

4-23-2007

The functional role of biodiversity in ecosystems: incorporating trophic complexity

J. Emmett Duffy
Virginia Institute of Marine Science

Bradley J. Cardinale

Kristin E. France

Peter B. McIntyre

Elisa Thebault

See next page for additional authors

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Terrestrial and Aquatic Ecology Commons](#)

Recommended Citation

Duffy, J. Emmett; Cardinale, Bradley J.; France, Kristin E.; McIntyre, Peter B.; Thebault, Elisa; and Loreau, Michel, The functional role of biodiversity in ecosystems: incorporating trophic complexity (2007). *Ecology Letters*, 10(6), 522-538.
<https://scholarworks.wm.edu/vimsarticles/657>

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

Authors

J. Emmett Duffy, Bradley J. Cardinale, Kristin E. France, Peter B. McIntyre, Elisa Thebault, and Michel Loreau

REVIEW AND
SYNTHESISThe functional role of biodiversity in ecosystems:
incorporating trophic complexity

J. Emmett Duffy,^{1*} Bradley J. Cardinale,² Kristin E. France,¹ Peter B. McIntyre,³ Elisa Thébault⁴ and Michel Loreau⁵
¹*School of Marine Science and Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, VA 23062-1346, USA*

²*Department of Ecology, Evolution and Marine Biology, University of California-Santa Barbara, Santa Barbara, CA 93106, USA*

³*Department of Biological Sciences, Wright State University, Dayton, OH 45345, USA*

⁴*NERC Centre for Population Biology, Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*

⁵*Department of Biology, McGill University, Montreal, Québec, Canada H3A 1B1*

*Correspondence: E-mail: jeduffy@vims.edu

Abstract

Understanding how biodiversity affects functioning of ecosystems requires integrating diversity within trophic levels (horizontal diversity) and across trophic levels (vertical diversity, including food chain length and omnivory). We review theoretical and experimental progress toward this goal. Generally, experiments show that biomass and resource use increase similarly with horizontal diversity of either producers or consumers. Among prey, higher diversity often increases resistance to predation, due to increased probability of including inedible species and reduced efficiency of specialist predators confronted with diverse prey. Among predators, changing diversity can cascade to affect plant biomass, but the strength and sign of this effect depend on the degree of omnivory and prey behaviour. Horizontal and vertical diversity also interact: adding a trophic level can qualitatively change diversity effects at adjacent levels. Multitrophic interactions produce a richer variety of diversity-functioning relationships than the monotonic changes predicted for single trophic levels. This complexity depends on the degree of consumer dietary generalism, trade-offs between competitive ability and resistance to predation, intraguild predation and openness to migration. Although complementarity and selection effects occur in both animals and plants, few studies have conclusively documented the mechanisms mediating diversity effects. Understanding how biodiversity affects functioning of complex ecosystems will benefit from integrating theory and experiments with simulations and network-based approaches.

Keywords

Ecosystem functioning, grazing, horizontal diversity, niche breadth, top-down control, trophic cascade, vertical diversity.

Ecology Letters (2007) 10: 522–538

INTRODUCTION

Global biodiversity is increasingly threatened by human domination of natural ecosystems and concomitant impacts that accelerate rates of population and species extinction, and homogenization through invasion (Vitousek *et al.* 1997; Sala *et al.* 2000). These changes raise fundamental questions, such as: What are the community and ecosystem-level consequences of biodiversity loss? Will extinctions alter basic ecosystem processes, including those that produce food, purify air and water, and decompose harmful wastes? To address such questions, the relationship between biodiversity and ecosystem functioning has emerged during the last decade as a vigorous new research area linking community and ecosystem ecology (see general syntheses in Loreau *et al.* 2001, 2002; Hooper *et al.* 2005).

Well before the recent surge of interest in the functional significance of biodiversity, ecologists recognized that community structure can strongly affect the functioning of ecosystems. In particular, a large body of research had shown that loss of predator species can have impacts that cascade down a food chain to plants, altering basic ecosystem processes. One classic example is the kelp – sea urchin – sea otter food chain in the northeast Pacific. Hunting of sea otters by fur traders in the late 19th century caused a population explosion of their sea urchin prey, and consequent overgrazing of kelp forests (Estes & Palmisano 1974). Loss of kelp led to local extirpation of numerous other species that depend on kelp for habitat, as well as increased coastal erosion and storm damage since kelp was a primary buffer from wave action. Similar cascading effects of predator removal have

since been documented in a wide variety of ecosystems (Pace *et al.* 1999; Borer *et al.* 2005).

In contrast to the well-documented evidence that reducing the number of trophic levels, or removing predator species, strongly affects ecosystem-level processes, comparatively little was known about how these same processes are affected by the number of species within trophic levels. Thus, in the 1990s, a new wave of studies began to use model systems to address this issue. With notable exceptions (Naeem *et al.* 1994; McGrady-Steed *et al.* 1997), early studies focused on assemblages of primary producers, asking how plant diversity influenced aggregate (ecosystem-level) production or biomass accumulation and resource use. Most experiments found that increasing plant diversity enhanced primary producer biomass and nutrient retention (reviewed by Hooper *et al.* 2005), and attributed these biodiversity effects to two classes of mechanisms – sampling effects and complementarity (Tilman *et al.* 1997; Loreau & Hector 2001). The sampling effect refers to the greater probability of including (sampling) a highly productive species in an assemblage as species richness increases, and is based on the assumption that the most productive species is also the strongest competitor, which comes to dominate the mixture (Tilman *et al.* 1997; Huston 1997). This phenomenon was later generalized to selection effects (Loreau & Hector 2001), which can take positive or negative values depending on whether the species that ultimately dominates the mixture has relatively high or low productivity, respectively. In contrast to these competition-driven effects of changing diversity, complementarity refers to a class of processes that result in higher performance of a mixture than would be expected from the separate performances of each component species. Complementarity is often attributed to niche partitioning or facilitation (Tilman *et al.* 1997; Loreau & Hector 2001), but since it is defined statistically as the sum of all effects not attributable to selection, complementarity may also arise from indirect effects or non-linear functional responses (Sih *et al.* 1998; Ives *et al.* 2005).

Although recent studies have rapidly advanced our knowledge of diversity–function relationships, understanding the consequences of biodiversity loss in complex, natural ecosystems requires that we move beyond simple systems of competing species to incorporate processes that occur both within and among trophic levels and, importantly, the interactions of these ‘horizontal’ and ‘vertical’ processes. This integration with trophic ecology is especially important in light of growing evidence that a variety of human impacts cause preferential extinction of top predators (Dobson *et al.* 2006) and that top-down control extends farther, on average, through food webs than do bottom-up effects of resource supply (Borer *et al.* 2006). We believe that further progress in understanding how biodiversity affects ecosys-

tem functioning requires integrating the largely separate bodies of research on trophic interactions across levels and diversity effects within trophic levels. In this paper, we first suggest a conceptual framework based on an expanded concept of biodiversity–ecosystem functioning (BEF) relationships that incorporates both horizontal and vertical dimensions of diversity. Second, we review the results of recent theoretical and experimental work, focusing on four key questions as a foundation for synthesis: (1) Do biodiversity effects on resource capture and biomass production differ among trophic levels? (2) Does prey diversity influence vulnerability to consumers? (3) Do diversity effects influence the strength of cascading top-down control? (4) Do diversity effects at one trophic level depend on presence or diversity of another trophic level?

The influence of trophic interactions on ecosystem processes is potentially quite broad, and space constraints mandate some restrictions on the scope of our review. First, although ‘ecosystem functioning’ encompasses a wide variety of processes, we focus primarily on two addressed by the majority of prior work, namely changes in the combined standing stocks of all species in a trophic level, and the efficiency by which these assemblages capture resources. Second, we emphasize food webs based on living plants, and in terrestrial systems primarily the above-ground community, while recognizing the important roles of detritus (Moore *et al.* 2004), and of interactions between above- and below-ground components of food webs (e.g. Wardle *et al.* 2004; Hättenschwiler *et al.* 2005). Finally, we emphasize how horizontal and vertical diversity impact average values of ecosystem properties, while acknowledging that the temporal aspect of species interactions provides a third functional dimension, which influences how biodiversity affects community stability (Cottingham *et al.* 2001) and is an important topic in its own right. We conclude by suggesting some key challenges and opportunities for future research.

HEURISTIC FRAMEWORK: TWO-DIMENSIONAL BIODIVERSITY

We start from the premise that biodiversity can be characterized in two principal dimensions, horizontal and vertical, which interact to regulate the structure and functioning of ecosystems. These aspects can be visualized using the traditional two-dimensional depiction of a food web or interaction web (Fig. 1). Functionally, both dimensions entail two hierarchical levels of diversity: (1) within-species variation, corresponding to degree of omnivory (vertical niche breadth) in the vertical dimension, or degree of resource generalism (horizontal niche breadth) in the horizontal dimension; and (2) among-species variation, describing the number of trophic levels in the vertical

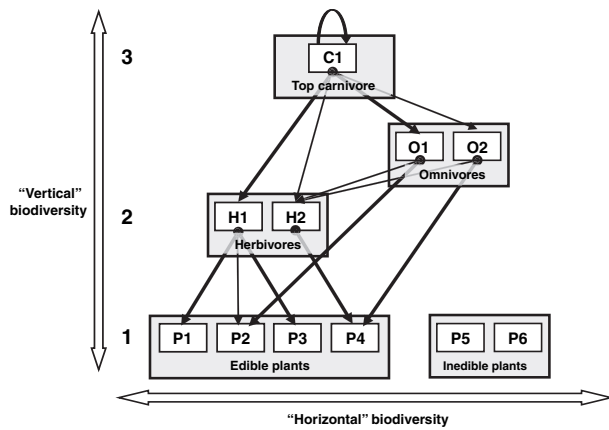


Figure 1 Schematic food web illustrating components of horizontal and vertical diversity discussed in the text. The web consists of 11 species. Components of vertical diversity include an average food chain length of 2.58 (averaging across all eight food chains in the web, with thick arrows = 1.0, and thin arrows = 0.1), and the presence of species with smaller (herbivores) and larger (omnivores, and cannibalistic top carnivore) vertical niche width. Components of horizontal diversity include, at the basal level, two functional groups containing two and four species each; consumer species with narrow and broader horizontal niche widths, represented by the specialist (H2) and generalists (H1, O1 and O2), respectively. For clarity, competitive interactions are not shown.

dimension (food chain length, FCL), and number of species within a trophic level in the horizontal dimension. The separation between horizontal and vertical diversity is incomplete in that omnivory can entail increased niche breadth in both the horizontal and vertical dimensions. However, distinguishing these two dimensions clarifies how ecosystem functioning may be affected separately or simultaneously by consumptive interactions across trophic levels and competitive processes within levels (Table 1). In principle, the two-dimensional approach links the largely separate but clearly interdependent fields of BEF (focusing on horizontal diversity), trophic and predator–prey ecology (vertical diversity), and food web ecology.

Horizontal diversity

Horizontal diversity constitutes the taxonomic or functional richness and evenness of entities (species, genes, etc.) within a single trophic level.

Species and functional diversity

Species richness and evenness are the two most widely used metrics of horizontal diversity, recognizing the species as a fundamental unit in biology. Realized diversity is affected by the relative abundance of species, which is often strongly

skewed in natural communities due to the large number of rare species (i.e. evenness is low). Nevertheless, species richness defines the variety of phenotypic traits that can be expressed in a system, and thus the range of functional traits available as conditions change. The few available studies indicate that richness of genotypes within a population can affect ecosystem properties in ways qualitatively similar to those of species richness (e.g. Hughes & Stachowicz 2004; Crutsinger *et al.* 2006). An underlying assumption of research linking species diversity to ecosystem functioning is that species richness serves as a useful proxy for the diversity of functionally distinct entities. Several approaches have aimed to quantify functional diversity more explicitly, ranging from subjective functional groups to quantitative metrics that summarize differences among species in multivariate trait space (reviewed by Petchey & Gaston 2006). A central issue is whether easily measured, species-level traits (e.g. body size) are valid predictors of contributions to ecosystem functioning.

Horizontal niche breadth

Resource specificity is of central importance in mediating the strength and nature of interspecific competition, and to indirect effects such as apparent competition. For these reasons, the degree of resource specialization influences the relationship between species and functional diversity, and has correspondingly important effects on how species diversity mediates ecosystem processes. For example, niche models show that, all else being equal, specialization in resource use causes aggregate resource and consumer densities to increase linearly with species richness (Thébaud & Loreau 2003; Ives *et al.* 2005). In contrast, increasing the richness of generalists often does not affect standing stocks of resources or consumers, and intermediate levels of specialization can cause standing stocks to become a unimodal function of diversity (Ives *et al.* 2005). Thus, both the quantitative and qualitative forms of diversity–function relationships depend strongly on the degree of resource specialization.

Vertical diversity

A large body of studies in classical trophic ecology has demonstrated the mechanisms and impacts of trophic interactions on ecosystems (e.g. Pace *et al.* 1999; Chase *et al.* 2002; Borer *et al.* 2005, 2006). Well-developed theory also has explored the role of FCL and degree of omnivory in regulating the distribution of biomass and productivity among trophic levels (e.g. Hairston *et al.* 1960; Fretwell 1977; Oksanen *et al.* 1981; Leibold 1989; Polis & Holt 1992). Most of this research, however, has focused on effects of single predator species (but see Sih *et al.* 1998), and has yet to be integrated with research focusing on effects of

Table 1 Summary of hypothesized effects of changing horizontal and vertical diversity, and the theoretical and experimental studies addressing those hypotheses that are discussed in the text. Consumer and prey biomass refer to aggregate, community-level properties.

Diversity component	Ecosystem response	Hypothesized effects of diversity	Theory: references	Empirical tests of hypotheses: references
(A) Horizontal diversity				
Consumer species richness	Resource capture and consumer biomass production	Increasing consumer richness increases consumer biomass, reduces resource standing stock	Tilman <i>et al.</i> (1997); Loreau (2000); Loreau & Hector (2001)	Denoth <i>et al.</i> (2002, review); Balvanera <i>et al.</i> (2006, meta-analysis); Cardinale <i>et al.</i> (2006a, meta-analysis)
Consumer species richness	Resource capture and consumer biomass production	Effects of increasing richness on focal trophic level biomass and resource capture are similar across levels	Sih <i>et al.</i> (1998); Holt & Loreau (2002); Duffy (2002); Fox (2003, 2004); Thébault & Loreau (2003, 2005); Ives <i>et al.</i> (2005)	Balvanera <i>et al.</i> (2006, meta-analysis); Cardinale <i>et al.</i> (2006a, meta-analysis)
Consumer species richness	Standing stock of prey's resource (trophic cascade strength)	Increasing consumer richness indirectly increases resource standing stock through a trophic cascade	Strong (1992); Duffy (2002)	Cardinale <i>et al.</i> (2003); Wardle <i>et al.</i> (2004); Borer <i>et al.</i> (2005, meta-analysis); Bruno & O'Connor (2005); Finke & Denno (2005); Wilby <i>et al.</i> (2005); Byrnes <i>et al.</i> (2006); Cardinale <i>et al.</i> (2006b); Snyder <i>et al.</i> (2006)
Prey species richness	Prey biomass in presence of consumer	Increasing prey richness reduces consumer impact on total prey community biomass (general hypothesis)	Leibold (1989); Strong (1992); Duffy (2002)	Andow (1991); Schmitz <i>et al.</i> (2000); Hillebrand & Cardinale (2004, meta-analysis); Borer <i>et al.</i> (2005, meta-analysis); Wojdak (2005); Duffy <i>et al.</i> (2005)
Prey species richness	Prey biomass in presence of consumer	Increasing prey richness reduces consumer impact on total prey community biomass (variance in edibility hypothesis)	Leibold (1989); Holt & Loreau (2002); Thébault & Loreau (2003, 2005)	Steiner (2001); Duffy <i>et al.</i> (2005)
Prey species richness	Prey biomass in presence of consumer	Increasing prey richness reduces consumer impact on total prey community biomass (dilution or resource concentration hypothesis)	Root (1973); Ostfeld & LoGiudice (2003); Joshi <i>et al.</i> (2004); Keesing <i>et al.</i> (2006)	Wilsey & Polley (2002); Otway <i>et al.</i> (2005); Keesing <i>et al.</i> (2006)
Prey species richness	Prey biomass in presence of consumer	Increasing plant richness reduces herbivore impact on total plant community biomass (enemies hypothesis)	Root (1973)	Andow (1991)
Prey species richness	Consumer biomass production/performance	Increasing prey richness increases consumer performance (balanced diet hypothesis)	DeMott (1998)	DeMott (1998); Pfisterer <i>et al.</i> (2003); Worm <i>et al.</i> (2006)
Consumer niche breadth	Prey capture and consumer biomass/production	Increasing consumer generalism (horizontal niche breadth) reduces or alters the impact of consumer richness on prey biomass	Thébault & Loreau (2003, 2005); Ives <i>et al.</i> (2005); Casula <i>et al.</i> (2006)	Bruno & O'Connor (2005); Finke & Denno (2005)

Table 1 (continued)

Diversity component	Ecosystem response	Hypothesized effects of diversity	Theory: references	Empirical tests of hypotheses: references
(B) Vertical diversity				
Food chain length (odd number of levels)	Plant biomass	Removal of predators from a food chain with odd number of levels reduces plant biomass (trophic cascade)	Hairston <i>et al.</i> (1960); Fretwell (1977); Oksanen <i>et al.</i> (1981)	Borer <i>et al.</i> (2006, meta-analysis)
Food chain length (even number of levels)	Plant biomass	Removal of predators from a food chain with even number of levels increases plant biomass (trophic cascade)	Hairston <i>et al.</i> (1960); Fretwell (1977); Oksanen <i>et al.</i> (1981)	Borer <i>et al.</i> (2006, meta-analysis)
Average degree of omnivory (including intraguild predation)	Plant biomass (trophic cascade strength)	Increasing omnivore richness reduces plant biomass; increasing carnivore diversity increases plant biomass	Polis & Strong (1996)	Bruno & O'Connor (2005); Finke & Denno (2005)
(C) Horizontal and vertical diversity				
Prey species richness × food chain length	Prey biomass	Removal of predators alters relationship between prey richness and prey biomass	Holt & Loreau (2002); Thébault & Loreau (2003, 2005)	Mulder <i>et al.</i> (1999); Duffy <i>et al.</i> (2005); Hättenschwiler & Gasser (2005); Wojdak (2005)
Prey species richness × food chain length	Basal resource standing stock (trophic cascade strength)	Increasing herbivore richness reduces predator impact on total plant biomass (trophic cascade strength)	Duffy (2002)	Schmitz <i>et al.</i> (2000, meta-analysis); Borer <i>et al.</i> (2005, meta-analysis)
Plant species richness × decomposer species richness	Plant biomass	Changing plant richness and changing decomposer richness have opposing effects on plant biomass	Loreau (2001)	Naeem <i>et al.</i> (2000)
Consumer species richness × prey species richness (factorial)*	Consumer and prey biomass	Increasing consumer richness alters relationship between prey richness and prey biomass in complex ways, depending on assumptions	Holt & Loreau (2002)	Fox (2004); Aquilino <i>et al.</i> (2005); Gamfeldt <i>et al.</i> (2005)
Consumer species richness × prey species richness (parallel)†	Consumer and prey biomass	Increasing richness at multiple trophic levels simultaneously has complex effects on ecosystem properties (e.g. plant biomass), depending on assumptions	Thébault & Loreau (2003, 2005); Worm & Duffy (2003)	Naeem <i>et al.</i> (1994); McGrady-Steed <i>et al.</i> (1997); Mikola & Setälä (1998); Downing (2005)

*Factorial: species richness at consumer and prey levels was manipulated in factorial design.

†Parallel: species richness at consumer and prey levels was manipulated simultaneously in parallel.

(horizontal) diversity on ecosystem-level productivity and resource capture. We use vertical diversity as a general term to summarize the functional complexity of a system in the vertical dimension. Although vertical diversity could encompass several characteristics of the food web, we focus on two components that have clear functional importance and that have analogues in the horizontal dimension, namely FCL and degree of omnivory.

Food chain length

FCL describes the average number of times that energy is transferred as it moves from basal resources to top predators. FCL is the simplest starting point for quantifying vertical diversity of a community, and because it strongly influences magnitude and efficiency of trophic transfer, FCL is directly related to ecosystem functioning. Mean FCL of a community can be quantified as a weighted average across all its component food chains (Williams & Martinez 2004; Fig. 1). Theory (Fretwell 1977; Oksanen *et al.* 1981) and empirical research (e.g. Pace *et al.* 1999; Borer *et al.* 2005, 2006) show that FCL often has wide-ranging impacts on the structure and functioning of ecosystems mediated by the cascading influence of predators.

Vertical niche breadth

Although discrete trophic levels are indeed apparent in many real food webs (Williams & Martinez 2004), omnivory, intraguild predation, cannibalism and ontogenetic diet shifts are common (Polis & Strong 1996), potentially blurring the boundaries among trophic levels. Here we consider omnivory in the general sense as feeding from more than one trophic level. Intraguild predation is a subset of omnivory in which consumers feed on prey at both their own and the next lower level. Just as the degree of resource specialization plays an important role in how horizontal diversity affects ecosystem functioning, vertical niche breadth influences the strength of top-down control and consequent ecosystem effects (Polis & Holt 1992). For example, omnivory should blur the alternating bottom-up and top-down control expected at alternating levels in simple models (e.g. Hairston *et al.* 1960), with fundamental implications for the distribution of biomass and productivity among levels. The average degree of omnivory could yield an estimate of vertical niche breadth at the community level (e.g. Williams & Martinez 2004) analogous to the degree of resource generalism in the horizontal dimension.

Integrating horizontal and vertical diversity

Theoretical efforts to merge research on functional effects of trophic interactions and diversity have appeared only recently (Holt & Loreau 2002; Fox 2003, 2004; Thébault & Loreau 2003, 2005; Ives *et al.* 2005; Casula *et al.* 2006).

These interactions between vertical and horizontal processes are at the heart of several important problems in ecology (Table 1), which we consider in detail in the subsequent sections. For example, how prey diversity influences vulnerability to consumers is central to long-standing debates about the factors controlling ecological efficiency in food chains, and the regulation of trophic cascades and top-down control generally. Whether diversity effects at one trophic level depend on presence or diversity of another level is critical to evaluating the generality of the last decade's research on ecosystem effects of biodiversity, much of which has been conducted in experimental systems with a single trophic level. And how diversity loss at different trophic levels affects ecosystem function is important to understanding how ecosystems will respond to trophic skew in extinction (Duffy 2003; Dobson *et al.* 2006).

Limitations of a two-dimensional concept of biodiversity

Although we believe vertical diversity provides a useful, general term to summarize the complexity of trophic structure and interactions, the concept has limitations in potentially lumping several aspects of trophic structure that can influence ecosystem functioning in different ways. The same could be said of the very general term 'biodiversity', which has traditionally been used in the BEF literature to convey several aspects of variation within a trophic level, and has nonetheless proved useful as a summary term. Although our concepts of vertical and horizontal diversity have some parallels, we emphasize that interactions among vs. within trophic levels are clearly distinct and entail different mechanisms. For example, increases in FCL are hypothesized to have alternating positive and negative effects on total plant biomass (Hairston *et al.* 1960), in contrast to the monotonic increase in plant biomass expected with increasing horizontal diversity (Tilman *et al.* 1997; Loreau 2000). Thus, our conceptual framework is meant primarily to emphasize that ecosystem functioning depends jointly on the complexity of trophic processes among levels and of competitive and facilitative interactions within levels, and to organize our discussion of those interactions. We also note that BEF research has many ideas that parallel classical trophic ecology, and that the two areas of research need to be merged to better understand the functional significance of biodiversity in the broadest sense.

BIODIVERSITY EFFECTS ON RESOURCE CAPTURE AND PRODUCTION AT DIFFERENT TROPHIC LEVELS

To date, well over half of diversity–functioning experiments have focused on primary producers (Balvanera *et al.* 2006;

Cardinale *et al.* 2006a). Recently, however, an increasing number of theoretical and empirical studies have addressed the functional effects of biodiversity at higher trophic levels. As a first step towards integrating horizontal and vertical diversity, it is important to ask whether there are general patterns in these studies, that is, are the effects of horizontal diversity on production and resource use comparable use across trophic levels?

Theoretical predictions

Most mathematical models predict that plant biomass and primary production increase with plant species richness as a result of both functional complementarity and selection of highly productive species (Tilman *et al.* 1997; Loreau 2000; Loreau & Hector 2001). Heuristic theory has suggested that fundamental biological differences between animals and plants may produce qualitatively different impacts of diversity changes at higher vs. lower trophic levels on ecosystem properties (Duffy 2002). The rationale for this prediction is that animals consume biological resources with density-dependent dynamics that can be overexploited and collapse, unlike the donor-controlled inorganic nutrients consumed by plants (Ives *et al.* 2005), that animals commonly exhibit omnivory, intra-guild predation (Polis & Holt 1992), and complex behaviours (Werner & Peacor 2003), and that their mobility adds greater spatial complexity to interactions (Polis *et al.* 1997).

Mathematical models are partly consistent with these heuristic predictions. First, in Lotka–Volterra models, the continuous, ‘donor-controlled’ supply of inorganic resources causes plant biomass to increase monotonically with plant richness, whereas animal consumers can potentially drive their dynamic prey extinct, resulting in a concave–down relationship between consumer richness and consumer biomass (Ives *et al.* 2005). Second, when competitive superiority results from high assimilation efficiencies (which is most likely for plants), trophic group biomass is a monotonically increasing function of diversity. In contrast, when competitive dominance is achieved by high resource capture rates (which is more likely for animals), a superior species can simultaneously drive down its prey and, in turn, its own equilibrium population size (Holt & Loreau 2002; Ives *et al.* 2005). As a result, consumer biomass again becomes a concave–down function of diversity. Mathematical models also show that predator diversity can differentially affect prey biomass depending on levels of intraguild predation and additivity of interactions (Ives *et al.* 2005; Casula *et al.* 2006).

Perhaps surprisingly, the addition of these more complex interactions may only modify the magnitude, and not the qualitative form, of diversity effects that are

established by resource partitioning and sampling (Ives *et al.* 2005), which tend to be the principal mechanisms underlying diversity effects and are fundamentally similar across trophic levels (Holt & Loreau 2002; Fox 2003, 2004; Thébault & Loreau 2003, 2005; Ives *et al.* 2005). Moreover, in all these models, increasing consumer species richness reduces total resource (prey) standing stock more, and tends to increase total consumer biomass more, when consumers are specialists (low horizontal niche breadth) than when they are generalists (greater horizontal niche breadth). When consumers are generalists, however, the qualitative forms of these relationships can change depending on the extent of resource overlap (Ives *et al.* 2005).

Finally, animal consumers may also affect prey biomass indirectly by changing prey diversity (Chase *et al.* 2002), which in turn can affect prey secondary production (Ives *et al.* 2005). Thus, increasing consumer diversity can decrease total prey biomass through any of three mechanisms: (1) overexploitation of prey; (2) reduction in prey species richness and consequently reduced prey production; and (3) dominance by less competitive prey species when there is a trade-off between competitive ability and resistance to predation (Thébault & Loreau 2003).

Empirical results

Two recent meta-analyses provide the first rigorous tests of whether diversity effects on ecosystem properties differ among trophic levels. Cardinale *et al.* (2006a) collected data from 111 experimental manipulations of diversity encompassing a broad range of trophic groups and habitats, and presented two key results. First, on average, experimental reduction of species richness decreased the abundance or biomass of the focal trophic group, and resulted in less complete resource use by that group. Second, the standing stock of, and resource depletion by, the most diverse polycultures were statistically indistinguishable from those of the single species that performed best in monoculture. Both of these results were quite consistent across four trophic groups, including primary producers assimilating inorganic nutrients or water, herbivores consuming live plant tissue, predators consuming live prey, and detritivores consuming dead organic matter. A parallel meta-analysis (Balvanera *et al.* 2006), which included observational studies and a broader range of experimental designs, confirmed the first result of Cardinale *et al.* (2006a), that increasing species richness increased average standing stocks and resource use, and that this effect was similar among trophic levels.

Most studies analysed by the two meta-analyses did not report the data necessary to confirm the underlying

mechanisms behind the diversity effects they documented. At this stage, the safest conclusion is that transgressive overyielding (i.e. mixture performance that exceeds even the best monoculture) is uncommon in studies conducted to date. This result shows some parallel with a recent meta-analysis of 167 biological control projects against weeds and insect pests, which concluded that the success of biological control frequently increased with the number of agents released, but that in most successful multiple-agent projects, a single species was responsible for successful control (Denoth *et al.* 2002). Although these studies are not strictly comparable with BEF experiments, because in biological control the target is usually a single (or few) species of pest rather than aggregate trophic-level biomass, the similarity in patterns is intriguing.

Summary and conclusions

Heuristic predictions that diversity in higher trophic levels should have different impacts on ecosystem functioning than diversity at lower trophic levels are not borne out by currently available data. Meta-analyses of diversity–function experiments reveal strikingly consistent effects of diversity on standing stock and resource capture by different trophic groups. On average, decreasing species richness leads to lower standing stocks and, in turn, lower rates of resource capture. But diverse communities rarely performed differently than the best-performing monocultures. Both of these patterns are independent of trophic level. In most cases, however, there is insufficient evidence to judge which biological mechanisms underlie these patterns.

There are at least two important caveats in interpreting existing data. First, studies of diversity effects at higher trophic levels are still relatively rare, and almost entirely lacking for vertebrates, which have relatively stronger top-down impacts on ecosystems, on average, than invertebrates (Borer *et al.* 2005). Second, the spatial complexity of interactions between mobile animals and their resources has rarely been incorporated into BEF experiments (France & Duffy 2006), yet a key feature of top predators is their high mobility and ability to connect dynamics of spatially or functionally distinct communities through their movements (McCann *et al.* 2005). Thus, further research will be required to resolve whether the similarity among trophic levels in the effects of species richness represents a broad generality.

PREY DIVERSITY AND THE STRENGTH OF TOP-DOWN CONTROL

Most previous studies of biodiversity effects on ecosystem functioning, both theoretical and empirical, have addressed

how the diversity of consumers (including plants) influences the capture of resources (prey or inorganic nutrients) and conversion to biomass. An important step in broadening our view is to ask the converse question: How does diversity at a focal trophic level influence its vulnerability to its own predators – that is, how does prey diversity affect the strength of top-down control?

Theoretical predictions

A number of verbal hypotheses have been proposed to explain how the diversity of resources might affect consumer impact on those resources, including the following. (1) The ‘variance in edibility hypothesis’, argues that a resource base with more species is more likely to contain at least one species that is resistant to consumption and can dominate in the presence of consumers (Leibold 1989; Duffy 2002; Hillebrand & Shurin 2005); this is analogous to a selection effect (Loreau & Hector 2001) at the resource rather than consumer level. (2) The ‘dilution or resource concentration hypothesis’ (Root 1973; Ostfeld & LoGiudice 2003; Joshi *et al.* 2004, Keesing *et al.* 2006) suggests that a more diverse resource base reduces both the relative and absolute abundances of resources available to specialist consumers, leading to lower efficiency of the consumer community. (3) The ‘enemies hypothesis’, developed for arthropod assemblages on terrestrial plants, argues that natural enemies of herbivores are more abundant in plant polycultures and, in turn, reduce herbivore populations (Root 1973). (4) Finally, the ‘balanced diet hypothesis’ holds that a more diverse resource assemblage provides a more complete range of nutritional resources, translating to higher consumer biomass (DeMott 1998), which could in turn result in stronger top-down control.

The variance-in-edibility hypothesis has been formalized mathematically, showing that the presence of inedible species can be a key factor that modifies the strength of top-down control in food webs (Leibold 1989; Holt & Loreau 2002). In models with two trophic levels and covarying plant and herbivore diversity, Thébaud & Loreau (2003, 2005) showed that the dependence of plant biomass on plant diversity can shift qualitatively from monotonically increasing to hump-shaped depending on the relationship between a plant’s resistance to herbivory and its competitive ability. Specifically, when plant species exhibit a trade-off between resistance and competitive ability, plant biomass decreases at the highest levels of diversity because dominance of consumer-resistant plant species is reduced by superior competitors that are losing biomass to herbivory. Thus, in multitrophic systems, species edibility could be an important mediator of diversity effects because it can lead to strong shifts in dominance, which in turn can strongly affect ecosystem properties.

Models have formalized the dilution hypothesis primarily in the context of how disease risk is influenced by diversity. For example, Ostfeld & LoGiudice (2003) used simulations to show that the prevalence of Lyme disease in mammalian hosts decreases as mammal diversity increases. Dilution effects in this model derive from the assumption that both the absolute and relative density of the focal resource species (mammalian hosts in this case) decrease as a function of increasing resource species diversity.

Empirical results

A considerable body of evidence supports the hypothesis that prey diversity often reduces the impact of consumers on aggregate prey standing stock. Perhaps the most comprehensive evidence comes from Andow (1991), who tallied results of 209 studies of 287 herbivorous arthropod species. In just over half (149) of the species examined, herbivores had lower population densities on plants in polycultures than in monocultures, whereas only 44 species had higher densities in polycultures. Andow concluded that the resource concentration hypothesis best accounted for these patterns, but also emphasized that there were many exceptions, and that responses of polyphagous (generalist) herbivores in particular were often unpredictable.

Hillebrand & Cardinale (2004) conducted a meta-analysis of data from 172 experimental manipulations of herbivores across a wide range of aquatic ecosystems to test the hypothesis that algal diversity modifies the magnitude of herbivory. Consistent with the hypothesis, and with Andow's (1991) results, herbivore impacts on algal biomass declined as algal diversity increased. Since algal diversity was not directly manipulated in these studies, however, the underlying cause of this pattern could not be determined.

Other studies have used controlled experiments to explore the potential mechanisms underlying the effects of prey diversity on consumer impact in controlled experiments. Steiner (2001) found support for the variance-in-edibility hypothesis, showing that inedible algae in a diverse planktonic assemblage flourished under intense grazing pressure, reducing total grazing impact at high algal diversity. Evidence consistent with the variance-in-edibility hypothesis was also found at the herbivore level in a seagrass system, where crab predators had weaker impact on a diverse assemblage of crustacean herbivore species than on the average herbivore monoculture (Duffy *et al.* 2005). In this case, the dominance of particular herbivore species under predation was probably due more to its resistance to capture than to lower edibility *per se*.

Support for the dilution hypothesis comes primarily from studies of host/disease dynamics. A recent review found that high host diversity often reduces disease risk, particularly when disease transmission is frequency-dependent

and greater within than between host species (Keesing *et al.* 2006). This occurs because high-diversity host assemblages tend to have lower density of any given host species and fewer opportunities for disease transmission. Examples of the dilution effect of diversity in macroscopic consumer-prey systems are scarcer, but reduced plant evenness enhanced the density of spittlebug pests, evidently by increasing intraspecific density of their hosts (Wilsey & Polley 2002). Plant diversity can also reduce infestation by specialist insect parasites, probably for similar reasons (Otway *et al.* 2005). Increasing plant diversity also often increases the density of arthropod parasitoids and predators, consistent with the enemies hypothesis, but the greater abundance of enemies correlates with lower abundance of insect herbivores only for specialized (monophagous) species (Andow 1991).

Several empirical studies are consistent with the balanced diet hypothesis in that mixed diets of primary producers enhanced herbivore growth and biomass accumulation compared with single-species diets (e.g. DeMott 1998; Pfisterer *et al.* 2003; Worm *et al.* 2006). To date, however, neither theory nor experiments have considered how the benefits to predators of a mixed diet might feed back to affect prey biomass or productivity.

Summary and conclusions

Heuristic theory proposes at least three hypotheses by which increasing prey diversity can alter total impact of higher trophic levels: (1) the variance in edibility hypothesis; (2) the dilution or resource concentration hypotheses; and (3) the enemies hypothesis. Although there are exceptions, the balance of evidence from herbivores consuming freshwater algae, predators attacking marine invertebrates, and insects on plants indicates that increasing prey diversity often leads to lower total consumption or impact by higher trophic levels, and both the variance in edibility, and the dilution hypotheses have received empirical support. In contrast, the enemies hypothesis has received mixed support from experiments (Andow 1991).

BIODIVERSITY AND THE STRENGTH OF CASCADING TOP-DOWN CONTROL

The previous sections show that experimental manipulations of diversity at either predator or prey levels commonly affect transfer of resources between trophic levels. Since trophic cascades to non-adjacent levels also are well documented across a range of ecosystems (Pace *et al.* 1999; Borer *et al.* 2005), we now turn to the question: do effects of diversity, at either prey or predator levels, influence the cascading effects of predators on non-adjacent trophic levels?

Theoretical predictions

In an influential paper, Strong (1992) argued that trophic cascades are more common in aquatic than in terrestrial systems, and that this proposed difference stems from greater functional diversity of terrestrial than aquatic vegetation. Although the suggested paucity of trophic cascades on land has proven controversial (Strong 1992; Pace *et al.* 1999; Terborgh *et al.* 1999), Strong's suggestion focused attention on the potential influence of functional diversity on the balance between bottom-up and top-down control in food webs. It seems reasonable to expect that the same mechanisms that mediate impacts of consumer and prey diversity on prey capture in models of two-trophic level systems (Thébault & Loreau 2003, 2005; Ives *et al.* 2005), and in experiments, might also mediate the cascading indirect effects of carnivores on plants. Yet the effects of diversity on ecosystem functioning at non-adjacent trophic levels have scarcely been studied using theoretical approaches.

Empirical results

How does prey diversity affect the strength of trophic cascades? Although the experiments reviewed in the previous section support the idea that prey diversity can dampen top-down control, explicit tests of how diversity affects trophic cascades (i.e. in systems with three or more trophic levels) are rare. Perhaps the most comprehensive study manipulated species richness of grazing pond snails in combination with nutrient loading and presence of predatory water bugs (Wojdak 2005). Although predators generally reduced grazer biomass, this effect did not change with grazer diversity, and predator effects did not consistently cascade to increase primary producer biomass, apparently because of compensatory changes among functional groups in the different food web treatments. In contrast, manipulation of grazing crustaceans in a seagrass system indicated that the effect of predatory crabs on grazer biomass declined with grazer richness, but that this damping effect of diversity did not cascade to algal biomass, which was strongly enhanced by predators regardless of grazer richness (Duffy *et al.* 2005). Thus, the very few experiments available provide no support for a dampening effect of prey diversity on trophic cascade strength.

How does predator diversity affect the strength of trophic cascades? Several experiments have manipulated predator diversity and directly measured the indirect cascading effects on plants. Some of these have shown that increasing predator diversity indirectly increases plant performance in agricultural (Cardinale *et al.* 2003; Wilby *et al.* 2005; Snyder *et al.* 2006), salt marsh (Finke & Denno 2005), and kelp forest systems (Byrnes *et al.* 2006). In agricultural systems, cascading effects of biodiversity were

attributed to non-additive interactions among predators, either positive (Cardinale *et al.* 2003) or negative (Cardinale *et al.* 2006b), illustrating emergent impacts of multi-predator assemblages (Sih *et al.* 1998). In both the salt marsh and kelp systems, cascading effects of predator diversity were mediated by changes in herbivore behaviour, with no corresponding impact on herbivore numbers. These results, although limited, are consistent with the growing evidence that cascading impacts of predators on primary producers often occur through trait-mediated indirect effects, specifically by modifying behaviour rather than via changes in herbivore density (Werner & Peacor 2003).

Experiments further suggest that a primary factor that influences diversity effects at higher trophic levels is the high frequency of omnivory and intraguild predation in real food webs – that is, broad vertical niche breadth of predators. For example, whereas increasing carnivore diversity would be expected to increase trophic cascade strength, an experiment in a marine rocky shore community found that increasing predator diversity instead reduced algal biomass because the most diverse predator communities contained omnivores that fed on both herbivores and algae (Bruno & O'Connor 2005). The influence of intraguild predation on cascading effects of predator diversity on plants was addressed explicitly in a salt marsh food web (Finke & Denno 2005): when all predators were 'strict' predators on lower-level consumers (no intraguild predation), higher predator diversity had no effect on herbivore numbers but nevertheless markedly increased biomass of marsh grass by altering herbivore behaviour. In contrast, increasing richness of intraguild predators had the opposite effect, reducing predation impact on herbivores with a concomitant reduction in marsh grass biomass. Thus, the cascading impacts of predator diversity differed in sign depending on whether or not predators fed on one another, potentially reflecting a shift between 'risk reduction' and 'risk enhancement' effects of multiple predators (Sih *et al.* 1998). Although several such experiments document emergent predator effects, meta-analysis of the relatively small number of studies available (Cardinale *et al.* 2006a) found no evidence that multi-predator systems generally perform differently than do the single best predator species, on average.

Finally, one can also approach the hypothesized role of diversity in trophic cascades indirectly, by comparing the strength of trophic cascades across experiments that differed in diversity. Meta-analysis of 14 terrestrial trophic cascade experiments found that cascading effects of predator removal on plant damage and reproduction were indeed weaker in systems with higher herbivore diversity (Schmitz *et al.* 2000). However, a more recent, comprehen-

sive analysis found no effect of species richness at predator, herbivore, or plant levels on cascade strength, either within or across ecosystem types (Borer *et al.* 2005). While these results are suggestive, such meta-analyses probably have low power to detect diversity differences since the range in diversity considered is often limited and natural variation in diversity generally covaries with environmental factors that may also influence cascade strength.

Summary and conclusions

Limited as they are, empirical data on cascading effects of predator diversity appear to be somewhat ahead of theory, which has not considered such effects explicitly. Meta-analyses of trophic cascades find mixed support for the hypothesis that prey species richness dampens cascade strength, and suggest that factors such as ecosystem type and predator metabolism are more important (Schmitz *et al.* 2000; Borer *et al.* 2005). At the predator level, available experiments show that increasing predator diversity can lead to either stronger or weaker cascading effects on plants, an important determinant being the degree of vertical niche width (omnivory) among predators. Few such experiments have explicitly compared the effects of strict vs. omnivorous predators, but the vertical niche width and plasticity of many animal species may give rise to a fundamental difference between the functional consequences of animal vs. plant species richness.

INTERACTIONS BETWEEN HORIZONTAL AND VERTICAL DIVERSITY

Thus far we have focused on the effects of changing diversity within a single trophic level. In real ecosystems, processes that influence diversity are likely to operate across multiple trophic levels simultaneously (Fig. 2), and changes in diversity at adjacent levels can have quite different effects on a given ecosystem process than those at a single level (Thébaud & Loreau 2003). A critical issue is whether the impacts on ecosystems of diversity loss in two dimensions are opposing or reinforcing, and additive or synergistic. Although the answer will likely depend on order and distribution of extinctions among trophic levels, we can ask two related questions as a first step towards understanding such interactions: (1) Do diversity effects within a trophic level depend on the number of trophic levels in the system (i.e. vertical diversity)? (2) Do they depend on horizontal diversity at adjacent trophic levels?

Theoretical predictions

Theory suggests that the influence of horizontal diversity at a focal trophic level indeed depends strongly on the

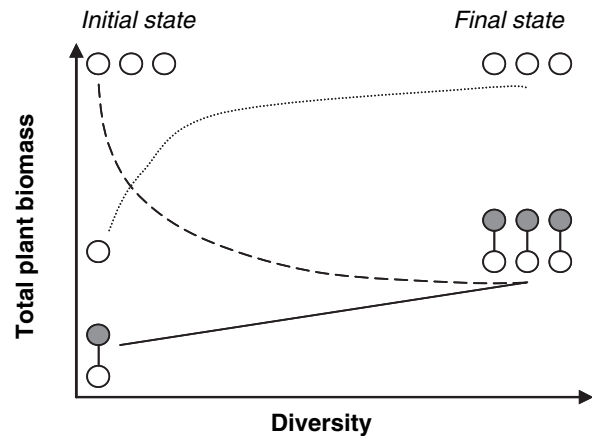


Figure 2 Predicted relationships between species diversity and total plant biomass depending on different scenarios of biodiversity change. The grey dotted line corresponds to an increase in plant diversity alone, in the absence of herbivores. The dashed line corresponds to an increase in herbivore diversity alone in the case of specialist herbivores. The solid line corresponds to a parallel increase of plant and herbivore diversity in the case of specialist herbivores. Plants are represented by white circles and herbivores by grey circles.

presence of adjacent trophic levels. For instance, addition of a trophic level can shift control of biomass in any single trophic level from limitation by resources to limitation by consumers. Holt & Loreau (2002) showed how such shifts can alter the relationship between plant species richness and plant production. Their results came from models of the 'sampling effect' of diversity, where systems initiated with some number of species at a trophic level eventually collapse to one dominant species with the highest carrying capacity. In the absence of herbivores, increasing initial plant richness led to higher plant biomass at equilibrium. Adding a single herbivore weakened the positive effect of plant richness as plant biomass was reduced at equilibrium. When plant species varied in edibility, however, equilibrium plant biomass again increased with plant richness as species more resistant to herbivory replaced less resistant species (i.e. bottom-up control was restored). Thus, herbivores could alter the relationship between plant richness and plant production, but this depends on how variance in edibility among plants moderates the relative importance of top-down vs. bottom-up control.

Thébaud & Loreau (2003) extended the results of Holt & Loreau (2002) in two ways. First, they explicitly demonstrated that trade-offs between plant competitive ability and resistance to herbivory dictate how plant diversity influences plant production. Second, they showed that herbivore specialization strongly influences the relationship between plant richness and production because it regulates both the magnitude of top-down control and the indirect

interactions among plants that stem from apparent competition. At the extreme of specialization, where each plant is controlled by a specialized herbivore, rather than by competition for resources, it will be unaffected by the addition of other plant species, which leads to an expected linear increase in total plant biomass as species richness increases in parallel at plant and herbivore levels (Thébault & Loreau 2003, Fig. 2). At the other extreme, when herbivores are generalists, total plant biomass has a nonlinear, and even sometimes hump-shaped relation to (jointly) increasing plant and herbivore diversity. In general, Thébault & Loreau (2003) found that addition of higher trophic levels tends to qualitatively alter diversity–production relationships at lower levels, but that the direction of these impacts was highly variable and depended on parameter values.

Given that presence of a higher trophic level can modify diversity effects, how does changing diversity at that higher trophic level interact with changing diversity at the lower level? Answers to this question from theory are mixed. Several models suggest that simultaneous loss of species from adjacent trophic levels leads to countervailing effects on total resource biomass (Holt & Loreau 2002; Thébault & Loreau 2003, 2005). This occurs because diversity of consumers tends to depress resource biomass, while diversity of the resources tends to increase resource biomass. But Fox (2004), who analysed a common set of predator–prey models, showed that the joint response of prey biomass to prey and predator diversity was more complex, and did not always predict countervailing effects of diversity loss among trophic levels. While predator diversity generally decreased prey biomass, prey diversity could increase or decrease biomass depending on which trade-offs led to coexistence.

Plant interactions with decomposers are also key to ecosystem processes and also can be affected by diversity at both levels. Models show that increasing decomposer diversity can enhance nutrient recycling, and thus plant production, either via enhanced microbial exploitation of organic matter or complementary niches (Loreau 2001); however, increasing plant diversity (and diversity of plant organic compounds) is antagonistic to plant production in plant–decomposer systems as it reduces the efficiency of microbial exploitation, and thus of recycling of nutrients.

Empirical results

Several recent experiments have found that an increase in FCL (addition of higher-level consumers) changed the relationship between prey diversity and biomass accumulation. First, Mulder *et al.* (1999) studied a two-level system of insect herbivores feeding on grassland plant assemblages that differed in species richness. They found that, in the

absence of herbivores (the one-level system), aggregate plant biomass increased with plant diversity. When insects were present (the two-level system), however, they fed heavily on the species with intermediate biomass, decreasing plant evenness in polycultures. Thus, addition of a trophic level (insect herbivores) weakened the relationship between plant diversity and biomass. The opposite pattern was found in a seagrass system, where functional effects of herbivore diversity were stronger in the presence of predatory crabs (three-level system) than in their absence (two-level system): higher grazer diversity enhanced grazer biomass, epiphyte grazing, and seagrass biomass only when predators were present (Duffy *et al.* 2005). In the seagrass system, the results appeared to arise from among-species trade-offs between predation resistance and competitive ability. A variation on this theme comes from an experiment that manipulated algal diversity in the presence and absence of decomposers (bacteria) rather than herbivores (Naeem *et al.* 2000). In this case, as in that of grassland plants discussed above, heterotrophic consumers reduced the positive effect of algal diversity on primary production. Finally, in other experiments, addition of a higher trophic level changed not only the magnitude but also the sign of the diversity–function relationship at the prey level, sometimes in complex ways (e.g. Hättenschwiler & Gasser 2005; Wojdak 2005).

Experiments comparing the effects of simultaneously changing horizontal diversity at different trophic levels have addressed two distinct situations in which interactions among levels are expected to differ. First, interactions between producers and decomposers are expected to be primarily mutualistic in that decomposers require organic products of the producers, but do not consume them alive, while producers require inorganic resources regenerated by decomposers (Loreau 2001). Naeem *et al.* (2000) tested how simultaneously changing diversity at both algal and bacterial levels interacted to affect biomass accumulation and resource use. First, in the absence of added bacteria, algal biomass increased significantly with algal species richness. When bacteria were added, however, net algal production depended on a complex interaction between algal and bacterial richness. Production of decomposer bacteria increased on average with bacterial species richness, but was also affected by the interaction of bacterial and algal richness (Naeem *et al.* 2000). Mechanistically, these patterns involved the greater range of carbon sources produced by diverse algal assemblages, and the greater ability of diverse bacterial assemblages to use these resources efficiently.

The second situation involves predator/prey (including herbivore/plant) interactions, which are generally antagonistic in that the interaction benefits one party more strongly than the other. Contrasting results of two experiments that factorially manipulated algal and protistan herbivore diver-

sity shed some light on the conditions under which diversity at different trophic levels interact. In one experiment, there were no significant effects of either algal diversity on herbivore biomass, nor of herbivore diversity on algal biomass (Fox 2004). Apparently, the absence of effects occurred because of the lack of diet specialization among herbivore species and the absence of any trade-off between competitive ability and edibility in the algae (Fox 2004). In contrast, a separate study indicated that increasing herbivore diversity enhanced both herbivore biomass accumulation and impact on algal biomass accumulation (Gamfeldt *et al.* 2005). Interestingly, when both algal and herbivore diversity increased, the effects of herbivore diversity dominated, reducing algal biomass, probably reflecting the absence of inedible algal species (Gamfeldt *et al.* 2005). The latter authors also found that increasing algal richness enhanced herbivore biomass accumulation, consistent with the balanced diet hypothesis. Aquilino *et al.* (2005), working in an agricultural system, took the unique approach of factorially manipulating diversity of predators and plants, and measuring their main and interactive effects on the herbivorous aphids between them. They found that increasing enemy richness reduced aphid densities, and that increasing plant richness increased aphid survival by approximately the same amount, with diversity effects at different trophic levels essentially cancelling one another out, as suggested by Worm & Duffy (2003).

Finally, a third group of studies has simultaneously manipulated diversity at multiple trophic levels (Naeem *et al.* 1994; McGrady-Steed *et al.* 1997; Mikola & Setälä 1998; Downing 2005). These experiments have often found significant effects of changing species richness on ecosystem-level properties, which appear to be mediated by intriguing indirect effects. Their designs limit the potential for mechanistic interpretation in terms of which trophic levels are driving changes in functioning. However, since ecosystem processes responded despite proportional diversity changes at different trophic levels, these results suggest that effects of diversity changes at adjacent levels generally do not simply cancel one another out.

Summary and conclusions

The interaction of horizontal and vertical diversity has received little attention to date. Both theory and limited experimental data suggest that effects of diversity at a focal trophic level can be quantitatively and sometimes qualitatively altered by presence of a higher trophic level, and that key factors influencing this interaction include consumer niche breadth – both horizontal and vertical – and presence of trade-offs between prey growth rate and resistance to predation. Because the available studies are few, it is not yet possible to draw general conclusions regarding the strength

or sign of interacting horizontal and vertical diversity effects. This will be a fertile area for future progress in both basic and applied ecology.

SYNTHESIS AND FUTURE DIRECTIONS

From the beginning, research on BEF has had two distinct and sometimes opposing aims: (1) to understand the fundamental mechanisms that mediate the functioning of diverse ecosystems; and (2) a more practical goal of predicting the consequences of rapid changes in Earth's biodiversity (Srivastava & Vellend 2005). Our review highlights that considerable progress has been made on the first of these goals with little more than a decade of research (Table 1). Tackling the second goal will require building on this strong foundation by focusing more directly on realistic scenarios of extinction and incorporating more of the important biology of animals at higher trophic levels.

Although seminal BEF experiments using random combinations of species have helped outline the general role of biodiversity in regulating ecosystem processes, these efforts must now be complemented by studies that mimic more realistic scenarios of extinction. Results of extinction simulations echo theoretical predictions (Gross & Cardinale 2005) that two issues are critical for predicting the consequences of non-random extinction: (1) the covariance between traits affecting extinction and those affecting ecosystem processes; and (2) the potential for functional compensation among surviving species. For example, strong interactors may be especially common among large animals at high trophic levels (e.g. Duffy 2003; Ebenman *et al.* 2004), and both body size and trophic position also predict vulnerability to population decline and extinction (Pauly *et al.* 1998; Dobson *et al.* 2006). Since large predators are naturally low in species diversity, a few extinctions may result in loss of the entire top predator trophic level, with disproportionately large effects on ecosystem properties and processes (Duffy 2002; Borer *et al.* 2006).

Another challenge in BEF research is to more fully consider the variety of ecosystem processes that communities perform. Although communities influence many ecosystem processes at once, BEF researchers have tended to focus on one dependent variable at a time. This univariate perspective has the potential to generate erroneous conclusions about the functional role of biodiversity (Rosenfeld 2002; Duffy *et al.* 2005; Srivastava & Vellend 2005). Although one or a select few species may be able to maximize the rates of any single process, it seems less likely that those same species can maximize the broad array of processes that communities perform simultaneously (Duffy *et al.* 2003 have referred to this as 'multivariate dominance'). For example, contributions to nitrogen and phosphorus recycling are only weakly correlated among tropical fresh-

water fish species (McIntyre *et al.* 2007). A related challenge is to simultaneously consider the processes performed by interacting components of a food web. For example, efforts have now expanded BEF research to consider the role of biodiversity in below-ground processes, and linking these to the functional role of diversity in aboveground processes is an emerging area of research (Wardle *et al.* 2004). Similarly, a considerable amount of BEF research has now focused on detrital-based systems (Hättenschwiler *et al.* 2005), and interactions among the 'green' and 'brown' portions of the food-web have the potential to alter conclusions about the functional role of biodiversity (Naeem *et al.* 2000). Clearly, considering the variety of processes performed by different components of the food web is a key direction for future BEF research.

Another pressing question, common to ecology in general, is whether and how insights from simple model systems scale up to complex natural ecosystems. This question is especially pressing given that most studies have focused on relatively sessile organisms placed in 'closed' experimental units that have been intentionally isolated from dispersal, disturbance, and other regional processes to maximize experimental control (Hooper *et al.* 2005). One limitation of this approach is that we know ecosystems are not closed. Spatial exchanges of energy and matter across habitats and ecosystem boundaries appear to be the norm in nature (Underwood & Fairweather 1989; Polis *et al.* 1997), and real populations exhibit source-sink dynamics that connect habitats together as meta-populations and meta-communities (reviewed by Leibold *et al.* 2004). Integrating more mobile organisms (e.g. large vertebrates) into BEF research is an especially difficult challenge given that it severely limits use of the complex factorial experiments that have been the foundation of BEF research on plants and invertebrates. Even so, theory and experiment clearly predict that animal migration can strongly modify the impact of diversity on ecosystem processes (Holt & Loreau 2002; France & Duffy 2006), and that mobile top predators can stabilize spatially and functionally distinct food webs (McCann *et al.* 2005). Furthermore, we know that animal migration and aggregation can lead to spatially variable effects of biodiversity (McLain *et al.* 2003; Cardinale *et al.* 2006a,b). Thus, future BEF research must begin to tackle the unique challenges of integrating the movement of organisms and their resources across heterogeneous landscapes to consider space more explicitly.

Given the emerging questions and challenges we have outlined above, we are convinced that predicting the functional consequences of biodiversity loss from complex, real food-webs will require that ecologists embrace a broader suite of approaches than has been the norm. Promising avenues include (1) taking advantage of the burgeoning field of network theory, which is being widely

used to relate the structural and functional properties of complex biological, social, and abiotic networks (Proulx *et al.* 2005); (2) using biogeographic comparisons that detail the natural ecological associations between species diversity and productivity of large-scale, whole ecosystems (e.g. Worm *et al.* 2006); (3) using simulations to model the consequences of extinction for systems where experimental tests are impractical, as has been done for mammalian vectors of lyme disease (Ostfeld & LoGiudice 2003), bioturbation by marine invertebrates (Solan *et al.* 2004), carbon sequestration by tropical trees (Bunker *et al.* 2005), and nutrient cycling by freshwater fishes (McIntyre *et al.* 2007), among others; (4) using paleoecological datasets to reconstruct the historical relationships between biodiversity and global ecosystem processes that have dominated through geologic time, or that have occurred during mass extinction and radiation events (Rothman 2001); and (5) taking advantage of emerging phylogenetic techniques that help predict how evolutionary divergence and trait differentiation lead to functional differentiation among species (Webb *et al.* 2002). Like all approaches, each of these has strengths and limitations. However, each has the potential to complement the knowledge we gain from controlled experiments. Only by finding converging support from multiple lines of inquiry can we draw robust conclusions about the functional consequences of the modern biodiversity crisis.

ACKNOWLEDGEMENTS

We are grateful to participants in the symposium 'Incorporating trophic diversity into the biodiversity–ecosystem functioning debate: lessons from aquatic ecosystems' at the Ecological Society of America's 2005 annual meeting, participants in the BioMerge and Diversitas networks, and the NCEAS working group 'Linking marine biodiversity and ecosystem services' for stimulating discussions that influenced our thinking, and to Jonathan Chase, Alex Flecker and three anonymous referees for comments that improved the MS. For support, we acknowledge the National Science Foundation (OCE-0352343 to JED; INT-872612445 to PBM and A.S. Flecker), and a Discovery grant of the Natural Sciences and Engineering Research Council of Canada (ML). This is VIMS contribution no. 2821.

REFERENCES

- Andow, D.A. (1991). Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.*, 36, 561–586.
- Aquilino, K.M., Cardinale, B.J. & Ives, A.R. (2005). Reciprocal effects of host plant and natural enemy diversity on herbivore suppression: an empirical study of a model tritrophic system. *Oikos*, 108, 275–282.

- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146–1156.
- Borer, E.T., Halpern, B.S. & Seabloom, E.W. (2006). Asymmetry in community regulation: Effects of predators and productivity. *Ecology*, 87, 2813–2820.
- Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B. *et al.* (2005). What determines the strength of a trophic cascade? *Ecology*, 86, 528–537.
- Bruno, J.F. & O'Connor, M.I. (2005). Cascading effects of predator diversity and omnivory in a marine food web. *Ecol. Lett.*, 8, 1048–1056.
- Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.C., Perfecto, I., Phillips, O.L. *et al.* (2005). Species loss and aboveground carbon storage in a tropical forest. *Science*, 310, 1029–1031.
- Byrnes, J., Stachowicz, J.J., Hultgren, K.M., Hughes, A.R., Olyarnik, S.V. & Thornber, C.S. (2006). Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecol. Lett.*, 9, 61–71.
- Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003). Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecol. Lett.*, 6, 857–865.
- Cardinale, B.J., Duffy, D., Wright, J.E., Downing, J.P., Sankaran, A.L., Srivastava, M. *et al.* (2006a). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989–992.
- Cardinale, B.J., Weis, J.J., Forbes, A.E., Tilmon, K.J. & Ives, A.R. (2006b). Biodiversity as both a cause and consequence of resource availability: A study of reciprocal causality in a predator–prey system. *J. Anim. Ecol.*, 75, 497–505.
- Casula, P., Wilby, A. & Thomas, M.B. (2006). Understanding biodiversity effects on prey in multi-enemy systems. *Ecol. Lett.*, 9, 995–1004.
- Chase, J.M., Abrams, P.A., Grover, J., Diehl, S., Chesson, P., Holt, R.D. *et al.* (2002). The interaction between predation and competition: a review and synthesis. *Ecol. Lett.*, 5, 302–315.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313, 966–968.
- DeMott, W.R. (1998). Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology*, 79, 2463–2481.
- Denoth, M., Frid, L. & Myers, J.H. (2002). Multiple agents in biological control: improving the odds?. *Biol. Control*, 24, 20–30.
- Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, J., McGlade, J. *et al.* (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87, 1915–1924.
- Downing, A.L. (2005). Relative effects of species composition and richness on ecosystem properties in ponds. *Ecology*, 86, 701–715.
- Duffy, J.E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99, 201–219.
- Duffy, J.E. (2003). Biodiversity loss, trophic skew, and ecosystem functioning. *Ecol. Lett.*, 6, 680–687.
- Duffy, J.E., Richardson, J.P. & Canuel, E.A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol. Lett.*, 6, 637–645.
- Duffy, J.E., Richardson, J.P. & France, K.E. (2005). Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol. Lett.*, 8, 301–309.
- Ebenman, B., Law, R. & Borrvall, C. (2004). Community viability analysis: The response of ecological communities to species loss. *Ecology*, 85, 2591–2600.
- Estes, J.A. & Palmisano, J.F. (1974). Sea otters: their role in structuring nearshore communities. *Science*, 185, 1058–1060.
- Finke, D.L. & Denno, R.F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Lett.*, 8, 1299–1306.
- Fox, J.W. (2003). The long-term relationship between plant diversity and total plant biomass depends on the mechanism maintaining diversity. *Oikos*, 102, 630–640.
- Fox, J.W. (2004). Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology*, 85, 549–559.
- France, K.E. & Duffy, J.E. (2006). Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, 441, 1139–1143.
- Fretwell, S.D. (1977). The regulation of plant communities by food chains exploiting them. *Perspectives Biol. Med.*, 20, 169–185.
- Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2005). Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol. Lett.*, 8, 696–703.
- Gross, K. & Cardinale, B.J. (2005). The functional consequences of random vs. ordered species extinctions. *Ecol. Lett.*, 8, 409–418.
- Hairton, N.G., Smith, F.E. & Slobodkin, L.G. (1960). Community structure, population control, and competition. *Am. Nat.*, 94, 421–425.
- Hättenschwiler, S. & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proc. Natl. Acad. Sci.*, 102, 1519–1524.
- Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Syst.*, 36, 191–218.
- Hillebrand, H. & Cardinale, B.J. (2004). Consumer effects decline with prey diversity. *Ecol. Lett.*, 7, 192–201.
- Hillebrand, H. & Shurin, J. (2005). In: *Aquatic Food Webs* (eds Belgrano, A., Scharler, U.M., J.Dunne, J. & Ulanowicz, R.E.). Oxford University Press, Oxford, pp. 184–197.
- Holt, R.D. & Loreau, M. (2002). Biodiversity and ecosystem functioning: the role of trophic interactions and the importance of system openness. In: *The Functional Consequences of Biodiversity. Empirical Progress and Theoretical Expectations* (eds Kinzig, A.P., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, PA, pp. 246–262.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Hughes, A.R. & Stachowicz, J.J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci.*, 101, 8998–9002.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.

- Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2005). A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.*, 8, 102–116.
- Joshi, J., Otway, S.J., Koricheva, J., Pfisterer, A.B., Alpehi, J., Roy, B.A. *et al.* (2004). Bottom-up effects and feedbacks in simple and diverse experimental grassland communities. In: *Insects and Ecosystem Function* (eds Weisser, W.W. & Siemann, E.). Springer-Verlag, Berlin, Heidelberg, pp. 115–134.
- Keesing, F., Holt, R.D. & Ostfeld, R.S. (2006). Effects of species diversity on disease risk. *Ecol. Lett.*, 9, 485–498.
- Leibold, M.A. (1989). Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.*, 134, 922–949.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.
- Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3–17.
- Loreau, M. (2001). Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model. *Proc. R. Soc. Lond. B*, 268, 303–309.
- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loreau, M., Naeem, S. & Inchausti, P., eds. (2002). *Biodiversity and Ecosystem Functioning. Synthesis and Perspectives*. Oxford University Press, New York.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.
- McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett.*, 8, 513–523.
- McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, 390, 162–165.
- McIntyre, P.B., Jones, L.E., Flecker, A.S. & Vanni, M.J. (2007). Fish extinctions alter nutrient recycling in tropical freshwaters. *Proc. Natl. Acad. Sci. U.S.A.*, 104, 4461–4466.
- McLain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M. *et al.* (2003). Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, 6, 301–312.
- Mikola, J. & Setälä, H. (1998). Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. *Oikos*, 83, 180–194.
- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A. *et al.* (2004). Detritus, trophic dynamics and biodiversity. *Ecol. Lett.*, 7, 584–600.
- Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Hogberg, P. & Joshi, J. (1999). Insects affect relationships between plant species richness and ecosystem processes. *Ecol. Lett.*, 2, 237–246.
- Naeem, S., Hahn, D.R. & Schuurman, G. (2000). Producer–decomposer co-dependency influences biodiversity effects. *Nature*, 403, 762–764.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, 118, 240–261.
- Ostfeld, R.S. & LoGiudice, K. (2003). Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology*, 84, 1421–1427.
- Otway, S.J., Hector, A. & Lawton, J.H. (2005). Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *J. Anim. Ecol.*, 74, 234–240.
- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14, 483–488.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing down marine food webs. *Science*, 279, 860–863.
- Petchey, O.L. & Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecol. Lett.*, 9, 741–758.
- Pfisterer, A.B., Diemer, M. & Schmid, B. (2003). Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. *Oecologia*, 135, 234–241.
- Polis, G.A., Anderson, W.B. & Holt, R.D. (1997). Toward and integration of landscape and food-web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.*, 28, 289–316.
- Polis, G.A. & Holt, R.D. (1992). Intraguild predation – the dynamics of complex trophic interactions. *Trends Ecol. Evol.*, 7, 151–154.
- Polis, G.A. & Strong, D.R. (1996). Food web complexity and community dynamics. *Am. Nat.*, 147, 813–846.
- Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). Network thinking in ecology and evolution. *Trends Ecol. Evol.*, 20, 345–353.
- Root, R.B. (1973). Organization of a plant–arthropod association in simple and diverse habitats – fauna of collards (*Brassica oleracea*). *Ecol. Monog.*, 43, 95–120.
- Rosenfeld, J.S. (2002). Logical fallacies in the assessment of functional redundancy. *Cons. Biol.*, 16, 837–839.
- Rothman, D.H. (2001). Global biodiversity and the ancient carbon cycle. *Proc. Natl. Acad. Sci. U.S.A.*, 98, 4305–4310.
- Sala, O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R. *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
- Schmitz, O.J., Hamback, P.A. & Beckerman, A.P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.*, 155, 141–153.
- Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.
- Snyder, W.E., Snyder, G.B., Finke, D.L. & Straub, C.S. (2006). Predator biodiversity strengthens herbivore suppression. *Ecol. Lett.*, 9, 789–796.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. & Srivastava, D.S. (2004). Extinction and ecosystem function in the marine benthos. *Science*, 306, 1177–1180.
- Srivastava, D.S. & Vellend, M. (2005). Biodiversity–ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Syst.*, 36, 267–294.
- Steiner, C.F. (2001). The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. *Ecology*, 82, 2495–2506.

- Strong, D.R. (1992). Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology*, 73, 747–754.
- Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heger, D., Miller, B.J. *et al.* (1999). The role of top carnivores in regulating terrestrial ecosystems. In: *Continental Conservation* (eds Soulé, M.E. & Terborgh, J.). Island Press, Washington, DC, pp. 39–64.
- Thébault, E. & Loreau, M. (2003). Food-web constraints on biodiversity–ecosystem functioning relationships. *Proc. Natl. Acad. Sci.*, 100, 14949–14954.
- Thébault, E. & Loreau, M. (2005). Trophic interactions and the relationship between species diversity and ecosystem stability. *Am. Nat.*, 166, E95–E114.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci.*, 94, 1857–1861.
- Underwood, A.J. & Fairweather, P.G. (1989). Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.*, 4, 16–20.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of Earth's ecosystems. *Science*, 277, 494–499.
- Wardle, D.A., Yeates, G.W., Williamson, W.M., Bonner, K.I. & Barker, G.M. (2004). Linking aboveground and belowground communities: the indirect influence of aphid species identity and diversity on a three trophic level soil food web. *Oikos*, 107, 283–294.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.
- Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.
- Wilby, A., Villareal, S.C., Lan, L.P., Heong, K.L. & Thomas, M.B. (2005). Functional benefits of predator species diversity depend on prey identity. *Ecol. Entomol.*, 30, 497–501.
- Williams, R.J. & Martinez, N.D. (2004). Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.*, 163, 458–468.
- Wilsey, B.J. & Polley, H.W. (2002). Reductions in grassland species evenness increase dicot seedling invasion and spittlebug infestation. *Ecol. Lett.*, 5, 676–684.
- Wojdak, J.M. (2005). Relative strength of top-down, bottom-up, and consumer species richness effects on pond ecosystems. *Ecol. Monogr.*, 75, 489–504.
- Worm, B. & Duffy, J.E. (2003). Biodiversity, productivity, and stability in real food webs. *Trends Ecol. Evol.*, 18, 628–632.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S. *et al.* (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314, 787–790.

Editor, Jonathan Chase

Manuscript received 22 December 2006

First decision made 22 January 2007

Manuscript accepted 15 March 2007