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The Role of Biodiversity in the Functioning of Freshwater and Marine Benthic Ecosystems

ALAN P. COVICH, MELANIE C. AUSTEN, FELIX BÄRLOCHER, ERIC CHAUVET, BRADLEY J. CARDINALE, CATHERINE L. BILES, PABLO INCHAUSTI, OLIVIER DANGLES, MARTIN SOLAN, MARK O. GESSNER, BERNHARD STATZNER, AND BRIAN MOSS

Empirical studies investigating the role of species diversity in sustaining ecosystem processes have focused primarily on terrestrial plant and soil communities. Eighteen representative studies drawn from post-1999 literature specifically examined how changes in biodiversity affect benthic ecosystem processes. Results from these small-scale, low-diversity manipulative studies indicate that the effects of changes in biodiversity (mostly synonymous with local species richness) are highly variable over space and time and frequently depend on specific biological traits or functional roles of individual species. Future studies of freshwater and marine ecosystems will require the development of new experimental designs at larger spatial and temporal scales. Furthermore, to successfully integrate field and laboratory studies, the derivation of realistic models and appropriate experiments will require approaches different from those already used in terrestrial systems.

Keywords: species loss, vulnerability, redundancy, coupled ecosystems, connectivity

During the last decade, much attention has centered on the question of whether altered species diversity (primarily species richness) affects the functioning of ecosystems (Loreau et al. 2002) and the goods and services they provide to society (Daily et al. 2000). Because one of the consequences of species loss may be the alteration or loss of certain ecosystem processes, understanding how changes in biodiversity affect the flow of energy and the cycling of nutrients and carbon remains a primary focus of ecological research (Kinzig et al. 2002, Loreau et al. 2002, Naeem and Wright 2003). Theory (Tilman 1999, Yachi and Loreau 1999, Loreau 2000) predicts that ecosystem functioning is likely

to be less affected by the loss of species in species-rich communities than in equivalent species-poor communities, but empirical data in support of this prediction were initially lacking. Although a wealth of knowledge exists both on the patterns of biodiversity changes and on ecosystem processes, firm conclusions from observational and experimental studies about the relationship between the two have often been hampered by confounding factors, by difficulties in experimental design, and by problems in the unequivocal interpretation of data (Mikola et al. 2002).

Stronger inferences about the effects of biodiversity loss on ecosystem-level processes have come from experiments that

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explicitly manipulated species richness (Hector et al. 1999). Some studies have reported idiosyncratic or statistically non-significant effects of changes in species richness on ecosystem functioning (Wardle et al. 1997, Mikola et al. 2002). Yet, after more than a decade of research in terrestrial habitats, the balance of evidence now suggests that declines in species numbers can adversely affect ecosystem processes (Kinzig et al. 2002, Loreau et al. 2002). When present, the relationship between increasing species richness and measures of ecosystem functioning typically levels off at relatively low levels of biodiversity (Loreau et al. 2002). Three mechanisms—species facilitation, resource-use complementarity, and sampling effects—have been proposed to explain enhanced ecosystem functioning with increasing biodiversity (Loreau et al. 2002). These mechanisms may act together to influence ecosystem processes. Understanding the sources and mechanisms of variability in ecosystem functioning, and the conditions under which individual species can influence ecosystem processes, remains an important challenge for predicting the environmental consequences of species loss (Naeem 2002).

If changes in biodiversity do affect the rates of ecosystem processes, it is important to determine whether these effects are similar in terrestrial, freshwater, and marine ecosystems. Most previous studies have been restricted to terrestrial ecosystems, mainly grasslands (Loreau et al. 2002), raising the question of whether these results can be extended to other biomes and ecosystems. Marine ecosystems represent the most extensive habitat on Earth (> 70 percent by area), and freshwater ecosystems are some of the most impaired parts of the biosphere, with some of the highest rates of species loss (Wall et al. 2001, Malmqvist and Rundle 2002). Benthic ecosystems at the bottom of rivers, wetlands, lakes, and oceans are of particular importance because of their high biodiversity and their global significance for the storage and cycling of materials, nutrients, and energy flow (Covich et al. 1999, Snelgrove 1999, Austen et al. 2002, Snelgrove and Smith 2002). In addition, because freshwater and marine ecosystems are notably different from terrestrial ones (especially with respect to the physicochemical environment), specific analyses of the relationship between biodiversity and ecosystem functioning in aquatic ecosystems may offer unique insights that help frame the general debate regarding the role of biodiversity in regulating ecosystem processes (Giller et al. 2004).

The goal of this paper is to summarize the existing knowledge on the functional consequences of species loss in benthic habitats, both marine and freshwater, and to identify gaps where future research could improve our ability to evaluate the effect of biodiversity changes on benthic ecosystem functioning. We begin by briefly describing some distinctive physical features of freshwater and marine ecosystems that need to be considered when assessing the functional consequences of species loss. This analysis is followed by an overview of recent marine and freshwater studies that have specifically assessed the effect of biodiversity changes on the functioning of benthic ecosystems, and by an outline of research needs and future research directions in this area.

Characteristics of benthic ecosystems and functional consequences of species loss

Both terrestrial and benthic habitats are composed of surfaces exposed to a moving fluid (air or water), but they differ in how fluid dynamics affect the physical habitat, community structure, and ecosystem processes. Although the same physical laws apply to moving air and water, the dynamic viscosity and density of water are about two (viscosity) to three (density) orders of magnitude greater than those of air (Vogel 1994). As a result, the dynamics of benthic ecosystems contrast with those of terrestrial ecosystems in that they are largely shaped by the surrounding fluid (water), which induces shear stress at the sediment–water interface (Kling et al. 2000, Gooday 2002). Fluid dynamics in freshwater and marine ecosystems affect the type and size of substrate in the benthic environment, the spatial configuration of habitat patches, the distribution of resources, and the structure of biotic communities, including species richness (Austen et al. 2002).

Ecologists are beginning to examine how functional relationships among species change under different flow regimes (Cardinale et al. 2002, Biles et al. 2003) and how benthic and pelagic components are coupled in thermally stratified lakes and oceans (Palmer et al. 2000, Smith et al. 2000). Benthic ecosystems occur in a broad range of physical conditions, from the highly variable and turbulent hydrodynamic regimes associated with the rocky and coarse substrates of headwater streams and exposed coastal habitats to the less variable hydrodynamic regimes and fine-grained, muddy, or sandy sediments of deeper water habitats. With the complex redistribution and transformation of sediments and organic matter by water flow, even seemingly homogeneous sediments can become patchy as a result of local, irregular inputs of organic matter. This redistribution and mixing (figure 1) of various types of organic matter is exacerbated by biological transformations mediated by microbial activity and by the feeding and burrowing behavior of infauna (Boudreau and Jørgensen 2001, Keegan et al. 2001, Biles et al. 2002).

Another important attribute that follows from the shaping influence of fluid dynamics in freshwater and marine ecosystems is the strength, scale, and preponderance of interhabitat coupling and its influence on benthic community structure and ecosystem processes (Palmer et al. 2000, Levin et al. 2001, Austen et al. 2002). Interhabitat coupling is the transfer of nutrients, organic matter, sediment, and propagules occurring between aquatic and adjacent terrestrial habitats, between pelagic and benthic zones, and horizontally between different parts of flowing-water ecosystems. The sediments of deep benthic ecosystems receive much of their input of energy and organic matter by large-scale current transport and by sinking from overlying, open-water communities (Austen et al. 2002), whereas those of shallow benthic ecosystems are typically linked to the input from both overlying waters and associated terrestrial habitats, including terrestrial vegetation.

In contrast to forested headwater streams, where inputs of organic matter are important sources of carbon, wide chan-

nels and tributary streams that lack riparian shading depend on in-channel, riverine plant productivity as a major source of carbon (Wallace and Webster 1996). Estuaries also receive inputs of terrestrial and riverine-derived organic matter and *in situ* primary productivity, and the relative importance of these resources varies greatly over time and location. Flowing-water ecosystems (streams, rivers, and estuaries) have many horizontal surface and subsurface linkages with floodplains and wetlands within their drainage basins. Rates of flows among these complex connections are often more variable, and with longer residence times, than among many standing-water ecosystems (marshes, bogs, ponds) (Kling et al. 2000, Poole 2002, Ward et al. 2002). Hydrological connections also provide important dispersal routes for benthic species and their propagules, especially in marine ecosystems. Many subtidal marine benthic species show adaptations for regional dispersal of larvae and post-larvae in major currents, as do many benthic species that are adapted for dispersal by downstream drift as well as upstream migration (Palmer et al. 1996). These regional pools of water column-dispersed benthic species provide the potential for relatively rapid recolonization of disturbed sites among coupled habitats (Palmer et al. 1996, Giller et al. 2004). Some freshwater species, however, are restricted within specific drainage basins or groundwaters, so their loss can be permanent (Malmqvist and Rundle 2002).

These two distinctive general features of benthic ecosystems—the strength of interhabitat coupling and the pervasive spatial heterogeneity of resources and particle size—make it difficult to consider local species diversity and ecosystem-level processes in

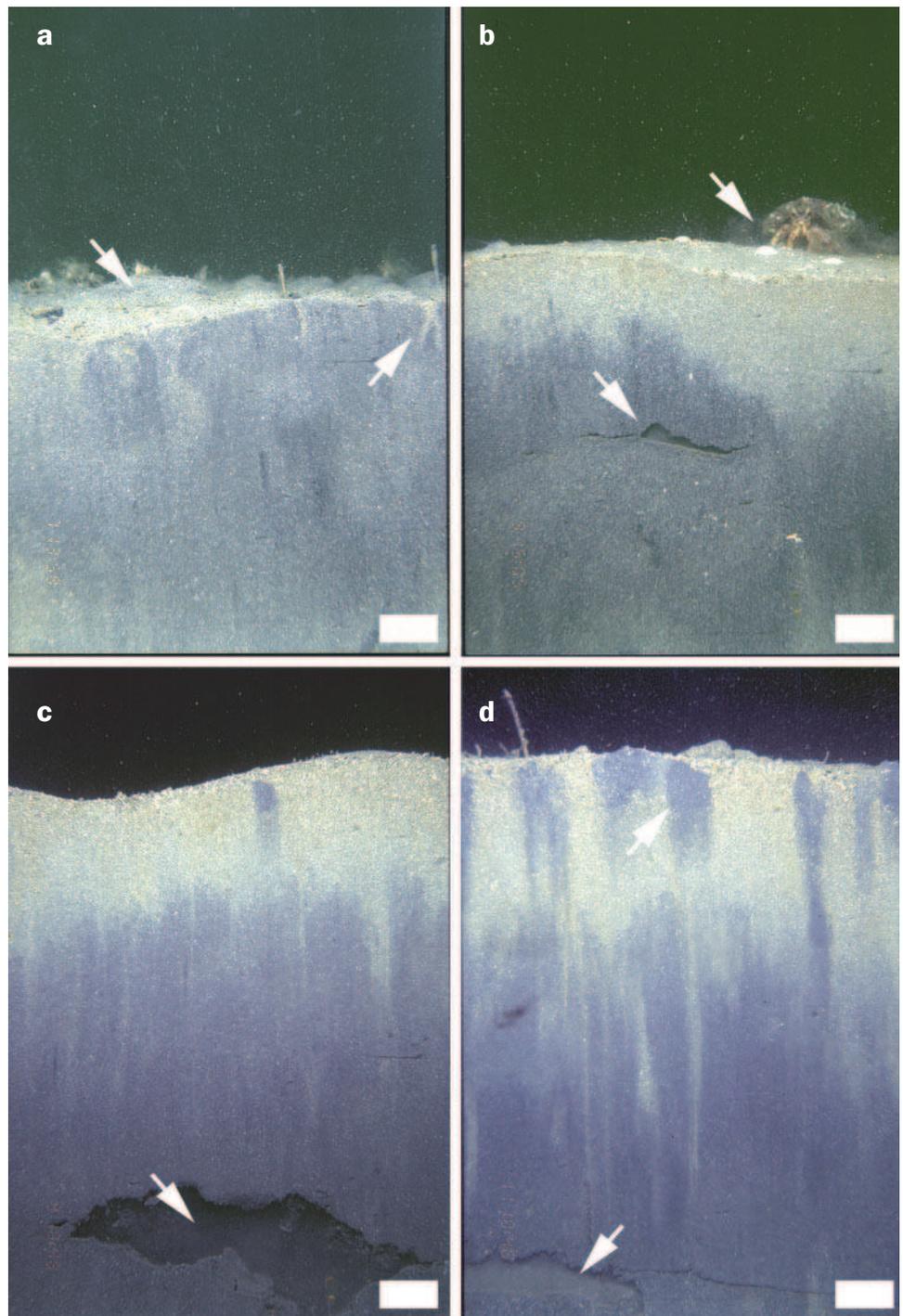


Figure 1. Sediment-profile images of the marine benthos showing the influence of invertebrate activity on sediment structure. Bioturbation results in (a) formation of mounds at the surface and zones of relatively oxygen-rich sediment around tube-worm structures; (b) epifaunal activity above the sediment-water interface by hermit crabs (*Pagurus bernhardus*) and subsurface activity by polychaete worms; (c) deep burrows, most likely formed by a spatangoid urchin (*Echinocardium cordatum*); and (d) the redistribution of oxygen-depleted, chemically reduced sediment (darker-colored sediments) from depth to the overlying mixed zone (lighter-colored sediments). These profiles contrast (a) biogenically dominated and (b, c, and d) physically dominated processes of particle redistribution. Arrows indicate specific features. Scale bars = 2.0 cm. Photographs: Martin Solan; used with permission from the University of South Carolina Press.

isolation from other habitats. Thus, when examining the functional implications of localized species loss, it is important to consider explicitly the spatial connections among various ecosystems. It is also important to consider the wide ranges of spatial heterogeneity and different residence times characterized by diverse sources of energy and nutrients in benthic ecosystems.

Linking biodiversity to the functioning of benthic ecosystems

Eighteen original, empirical studies published since 1999 examined the effects of changes in biodiversity on ecosystem processes in marine and freshwater benthic ecosystems (table 1). These studies related the average rate and temporal variability of an ecosystem process or ecosystem property to a measure of biodiversity such as species richness, evenness, or number of functional groups. The 18 studies examined a total of 32 relationships between biodiversity and ecosystem functioning, spanning a variety of ecological processes and aquatic habitat types (table 1). We categorized the relationships as positive, negative, or nonsignificant on the basis of the statistical analyses reported in the original studies. No efforts were made to search for nonlinear relationships, because the ranges of biodiversity used in most studies were generally too narrow to allow testing for curvilinear relationships between ecosystem functioning and changes in biodiversity. We also refrained from conducting a formal meta-analysis, given the small number of studies available; however, this approach will become more useful as the number of experimental studies assessing the link between benthic biodiversity and ecosystem functioning increases.

Fourteen experiments from 12 independent studies tested the relationship between biodiversity and elemental cycling. Sixteen of the 18 studies we reviewed used the number of species as the main or sole descriptor of biodiversity. Only three studies considered the potential importance of taxonomic evenness in benthic processes (Bärlocher and Graça 2002, Cardinale and Palmer 2002, Cardinale et al. 2002), but other studies recognized the importance of the relative biomass and abundance of the species that comprise an experimental community (Bolam et al. 2002). Although habitats such as ponds and wetlands were considered, only stream and estuarine benthic ecosystems were represented by multiple independent studies, and few manipulations included more than one trophic level. In most cases, the primary ecological process examined was related to elemental cycling (typically the release or retention of carbon, nitrogen, or phosphorus), productivity (usually primary production of algae or macrophytes), or organic matter decomposition (mostly allochthonous leaf litter in streams).

Results and discussion

The empirical evidence (table 1) indicates that changes in benthic species richness have highly variable effects on ecosystem functioning in terms of the magnitude and direction of responses. The variability in results observed across different

experiments in estuarine ecosystems (Raffaelli et al. 2003), where multiple studies with macroinvertebrates were carried out, suggests that either (a) thus far, evidence for strong linkages between ecosystem functioning and macrofaunal diversity in these ecosystems is lacking (Emmerson and Raffaelli 2000, Biles et al. 2003, Solan and Ford 2003), or (b) these linkages show important spatiotemporal variability (Emmerson et al. 2001, Zedler et al. 2001). Generally, even within a given experimental setting, different freshwater and marine ecosystem processes may show variable responses to the same changes in biodiversity (Bolam et al. 2002, Cardinale and Palmer 2002, Cardinale et al. 2002).

Other experiments with benthic marine and freshwater communities have demonstrated some effects of biodiversity on ecosystem functioning (table 1). For example, five of the seven studies that have explored the relationship between species richness and litter decomposition in fresh waters concluded that decomposer species diversity influenced decomposition rate (Jonsson and Malmqvist 2000, 2003a). Although decomposition of oak leaves by species mixtures of leaf-degrading fungi from streams was significantly greater than predicted from the average contributions of component species in single cultures (Bärlocher and Corkum 2003), this result was not supported by correlational evidence from a field survey (Bärlocher and Graça 2002). Likewise, Zedler and colleagues (2001) reported that the accumulation of plant biomass and nitrogen increased with the number of macrophyte species in experimental salt marsh plots (see also Engelhardt and Ritchie 2001, 2002). However, most of these experiments involved a narrow range of benthic biodiversity (typically up to six species; table 1), often specifically selected to maximize the number of functional groups present. Consequently, when biodiversity effects were detected in these studies, they occurred at rather low levels of species richness, as in biodiversity experiments that have assessed comparable effects on ecosystem processes in terrestrial environments (Loreau et al. 2002).

One difficulty in drawing general conclusions from benthic biodiversity experiments is that the results of many of the studies depend on the environmental context, and in particular on nutrient concentrations, temperature, water flow, and the frequency and severity of disturbance. For example, Cardinale and Palmer (2002) found that the effect of the number of filter-feeding species from streams (net-spinning caddisflies) on the flux of particulate organic matter and biofilm respiration varied with the experimentally manipulated disturbance regime. Similarly, the impact of dissolved nutrients (nitrogen and phosphorus) on the rate of litter decomposition appears to override effects induced by changes in fungal community composition. Experiments on the reciprocal exchange of decaying leaves between streams with distinct fungal communities demonstrated differences in dissolved nutrient concentrations and other abiotic characteristics (Suberkropp and Chauvet 1995). Microcosm experiments mimicking this fungal decomposition system also showed that nutrient effects on decomposition were

considerably greater than the effects of increases in species richness (Bärlocher and Corkum 2003). In a marine intertidal mudflat, Biles and colleagues (2003) investigated the modifying effects of water flow on the relationship between biodiversity and ecosystem functioning. They found that flow significantly affected nutrient flux in both natural and assembled macrofaunal communities, but it had no effect on nutrient flux in control systems that were free of macrofauna. Biles and colleagues concluded that flow generates a positive effect on nutrient flux by promoting changes in the bioturbatory activity of the infauna, which in turn causes greater disruption to the sediment. Such context dependency, which is probably more widespread than is currently believed, may partly account for seemingly equivocal results from different studies on benthic ecosystems.

Different mechanisms have been invoked when the effects of biodiversity on ecosystem functioning have been detected in benthic aquatic ecosystems. The sampling effect was the most commonly reported mechanism among the 14 studies that found a significant effect (table 1). Cardinale and Palmer (2002) found that in the absence of disturbance, the dominance of the superior competitor among three caddisfly species led to selected ecosystem processes being largely controlled by a single species. Engelhardt and Ritchie (2001) also concluded that the observed increase of total biomass and the reduction of phosphorus loss with increasing number of macrophyte species was mostly caused by the dominant species (see also Zedler et al. 2001), a clear case of a sampling effect. The mechanisms underlying the diversity effect observed by Bärlocher and Corkum (2003) were not clear, but they may have been the result of a sampling effect or complementarity. However, as yet there is no evidence of either pronounced species complementarity—for example, in enzymatic complements—or strong competitive interactions (interference) among fungal species that colonize decomposing leaves in streams. These results suggest that the scope for fungal biodiversity effects may be small, at least at the small spatial and short temporal scales of experiments to date.

Resource partitioning, one cause of species complementarity effects, was identified as the mechanism underlying diversity effects in a single study that showed a negative relationship between the probability of species invasion and local species diversity (Stachowicz et al. 1999). By contrast, facilitation was considered important in three studies (Cardinale and Palmer 2002, Cardinale et al. 2002, Jonsson and Malmqvist 2003b). The potential for diversity to induce facilitation, or other forms of nonadditive interaction among species, warrants particular attention in future studies. Positive interactions among species are now thought to be more prevalent than previously believed (Bruno et al. 2003), particularly in harsh or variable environments. If species diversity increases the probability or intensity of such interactions, then losses of diversity could lead to changes in ecosystem functioning that are greater than anticipated from the traits of individual species. Limited evidence suggests that declines

in the richness of stream benthic consumers can indeed reduce the probability of positive interactions and lead to non-additive decreases in carbon cycling (Cardinale and Palmer 2002, Cardinale et al. 2002, Jonsson and Malmqvist 2003b). However, the generality of these results and the mechanisms that underlie them are currently uncertain and require further testing.

Several benthic studies have highlighted the importance of changes in species diversity in response to natural or anthropogenic perturbations leading to local, nonrandom species extinctions (Crowl et al. 2001, Huryn et al. 2002, Dangles and Chauvet 2003, Larned et al. 2003, Dangles and Malmqvist 2004). Because species respond differently to different types of environmental changes, community disassembly is unlikely to be a random process. Jonsson and Malmqvist (2003b) studied the sequential loss of some benthic invertebrates involved in leaf decomposition in response to increasing levels of stream acidification and eutrophication. They found that in addition to indications of biodiversity effects, species identity also mattered greatly, with the sequence of species removal largely determining litter decomposition rate (Jonsson et al. 2002). Knowledge about such sequential losses is particularly important to predicting effects of species losses in response to environmental change in cases where deletion of a single species, or a few similarly vulnerable species, outweighs the effects of reduced species numbers per se. For example, along a gradient of pH (4.5 to 7.2) and alkalinity (0 to 800 microequivalents per liter) for headwater streams affected by acid deposition, a 60 percent reduction in macroinvertebrate richness (Guérol et al. 2000) was accompanied by an 85 percent reduction in leaf decomposition rate (Dangles and Guérol 2001). In the most acidified streams (pH < 5.0), this reduction was mediated by lower microbial activity and by changes in shredder communities. Underlying mechanisms included elevated concentrations of hydrogen and aluminum ions, which affect the ion regulation of shredders such as gammarids or trichopterans. Calcium deficiency adds to the pH and aluminum stress, especially for gastropods and crustaceans; calcium is also instrumental to the activity of fungal pectinases, a key enzyme in leaf degradation in streams. Rather than species richness, the abundance and biomass of a single acid-sensitive species, *Gammarus fossarum*, were good predictors of the variation in breakdown among streams. In this case, changes in shredder community structure through the loss of a key species caused by acidification had a profound effect on ecosystem functioning (Dangles et al. 2004a). Nevertheless, the overriding factor accounting for the drastically reduced decomposition rates appeared to be the elimination of a single species, an efficient leaf-shredding amphipod crustacean, that is particularly sensitive to stream acidification (Dangles and Guérol 2001). In some naturally acidic boreal streams, benthic diversity and leaf breakdown rates remain relatively high (Dangles et al. 2004a, 2004b).

Some fundamental problems limiting the scope for inference based on the currently available data about effects

Table 1. Summary of empirical research examining the relationship between biodiversity and ecosystem functioning in benthic habitats.

Habitat	Approach ^a	Experimental unit	Duration	Manipulated organisms	Functional or trophic group	Number of species	Diversity metric ^b	Aspect of ecosystem functioning ^b	Sign of observed effect ^c	Hypothesized mechanism	Reference ^d
Stream	O	Natural stream reaches	60 d	Aquatic hyphomycetes	Decomposer	7–20	Species richness and evenness	Litter decomposition	0	—	1
Stream	E	18-L laboratory flumes	7 d	Insects	Filter-feeder	1–3	Species richness and evenness	Carbon cycling	+	Facilitation	2
Stream	E	18-L laboratory flumes	14 d	Insects	Filter-feeder	1–3	Species richness	Carbon cycling Nutrient cycling (N, P) Periphyton production Periphyton respiration	0/+ (\$) 0/- (\$) 0/- (\$)	Facilitation Sampling effect Sampling effect	3
Stream	O	Natural stream reaches	30 d	Insects, isopods	Shredder	1–7	Species richness	Litter decomposition	+	—	4
Stream	E	1.5-L laboratory containers	46 d	Insects	Shredder	1–3	Species richness	Litter decomposition	+	—	5
Stream	E	1.0-L aquaria	48 d	Insects	Shredder	1–6	Species richness	Litter decomposition	+	Facilitation	6
Stream	O	Natural stream reaches	28 d	Insects	Shredder	1–11	Species richness	Litter decomposition	+	—	7
Stream	E	143-cm ² mesh bags in channels	14 d	Insects, amphipods	Shredder	1–3	Species richness	Litter decomposition	+	Sampling effect	8
Wetland	E	1.77-m ² tanks	4 mo	Macrophytes	Primary producer	1–3	Species richness	Phosphorus cycling	+	Sampling effect	9
Pond	E	300-L outdoor tanks	1.2 wk	Macrophytes, gastropods, amphipods, insects, frogs	Primary producer, herbivore, predator	3–15	Species richness	Litter decomposition Primary production Community respiration	0 0 +	—	10
Estuary	E	122-L outdoor tanks	6 wk	Isopods, amphipods	Herbivore	1–3	Species richness	Eelgrass production Periphyton production Herbivore production	0 0 0	—	11
Estuary	E	314-cm ² chambers in intertidal	19 hr	Polychaetes, amphipods, bivalves, gastropods	Bioturbator	1–5	Species richness	Nitrogen cycling	–	—	12
Estuary	E	314-cm ² chambers in intertidal	19 hr	Polychaetes, amphipods, bivalves, gastropods	Bioturbator	1–5	Functional group richness	Nitrogen cycling	+	—	12
Estuary	E	3.5-L aquaria	15 d	Polychaetes, amphipods, bivalves, gastropods	Bioturbator	1–5	Species richness	Nitrogen cycling	0/+	Sampling effect	13
Estuary	E	4-L aquaria	3 d	Polychaetes, amphipods, bivalves, gastropods, decapods	Bioturbator	1–5	Species richness	Nitrogen cycling	0/+	Sampling effect	14
Estuary	E	1-m ² intertidal field cages	6 wk	Macrofauna	Bioturbator	1–22	Species richness	Nitrogen cycling	0/+	—	15
Estuary	E	1-m ² intertidal field cages	6 wk	Macrofauna	Bioturbator	1–22	Species richness	Nitrogen cycling	0/+	—	15

Table 1. Continued.

Habitat	Approach ^a	Experimental unit	Duration	Manipulated organisms	Functional or trophic group	Number of species	Diversity metric ^b	Aspect of ecosystem functioning ^b	Sign of observed effect ^c	Hypothesized mechanism	Reference ^d
Estuary	E	4-m ² field plots	3 yr	Macrophytes	Primary producer	1–6	Species richness	Macrophyte production Nitrogen cycling	+	Sampling effect Sampling effect	16 16
Estuary	E	Greenhouse pots	2 yr	Macrophytes	Primary producer	1–6	Species richness	Macrophyte production Nitrogen cycling	+	Sampling effect Sampling effect	16 16
Intertidal	E	4-L aquaria	15 d	Polychaetes, amphipods, bivalves, gastropods, decapods	Bioturbator	1–4	Species richness	Nitrogen cycling	0/+ (‡)	Sampling effect	17
Intertidal	E	4-L aquaria	15 d	Polychaetes, amphipods, bivalves, gastropods, decapods	Bioturbator	Unknown	Functional group richness	Nitrogen cycling	0/+ (‡)	Sampling effect	17
Coastal	E	100-cm ² ceramic tiles	14 d	Bivalves, ascidians, bryozoans	—	1–4	Species richness	Community invasibility	–	Resource partitioning	18

cm², square centimeter; d, days; E, experimental; hr, hours; L, liter; m², square meter; mo, months; O, observational; wk, weeks; yr, years.

a. The approach of most studies was experimental (E), but three observational (O) studies are also included.

b. The biodiversity metric used and the variables reflecting ecosystem functioning are as reported in the original studies.

c. The § symbol indicates that the effect varied depending on the disturbance regime, and the symbol ‡, that the effect differed between study sites.

d. Reference key: 1: Bärlocher and Graça 2002; 2: Cardinale et al. 2002; 3: Cardinale and Palmer 2002; 4: Hurl et al. 2002; 5: Jonsson and Malmqvist 2000; 6: Jonsson and Malmqvist 2003b; 7: Jonsson et al. 2001; 8: Jonsson et al. 2002; 9: Engelhardt and Ritchie 2001; 10: Downing and Leibold 2002; 11: Duffy et al. 2001; 12: Biles et al. 2003; 13: Solan and Ford 2003; 14: Emmerson and Raffaelli 2000; 15: Bolam et al. 2002; 16: Zedler et al. 2001; 17: Emmerson et al. 2001; 18: Stachowicz et al. 1999.

Future research directions

Although a good start has been made in outlining the potential importance of biodiversity for benthic ecosystem functioning, additional studies are needed to determine how consistent and widespread the observed effects, or the lack thereof, may be. For example, information on the effects of benthic fish, and of meiofauna algal and bacterial diversity, is notably absent. Although manipulations involving invertebrate infauna in marine mudflats are well represented, there is a notable absence of studies on mobile epifauna. Moreover, experiments involving several trophic levels are essential to determine the full range of direct and indirect top-down and bottom-up effects in benthic food webs (Duffy 2002, Petchey et al. 2004). A critical question to address is the relative importance of mechanisms by which increasing

of benthic biodiversity on ecosystem functioning include the limited number of studies that have been carried out, the risk of observing artifacts in the microcosms used for experimentation, and the restriction of experiments to relatively small spatial and temporal scales. In most studies, experimentally rather than naturally assembled communities were used for analysis. Moreover, habitats were usually not “conditioned” with sufficient development of a natural microbial community before experiments were started, so it is not clear whether the experimental microbial communities actually resembled natural communities (see Biles and colleagues [2003] for an exception). Such habitat conditioning is particularly important in studies of elemental cycling in soft sediments (the focus of most biodiversity experiments in benthic marine studies), because sediment chemistry is highly dependent on recent disturbance, and disturbance is unavoidable during sediment sampling. The difficulties of experimentally controlling key abiotic factors, such as patterns of water flow, can also preclude experiments from simulating the full range of conditions experienced by natural benthic communities. Although the small spatial and short temporal scales of experiments carried out thus far have been useful for outlining the hypothesis that the number and kinds of species present affect the rates and variability of benthic ecosystem processes, the relevance of results observed in laboratory experiments needs further evaluation and verification in larger-scale field experiments. This expansion to field scales seems particularly important given that recent theory predicts the effects of species diversity on ecosystem processes will be most pronounced at large spatial and long temporal scales, where maximal heterogeneity allows the full range of species traits to be expressed (Loreau et al. 2003, Cardinale et al. 2004).

benthic species diversity may enhance ecosystem processes. In particular, what is the relative importance of species facilitation, resource partitioning, and sampling effects across different benthic habitats? Perhaps most important, future experiments aiming to assess the functional consequences of changes in benthic biodiversity need to address the spatial heterogeneity and interhabitat coupling known to moderate the coexistence of local species and the flux of materials in benthic ecosystems. Now that controlled experimental studies have outlined the potential for species richness to alter some ecosystem processes over several generations (Morin and McGrady-Steed 2004), the next step should be to move from relatively small, simple, closed experimental laboratory systems to larger, more open, interconnected experimental systems that more closely resemble natural ecosystems (Cardinale et al. 2004, Giller et al. 2004). Steps in this direction are to conduct longer-term experiments in outdoor mesocosms (Duffy et al. 2001) and to manipulate species diversity *in situ* (Parker et al. 2001, Bolam et al. 2002, Biles et al. 2003), with the results of such experiments being expected to have greater relevance for real-world phenomena than those obtained to date using a microcosm approach.

In conclusion, to better understand the role of biodiversity in regulating ecosystem processes in benthic ecosystems, it will be useful to (a) perform experiments with communities reflecting anticipated, nonrandom species losses that consider multiple effects of natural and anthropogenic disturbance; (b) consider a wider range of species that differ in their sizes, biomass, longevity, and other life-history traits; (c) extend measures of biodiversity beyond species richness; (d) incorporate multitrophic-level interactions; and (e) increase the spatial and temporal scales in experimental designs. Consideration of these points will improve the predictive value both of findings from experimental studies and of theoretical efforts to model biologically realistic scenarios of ecosystem-level effects resulting from projected species loss in benthic and other environments.

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