marine reserves. *Journal of Applied Ecology*, **46**, 735–42.

Loreau, M., Mouquet, N. and Gonzalez, A. (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences, USA*, **100**, 12765–70.

Matthiessen, B., Gamfeldt, L., Jonsson, P. R. *et al.* (2007) Effects of grazer richness and composition on algal biomass in a closed and open marine system. *Ecology*, **88**, 178–87.

Menge, B. A., Chan, F., Dudas, S. *et al.* (2009) Terrestrial ecologists ignore aquatic literature: Asymmetry in citation breadth in ecological publications and implications for generality and progress in ecology. *Journal of Experimental Marine Biology and Ecology*, **377**, 93–100.

Naeem, S. (2006) Expanding scales in biodiversity-based research: challenges and solutions for marine systems. *Marine Ecology-Progress Series*, **311**, 273–83.

Naeem, S. (2008) Advancing realism in biodiversity research. *Trends in Ecology and Evolution*, **23**, 414–16.

Naeem, S., Thompson, L. J., Lawler, S. P. *et al.* (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–7.

OUP CORRECTED PROOF – FINAL, 06/21/12, SPi

Nobre, A. M. and Ferreira, J. G. (2009) Integration of ecosystem-based tools to support coastal zone management. *Journal of Coastal Research* **2**, 1676–80.

O'Connor, M. I. and Bruno, J. F. (2009) Predator richness has no effect in a diverse marine food web. *Journal of Animal Ecology*, **78**, 732–40.

O'Connor, N. E. and Bruno, J. F. (2007) Predatory fish loss affects the structure and functioning of a model marine food web. *Oikos,* **116**, 2027–38.

O'Connor, N. E. and Crowe, T. P. (2005) Biodiversity loss and ecosystem functioning: Distinguishing between number and identity of species. *Ecology,* **86**, 1783–96.

O'Connor, N. E., Grabowski, J. H., Ladwig, L. M. *et al.* (2008) Simulated predator extinctions: Predator identity affects survival and recruitment of oysters. *Ecology,* **89**, 428–38.

Paine, R. T. (2002) Trophic control of production in a rocky intertidal community. *Science,* **296**, 736–9.

Petchey, O.L., Casey, T., Jiang, L. *et al*. (2002) Species richness, environmental fluctuations, and temporal change in total community biomass. *Oikos* **99**, 231–40.

Peters, R. H. (1991) *A Critique for Ecology,* Cambridge, Cambridge University Press.

Raffaelli, D., Solan, M. and Webb, T. J. (2005) Do marine and terrestrial ecologists do it differently? *Marine Ecology-Progress Series*, **304**, 283–9.

Raffaelli, D. G. (2006) Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology-Progress Series*, **311**, 285–94.

Romanuk, T. N., Vogt, R. J. and Kolasa, J. (2009) Ecological realism and mechanisms by which diversity begets stability. *Oikos,* **118**, 819–28.

Salomon, A. K., Shears, N. T., Langlois, T. J. *et al.* (2008) Cascading effects of fishing can alter carbon flow through a temperate coastal system. *Ecological Applications,* **18**, 1874–87.

Schmid, B., Balvanera, P., Cardinale, B. J. *et al.* (2009) Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem, S., Bunker, D. E., Hector, A. *et al.* (eds), *Biodiversity, Ecosystem Functioning, and Human Wellbeing: an ecological perspective.* Oxford, Oxford University Press.

Schmitz, O. J. (2007) Predator diversity and trophic interactions. *Ecology,* **88**, 2415–26.

Solan, M., Cardinale, B. J., Downing, A. L. *et al.* (2004) Extinction and ecosystem function in the marine benthos. *Science,* **306**, 1177–80.

Srivastava, D. S., Kolasa, J., Bengtsson, J. *et al.* (2004) Are natural microcosms useful model systems for ecology? *Trends in Ecology and Evolution,* **19**, 379–84.

Srivastava, D. S. and Vellend, M. (2005) Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology Evolution and Systematics,* **36**, 267–94.

Stachowicz, J. J., Best, R. J., Bracken, M. E. S. *et al.* (2008a) Complementarity in marine biodiversity manipulations: Reconciling divergent evidence from field and mesocosm experiments. *Proceedings of the National Academy of Sciences of the United States of America,* **105**, 18842–7.

Stachowicz, J. J., Bruno, J. F. and Duffy, J. E. (2007) Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology Evolution and Systematics,* **38**, 739–66.

Stachowicz, J. J., Fried, H., Osman, R. W. *et al.* (2002) Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology,* **83**, 2575–90.

Stachowicz, J. J., Graham, M., Bracken, M. E. S. *et al.* (2008b) Diversity enhances cover and stability of seaweed assemblages: The role of heterogeneity and time. *Ecology,* **89**, 3008–19.

Stachowicz, J. J., Whitlatch, R. B. and Osman, R. W. (1999) Species diversity and invasion resistance in a marine ecosystem. *Science,* **286**, 1577–9.

Symstad, A. J., Chapin Iii, F. S., Wall, D. H. *et al.* (2003) Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience,* **53**, 89–98.

Thompson, R. C., Norton, T. A. and Hawkins, S. J. (1998) The influence of epilithic microbial films on the settlement of Semibalanus balanoides cyprids—a comparison between laboratory and field experiments. *Hydrobiologia,* 375–376, 203–16.

Tilman, D., Naeem, S., Knops, J. *et al*. (1997) Biodiversity and ecosystem properties. *Science*, **278**, 1865–6.

Tilman, D., Wedin, D. and Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland systems. *Nature,* **379**, 718–20.

Trussell, G. C., Ewanchuk, P. J. and Bertness, M. D. (2003) Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology,* **84**, 629–40.

Tylianakis, J. M., Rand, T. A., Kahmen, A. *et al.* (2008) Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biology,* **6**, 947–56.

Underwood, A. J. (1995) Ecological research (and research into) environmental management. *Ecological Applications,* **5**, 232–47.

Underwood, A. J. (1997) *Experiments in ecology: their logistical design and interpretation using analysis of variance.*, Cambridge, Cambridge University Press.

OUP CORRECTED PROOF – FINAL, 06/21/12, SPi

Waldbusser, G. G., Marinelli, R. L., Whitlatch, R. B. and *et al.* (2004) The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnology and Oceanography,* **49**, 1482–92.

Walker, B. H. (1992) Biodiversity and ecological redundancy. *Conservation Biology,* **6**, 18–23.

Walters, C. (1986) *Adaptive management of renewable resources.* New York, McGraw Hill.

Zedler, J. B., Callaway, J. C. and Sullivan, G. (2001) Declining biodiversity: Why species matter and how their functions might be restored in Californian tidal marshes. *Bioscience,* **51**, 1005–17.