

Towards a food web perspective on biodiversity and ecosystem functioning

Bradley Cardinale, Emmett Duffy, Diane Srivastava, Michel Loreau, Matt Thomas, and Mark Emmerson

8.1 Introduction

One of the most common questions asked by researchers across a variety of scientific disciplines is ‘How does the number of nodes connected together into a network influence the efficiency and reliability of that network?’. While social scientists and epidemiologists might think of ‘nodes’ and ‘connections’ as people interacting within a social network, computer scientists, neurologists, and civil engineers would instead think of servers connected together in a world-wide web, synapses connecting neurons in the brain, or hubs connecting to other hubs in a transportation network or telecommunications grid (Albert and Barabasi 2002, Newman 2003). Regardless of the particular study system, all of these individuals ask similar questions about how the number of nodes and connections among nodes influence the efficiency and reliability by which information, disease, energy, or matter is transmitted throughout that network.

Within the field of ecology, one of the oldest and most fundamental questions asked by researchers is ‘How does the number of species interacting within a food web influence the efficiency and reliability by which energy and matter are transmitted through that web?’. Research on this topic can be broadly divided into two foci. Historically, much attention in ecology has focused on identifying those taxa that are the most influential nodes in a food web. For many years, it has been thought that some subset of species might represent ‘hubs’ of interactions and/or exhibit such strong interactions

that they exert a disproportionate influence over food web dynamics. This idea has fueled much debate over the prevalence of omnivory in food webs (Polis and Strong 1996, Thompson *et al.* 2007, Yodzis 1984) and whether the increased number of feeding links that result from omnivory increases or decreases the stability of energy flow through a food web (McCann *et al.* 1998, MacArthur 1955). Identifying species that represent influential nodes has also been one of the primary goals in the search for ‘ecosystem engineers’ (Jones *et al.* 1994), ‘keystone species’ (Paine 1966, Power *et al.* 1996) or other types of ‘strong interactors’ (Wootton and Emmerson 2005) that might have cascading effects on the diversity and biomass of species at a variety of different trophic levels (Paine 1966, Carpenter *et al.* 1987, Elser *et al.* 1988).

In the 1990s, ecologists began to pursue a slightly different perspective on food webs. This perspective focused not on the cascading impacts of individual species, but rather on how the number of species that comprise any single trophic level might control fluxes of energy and matter. Research in this area was generally referred to as Biodiversity effects on Ecosystem Functioning (BEF for short), and was often justified on grounds that (1) loss of biological diversity ranks among the most pronounced changes to the global environment (Sala *et al.* 2000, Pimm *et al.* 1995), and (2) reductions in diversity, and corresponding changes in species composition, may alter fluxes of energy and matter that underlie important services that ecosystems provide to

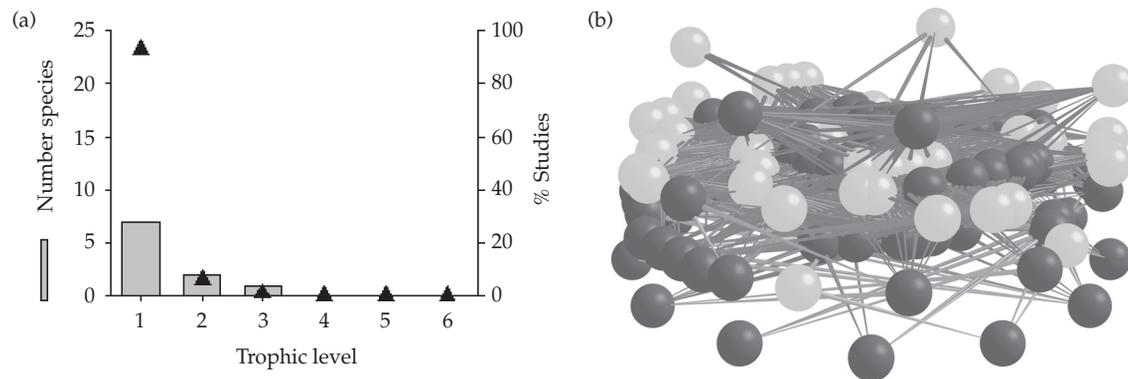


Figure 8.1 (a) Summary of the biological complexity of biodiversity-ecosystem functioning (BEF) studies performed to date. On the x -axis is the number of trophic levels included in different experiments. On the left-hand y -axis (plotted as grey bars) is the mean number of species per trophic level. On the right hand y -axis (plotted as triangles) is the percentage of studies that have included 1, 2, or more trophic levels. Note that 93 per cent of BEF experiments have focused on a single trophic level composed of a mean seven species. (b) An example of the complexity of a real, yet still relatively simple natural food web in a salt marsh (from Lafferty *et al.* 2007). Note that within this system there are dozens of species (nodes) and hundreds of feeding links (lines connecting nodes) among plants, herbivores, predators and parasites that span six or more trophic levels. Figure reproduced with permission from K. Lafferty.

humanity (e.g. production of food, pest/disease control, water purification, etc. Daily 1997, Chapin *et al.* 1998). While the value of BEF research for conservation biology and management has been questioned by some (Schwartz *et al.* 2000, Srivastava and Vellend 2005), there is a more fundamental reason for the recent prominence of this topic. BEF is one of the few research topics in ecology that examines how biological variation *per se* acts as an independent variable to regulate key community and ecosystem-level processes (Naeem 2002b). Understanding the ecological consequences of variation among species has shown much potential to complement our historical focus on the ecological impacts of highly influential species.

Although the BEF paradigm has evolved considerably over the past 15–20 years and been increasingly applied to a variety of organisms and ecosystems, studies have continued to focus mostly on simplified ‘model’ communities. In fact, the typical experiment has manipulated an average of just seven species in an average of just one trophic group (Fig. 8.1(a)). Such minimal levels of complexity are far from the realities of natural food webs, where, even for some of the simplest communities, species interact within webs composed of hundreds of species spanning many trophic levels (Lafferty *et al.* 2006, Polis 1991, Martinez 1992). At present, it is unclear whether such over-

simplifications are justified, or alternatively, whether they have led ecologists to potentially erroneous conclusions. However, what is clear is that a large body of research in ecology has shown that interactions of species across trophic levels can have cascading impacts that influence the diversity and biomass of organisms at numerous levels in a food web. At the very least, this suggests that the past focus of BEF on diversity within single trophic levels may be insufficient to quantitatively predict, and perhaps even qualitatively reflect, the ecological consequences of diversity loss.

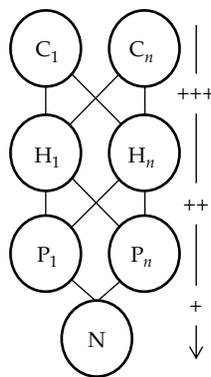
In this chapter, we continue with the development of an idea that originated with other authors who have argued that, in order to understand how extinction alters the functioning of whole ecosystems, ecologists will likely need to merge modern paradigms of BEF with much more classic ideas in food web ecology that consider not only the functional role of diversity within trophic levels, but the interactions of species across trophic levels (Duffy *et al.* 2007, Bruno and Cardinale 2008, Petchey *et al.* 2004a). Our chapter is organized as follows. In Section 8.2 we briefly review five hypotheses about how fluxes of energy and matter through a food web might depend on the diversity of species comprising a web. Those hypotheses are divided into those that

contrast diversity effects within different trophic levels versus those that focus on diversity effects across trophic levels. In Section 8.3 we outline the empirical support for or against these hypotheses, emphasizing that most are still unresolved and in need of testing. In the final Section 8.4, we outline just a few of the areas of research that we believe will be fruitful as ecologists move towards an integration of BEF into food-web ecology.

8.2 Five early hypotheses about multi-trophic biodiversity and ecosystem function

8.2.1 Diversity effects within trophic levels

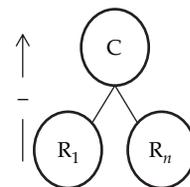
8.2.1.1 Top-down effects of diversity grow increasingly strong at higher trophic levels



Early hypotheses proposed that species extinction from higher trophic levels was likely to have greater impacts on the functioning of ecosystems than extinction from lower trophic levels (Table 8.1). Duffy (2002) argued that three characteristics potentially make ecological processes more sensitive to extinction by consumers than plants: (1) because species at higher trophic levels have lower population sizes and are under stronger anthropogenic pressure than most wild plants, higher trophic levels face greater risks of extinction and higher rates of species loss; (2) consumer assemblages have lower overall richness and higher degrees of resource specialization, leading to less 'functional redundancy' and limited potential for surviving species to compensate for processes performed by lost counterparts; and (3) unlike plants, consumers often have

impacts on processes that are disproportionate to their abundance or biomass. Duffy's (2002) paper was one of the first to call for a merger of BEF and food-web theory, and the hypotheses put forth in that paper were useful, in part, because they represented an alternative to those posed by a number of other authors. For example, some have argued that extinction at higher trophic levels may, in fact, have less impact on ecological processes than extinction at lower trophic levels. These arguments have usually been based on the idea that animals are more generalized in their use of resources than historically appreciated, either because the extent of omnivory and intra-guild predation has been underestimated (Rosenheim *et al.* 1995, Holt and Polis 1997, Polis and Holt 1992), or because animals can 'switch' among different prey species by moving across habitats (Polis *et al.* 1997, McCann *et al.* 2005). Resource generalization has been proposed to dampen the effects of consumer diversity on prey populations (Finke and Denno 2005, Snyder and Ives 2003).

8.2.1.2 Increasing diversity of a resource reduces the strength of top-down control by consumers



The majority of BEF studies performed to date have taken a 'top-down' perspective, meaning that they have examined how diversity within a given trophic level impacts the fraction of resources consumed, and production of biomass, by that focal trophic level. In contrast, diversity may also have 'bottom-up' effects on the dynamics of food webs, meaning that the diversity of resources may influence how efficiently those resources are consumed and converted into biomass by higher trophic levels (Table 8.1). At least three hypotheses have been proposed to explain how resource diversity might influence trophic dynamics: (2.1) the variance in edibility hypothesis argues that a more diverse prey assemblage is more likely to contain at least one species that is resistant to consumers (Leibold 1989,

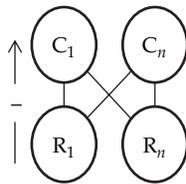
Table 8.1 Five early hypotheses about multi-trophic BEF. What do the data say?

Section	Hypothesis	Key reference(s)	Section	Balance of evidence	Certainty	Key references
8.2.1	Diversity effects within trophic levels					
8.2.1.1	Top-down effects of diversity grow increasingly strong at higher trophic levels.	Duffy (2002)	8.3.1.1	The balance of evidence is not consistent with this hypothesis. Recent meta-analyses have found no difference in the direction or magnitude of diversity effects for groups of producers, herbivores, detritivores, or predators. In fact, there tends to be considerable generality such that decreases in species richness decrease the efficiency of resource capture and the amount of biomass produced by any given trophic group.	Medium to high	Balvanera <i>et al.</i> (2006), Cardinale <i>et al.</i> (2006a, 2007)
8.2.1.2	Increasing diversity of resources reduces the strength of top-down control by consumers.	Leibold (1989), Duffy (2002), Ostfeld and LoGiudice (2003), Root (1973)	8.3.1.2	The balance of evidence is consistent with this hypothesis. Summaries suggest that consumption of lower by higher trophic levels is reduced when a resource base is more diverse. Note, however, that most of the available data comes from studies that have not directly manipulated the richness of resources. Several controlled experiments have provided counter-examples, so the generality of this hypothesis remains unclear.	Low to medium	Andow (1991), Hillebrand and Cardinale (2004)
8.2.2	Diversity effects across trophic levels					
8.2.2.1	Top-down effects of consumer diversity oppose the bottom-up effects of resource diversity.	Holt & Loreau (2002), Thébault and Loreau (2003, 2005)	8.3.2.2	Recent meta-analyses suggest that the top-down effects of consumer diversity are qualitatively different than the bottom-up effects of resource diversity. However, these effects have not been opposing as suggested by this hypothesis. Note, however, that few studies have simultaneously manipulated the richness of species at adjacent trophic levels, so conclusions are tentative.	Low	Shrivastava <i>et al.</i> (in press)
8.2.2.2	Diversity effects on biomass production and resource capture by a given trophic level are reduced in the presence of a higher trophic level.	Holt and Loreau (2002), Thébault and Loreau (2003)	8.3.2.1	The balance of evidence does not support this hypothesis. Of the few experiments that have manipulated species richness in the presence vs. absence of a higher trophic level, results are decidedly mixed. Analyses presented in this chapter further show no evidence that the effects of plant diversity on plant biomass differ for experiments performed in the presence vs. absence of herbivores.	Low	Mulder <i>et al.</i> (1999), Duffy <i>et al.</i> (2005), Wodjak (2005), and this chapter
8.2.2.3	Trophic cascades are weaker in diverse communities.	Strong (1992)	8.3.2.3	Experiments and data summaries to date have been equivocal and contradictory. At present, there is no clear reason to accept or reject this hypothesis.	None	Schmitz <i>et al.</i> (2000), Borer <i>et al.</i> (2005), Cardinale <i>et al.</i> (2003, 2006b), Wilby <i>et al.</i> (2005), Snyder <i>et al.</i> (2006), Finkle and Denno (2005), Bynes <i>et al.</i> (2006)

Duffy 2002); (2.2) the dilution hypothesis (Ostfeld and LoGiudice 2003), which has also been called the resource concentration hypothesis in the agro-ecology literature (Root 1973), suggests that specialist consumers become less efficient at finding and attacking their resource in a diverse prey assemblage; and (2.3) the balanced diet hypothesis suggests that a more diverse prey assemblage provides a more complete nutrition and, as a result, leads to higher consumer biomass (DeMott 1998). While hypotheses (1) and (2) predict that trophic efficiency will decrease as the diversity of resources increases, (2.3) predicts the opposite.

8.2.2 Diversity effects across trophic levels

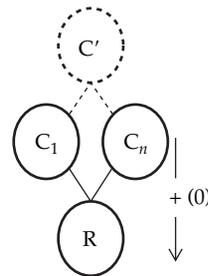
8.2.2.1 *Top-down effects of consumer diversity oppose the bottom-up effects of resource diversity*



An important, but still unresolved issue is whether the overall impacts of diversity loss at adjacent levels are opposing or reinforcing, antagonistic or synergistic. Hypotheses (2.1) and (2.2) suggest that consumer diversity tends to enhance the flux of resources from lower to higher trophic levels, whereas resource diversity tends to reduce these fluxes. Collectively, these two hypotheses lead to a third hypothesis: that extinction of species from adjacent trophic levels will have opposing impacts on the flux of energy and matter through a food web (Table 8.1). This prediction has received some theoretical support from mathematical models showing that simultaneous changes in diversity from consumers and their resource leads to countervailing effects on total resource use and biomass production (Thébault and Loreau 2003, Thébault and Loreau 2005, Holt and Loreau 2002). Fox (2004b) provided a counter example in which he used Lotka–Volterra models to show that the joint response of prey biomass to prey and predator diversity is poten-

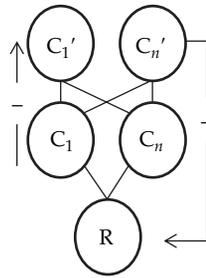
tially more complex. While predator diversity generally decreases prey biomass, prey diversity can increase or decrease biomass depending on how different life-history trade-offs influence the coexistence of prey.

8.2.2.2 *Diversity effects on biomass production and resource capture by any focal trophic level are reduced in the presence of higher trophic levels*



In their recent review, Duffy *et al.* (2007) used the terms ‘horizontal’ and ‘vertical’ diversity to distinguish between the richness of species within a trophic level and the richness of trophic levels that comprise a food web. They argued that one of the primary limitations in merging BEF with food-web theory is knowing how the impacts of diversity within trophic levels depend on the length of food chains (i.e. how horizontal and vertical diversity interact). The first step in overcoming this limitation is to ask how the diversity effects of any single trophic level are altered by the presence or absence of the next highest trophic level. Holt and Loreau (2002) used simple consumer–resource models to argue that the effects of plant diversity on nutrient uptake and plant biomass production are reduced in the presence of herbivores. This occurs because herbivory selects for dominance by poor plant competitors that are also the most tolerant to consumption by herbivores. Subsequent models by Thébault and Loreau (2003) also suggested that addition of higher trophic levels might qualitatively alter diversity–production relationships at lower levels; however, the direction of these impacts depends on both the nature of trade-offs between a plant’s competitive ability and ability to resist herbivory, and on the degree of consumer specialization.

8.2.2.3 Trophic cascades are weaker in diverse communities



In his seminal critique of the empirical evidence for trophic cascades, Strong (1992) argued that cascades are ‘a relatively unusual sort of food web mechanics... over the full range of ecological communities, evidence is that these cascades are restricted to fairly low-diversity places where great influence can issue from one or a few species’. He went on to suggest that trophic cascades are ‘all wet’, meaning they occur primarily in aquatic ecosystems where communities are characterized by linear, low-diversity food chains. In contrast, he argued that terrestrial food webs are more reticulate and ‘consumption is so differentiated in speciose systems that its overall effects are buffered’. The idea that diversity modifies the strength of trophic cascades can be broken down into at least two distinct hypotheses: (1) increasing the diversity of species comprising secondary consumers C' tends to decrease the strength of indirect effects on a basal resource R , and (2) increasing diversity of primary consumers C tends to decrease the indirect effects of C' on R . This latter hypothesis is very much an extension of hypotheses (2.1) and (2.2), as all of these rely on the assumption that an increasing diversity of resources tends to reduce the top-down impacts of consumers on food-web dynamics (Table 8.1).

8.3 What do the data say?

8.3.1 Diversity effects within trophic levels

8.3.1.1 Are diversity effects stronger at higher trophic levels? (Hypothesis 2.1)

Empirical evidence gathered to date does not appear to support the hypothesis that diversity

effects are stronger at higher trophic levels. Balvanera *et al.* (2006) reviewed 103 studies in which they could examine 400+ correlation coefficients relating species richness to a variety of ecological processes. They found no evidence for differential correlations between diversity and any of the response variables at various trophic levels. Similarly, Cardinale *et al.* (2006a) collated data from 111 experiments that have manipulated species richness and examined how this aspect of diversity impacts the capture of resources and production of biomass. Their analyses compared four trophic groups: (1) microalgal, macroalgal, or herbaceous plants assimilating nutrients or water, (2) protozoan or metazoan herbivores consuming live algal or herbaceous plant tissue, (3) protozoan or metazoan predators consuming live prey, and (4) bacterial, fungal or metazoan detritivores consuming dead organic matter. They showed that, on average, experimental reduction of species richness decreases the standing stock abundance or biomass of the focal trophic group, resulting in less complete resource use by that group (Fig. 8.2). However, the standing stock of, and resource depletion by, the most diverse polycultures were indistinguishable from those of species that performed best in monoculture. Importantly, the authors could not detect any statistical difference in the magnitude of diversity effects among the four trophic groups.

Collectively, these meta-analyses suggest there is considerable generality in the way that the diversity of species impact resource capture and biomass production in food webs. The fact that Cardinale (2006a) and Balvanera (2006) both found that the BEF relationships did not change dramatically across trophic levels could imply that, if niche complementarity is the main mechanism driving these patterns, then the degree of niche complementarity could be similar across trophic groups. Identifying whether the mechanisms that dictate BEF relationships are the same across different levels of biological organization is a key next step in BEF research (a point we return to in Section 8.4.1). Although studies to date show considerable generality in diversity effects across trophic levels, we should emphasize that there still tend to be fewer absolute numbers of species at

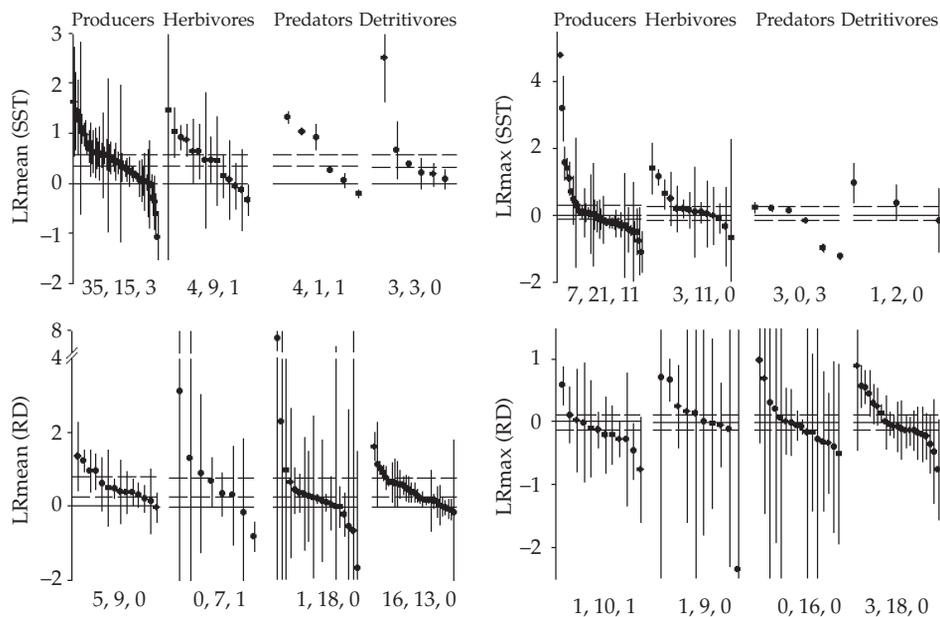


Figure 8.2 Summary of the results of experiments that have manipulated the richness of species in four trophic groups t (producers, herbivores, predators, and detritivores), and examined how richness impacts the standing stock abundance or biomass of t (SST – top graphs) or the fraction of resources depleted by t (RD – bottom graphs). The y -axes in all graphs give the diversity ‘effect size’, measured using two log ratios. LRmean (left graphs) compares SST and RD in the most diverse polyculture used in a study to the average of all monocultures. LRmax (right graphs) compares SST and RD from the most diverse polyculture used in a study to the species having the highest values of SST or RD in monoculture. Each data point is the mean effect size for all replicates in an experiment \pm 95 per cent CI. Dashed horizontal grey lines give the 95 per cent CI for all experiments combined based on results from a mixed model ANOVA. Numbers below each figure are the number of studies that have shown significantly positive effects of diversity, no effect, or negative effects of diversity. Data are from Cardinale *et al.* (2006a).

higher trophic levels, and that these species tend to be disproportionately prone to extinction (a point we return to in Section 8.4.2). Thus, it is still reasonable to hypothesize that food webs can tolerate fewer extinctions at higher trophic levels before ecosystem functioning is altered.

8.3.1.2 Does resource/prey diversity weaken the strength of top-down control? (Hypothesis 2.2)

Empirical evidence gathered thus far is mostly consistent with the hypothesis that increasing prey diversity tends to reduce the impacts of consumers on prey. Andow (1991) tallied the results of 200+ studies of herbivorous arthropods and found that more than half of the herbivore species had lower population sizes on plant polycultures as opposed to monocultures. He argued that the resource concentration hypothesis, in which specialist consumers have a more difficult time finding their

resource in a diverse prey assemblage, best accounted for the observed patterns. A summary of aquatic studies by Hillebrand and Cardinale (2004) tallied results from 172 experimental manipulations of herbivores and showed that consumption of algal biomass generally declined with increasing algal species richness. Although these patterns are consistent with hypothesis (2.2), some caution is warranted when interpreting these summaries, since the studies reviewed did not manipulate species diversity directly, and many potentially confounding factors were not controlled for. This caveat is particularly important when considering the mixed results from the limited number of experiments that have manipulated resource diversity directly. Several studies do provide evidence consistent with the variance-in-edibility hypothesis (Steiner 2001, Duffy *et al.* 2005), or for the dilution hypothesis (Keesing *et al.* 2006, Wilsey and

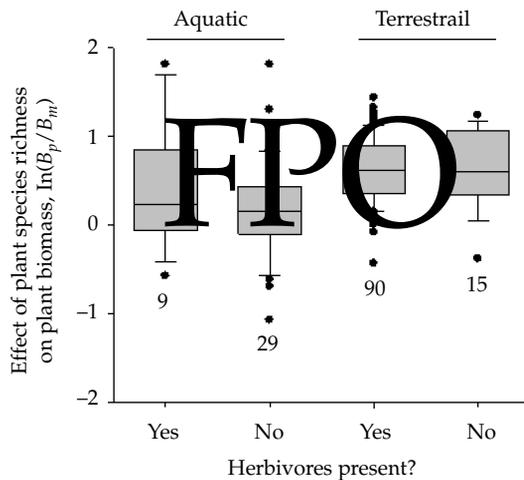


Figure 8.3 A summary of the impact of plant species richness on the production of plant biomass when herbivores are present or absent in experimental units. Data were taken from the summaries of Cardinale *et al.* (2006, 2007). The log ratio of plant biomass in the most diverse polyculture B_p to biomass in the average monoculture B_m was analyzed using a mixed model ANOVA with herbivores (y/n), ecosystem (aquatic vs. terrestrial), and their two-way interaction included as fixed effects, experiment accounted for as a random effect, and observations weighted by the inverse of their variance. Analyses indicate that the impacts of plant diversity on plant production do not differ when herbivores are absent vs. present ($F = 0.01$, $P = 0.92$), and that this conclusion is consistent among ecosystems ($F = 0.07$, $P = 0.80$ for interaction). These data and analyses should not be taken as conclusive evidence that herbivores do not impact plant diversity–biomass relationships since the studies summarized here differ in many ways that cannot be explicitly accounted for. However, these data can serve as a null hypothesis for experiments that explicitly manipulate plant diversity in the presence versus absence of higher trophic levels.

Polley 2002, Otway *et al.* 2005) where increasing diversity of resources leads to reduced consumption by higher trophic levels. Other studies provide support for the balanced diet hypothesis, showing that mixed diets of primary producers tend to enhance herbivore growth and biomass accumulation (Pfisterer *et al.* 2003, DeMott 1998). Thus, although the balance of evidence appears consistent with hypothesis (2.2), these conclusions should be considered tentative.

8.3.2 Diversity effects across trophic levels

8.3.2.1 Do top-down effects of diversity differ from bottom-up effects? (Hypothesis 2.1)

To date, studies that have simultaneously manipulated the richness of species at adjacent trophic levels are rare (Fig. 8.1(a)), and it is difficult to draw many general conclusions about the direction of top-down versus bottom-up effects of diversity in food webs. However, a recent meta-analysis by Srivastava *et al.* (2008) suggests that hypothesis (2.1) is not supported in detrital systems. These authors compiled the results of 90 experiments reported in 28 studies of detritivores to ask ‘Do changes in consumer (i.e. detritivore) diversity have the same effect on rates of resource consumption as changes in resource (i.e. detrital) diversity?’. To address this question, they compared the top-down effects of consumer (detritivore) diversity on the consumption of dead organic matter (decomposition) to the

bottom-up effects of resource (detrital) diversity on consumption of dead organic matter. Their meta-analysis indicated that reductions in detritivore diversity generally led to reductions in rates of decomposition, but changes in the diversity of detrital resources led to no detectable change in decomposition. The implication is that consumer, but not resource diversity, impacts consumption and energy flow in ‘brown’ food webs (detritus-consumer). However, an important point to keep in mind is that the resources studied by Srivastava *et al.* (2008) are ‘dead’, meaning they are non-living resources that have no potential to show dynamic coupling to their consumers. A number of mathematical models suggest that diversity–function relationships could be qualitatively different when resources are ‘living’, such as in ‘green’ food webs (i.e. plant-based systems) where populations have the potential to respond to changes in the density of their consumers (Loreau 2001, Ives *et al.* 2005). The potentially important contrast between systems that have dynamic (living) vs. non-dynamic (non-living) is an issue that we return to in Section 8.4.1. For now, suffice it to say that we do not know whether the results of Srivastava *et al.* (2008) are specific to detrital systems, or whether they hold more generally.

8.3.2.3 Are diversity effects at one trophic level altered by higher levels? (Hypothesis 2.2)

Only a handful of experiments have manipulated the richness of species in a focal trophic level and

then simultaneously manipulated the presence/absence of a higher trophic level. Mulder *et al.* (1999) varied plant diversity in the presence and absence of insect herbivores in a grassland plant assemblage. In the absence of herbivores, plant biomass increased with plant diversity, whereas when insects were present, they fed heavily on species with intermediate biomass, weakening the impact of plant diversity and biomass. Conversely, in a seagrass system, effects of herbivore richness on plant production were stronger in the presence of a higher trophic level (crabs) than in their absence (Duffy *et al.* 2005), which presumably occurred because of tradeoffs between species abilities to compete for resources versus resist predators. 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 (e.g. Hattenschwiler and Gasser 2005, Wojdak 2005).

We have been able to further examine hypothesis (2.2) by collating data from the meta-analyses of Cardinale *et al.* (2006a, 2007) for studies that have manipulated the richness of primary producers. We divided experiments into those that did versus did not allow herbivores access to experimental plots or pots, and then compared how plant diversity influence plant biomass between the two types of studies. Although plant species richness generally increased the production of plant biomass, we found no evidence that herbivores alter the magnitude of plant diversity effects (Figure 8.3). This was true for studies performed in both aquatic as well as terrestrial ecosystems. Although these analyses are far from conclusive, when taken with the mixed results of experiments they suggest that widespread support for hypothesis (2.2) is presently lacking.

8.3.2.4 *Are trophic cascades weaker in diverse communities? (Hypothesis 2.3)*

Experiments and data summaries that have addressed hypothesis (2.3) to date have been equivocal and contradictory. Schmitz *et al.* (2000) performed a meta-analysis of 14 terrestrial experiments that manipulated higher predators and found evidence that the cascading effects of predator removal on plant damage were weaker in systems that had higher herbivore diversity. A more comprehensive analysis of trophic cascades measured in a variety of

ecosystems found no evidence that variation in the strength of cascades was related to the richness of predators, herbivores, or plants (Borer *et al.* 2005). In contrast, a limited number of experiments have manipulated the diversity of predators at top trophic levels and shown that diversity can indirectly alter plant biomass by changing rates of herbivory. Cascading effects of predator diversity have been demonstrated in agricultural (Cardinale *et al.* 2003, Wilby *et al.* 2005, Snyder *et al.* 2006), salt marsh (Finke and Denno 2005), and kelp forest systems (Byrnes *et al.* 2006), and have been attributed to non-additive interactions (Cardinale *et al.* 2003, Cardinale *et al.* 2006b), omnivory (Bruno and O'Connor 2005), intra-guild predation (Finke and Denno 2005), and changes in herbivore behavior (Finke and Denno 2005, Byrnes *et al.* 2006). Yet, the magnitude and direction of predator richness impacts on plant biomass and production have been inconsistent among studies (see Bruno and Cardinale 2008 for a review). Thus, although predator richness frequently has cascading impacts on food-web properties, it is difficult at this point in time to predict whether these cascading effects generally increase or decrease plant biomass. Therefore, at present, there is no clear evidence that can be used to accept or reject Strong's (1992) hypothesis that trophic cascades are restricted to low-diversity linear food chains.

8.4 Where do we go from here?

8.4.1 Detailing mechanisms: niche partitioning and life-history tradeoffs

William Dillard, founder and Chairman of Dillard's department stores, once said that the three most important factors for the success of a business are 'location, location, location'. Similarly, we believe that the three most important factors that will determine the success of the BEF paradigm will be our ability to identify mechanisms, mechanisms, mechanisms! Understanding the mechanisms that underlie diversity effects essentially requires that researchers return to several of ecology's classic questions about how niche partitioning and life-history tradeoffs allow species to coexist. Chesson (2000) provided what is perhaps the most elegantly organized summary of the mechanisms that allow

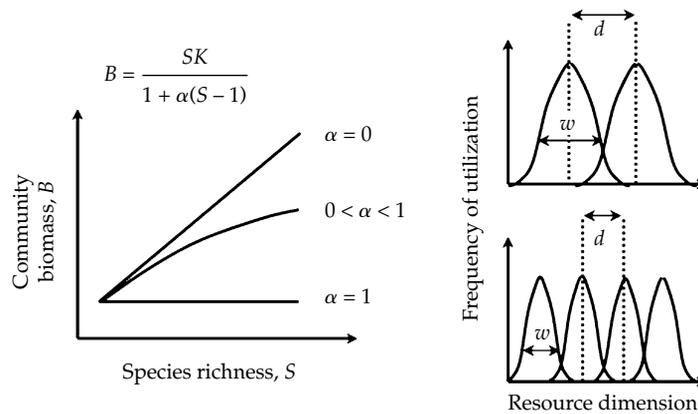


Figure 8.4 (a) Solutions to Lotka–Volterra competition equations showing how species richness affects community biomass production for differing levels of interaction strength. Note there is a positive, but decelerating relationship between B and γ for all $0 < \alpha < 1$. This is an inevitable consequence of niche packing (insets) where the addition of species to a system with finite resource forces the average species to occupy a smaller fraction of resource space. Thus, the more species there are, the less each species contributes to resource capture and biomass production, on average.

coexistence. He showed that, for a wide variety of mathematical models, coexistence is ultimately determined by the balance of two interacting forces, which he called *equalizing* and *stabilizing*. Equalizing forces are those that minimize differences in the fitness of species, causing interspecific interactions to have weaker influence over population dynamics. Hubbel’s (2001) neutral theory of biodiversity is the extreme case of an equalizing force where demographic parameters are assumed to be identical among species such that interacting with another species has the same per capita impact as interacting with a congener. Equalizing mechanisms are not mathematically stable and cannot allow long-term coexistence. Rather, equalizing mechanisms only serve to slow the inevitable outcome of species interactions. Thus, long-term coexistence requires some type of stabilizing force that involves niche differentiation in space or time. Regardless of whether niche differentiation occurs through partitioning of limited resources, shared predators, or some other dimension of a species niche, stabilizing forces all share the feature that they reduce interspecific relative to intraspecific interactions, leading to a per capita growth advantage of a species when rare.

The literature is ripe with models that examine how reductions in interspecific relative to intraspecific interactions regulate the impacts of species diversity on the production of single trophic-level

systems (Loreau 2004, Tilman *et al.* 1997c, Ives *et al.* 2005, Cardinale *et al.* 2004). The discrete time Lotka–Volterra models of competition serve as an example (Cardinale *et al.* 2004), where the biomass of any species i in a local community can be described as

$$b_i(t+1) = b_i(t) \exp \left[r_i \left(1 - \frac{b_i(t) + \alpha \sum_{j \neq i}^N b_j(t)}{K_i} \right) \right] \quad (8.1)$$

K_i is the equilibrium biomass of i in the absence of competitors, r_i is the intrinsic rate of increase in biomass, and α is the ratio of inter- to intra-specific interaction. If species have similar carrying capacities and symmetric interactions, then all species have the same biomass at equilibrium, $b(\infty)$, and for any local community

$$b(\infty) + \alpha(S-1)b(\infty) = K \quad (8.2)$$

From this, the total biomass of the community is

$$B(\infty) = \frac{SK}{1 + \alpha(S-1)} \quad (8.3)$$

For the extreme cases of $\alpha = 1$ or $\alpha = 0$, eq. 3 reduces to $B = K$ and $B = SK$, respectively, which shows that community biomass is independent of,

or a linear function of richness (Fig. 8.4). For all other scenarios where $0 < a < 1$, community biomass is a positive but decelerating function of species richness. Importantly, the curvilinearity of this function has nothing to do with how 'unique' or 'redundant' species are. Rather, the decelerating relationship is an inevitable consequence of packing more species into a finite niche axis. Even when all species are specialists with a unique niche, the contributions by any single species to resource capture and biomass production must decline as a function of richness (i.e. $b \propto 1/S$, (Eqn 8.2), causing each increase in diversity to contribute smaller increments to resource capture and biomass.

Equation (8.3) predicts a rather straightforward set of relationships between species diversity and community biomass for any trophic group that is supported by a non-dynamic resource (e.g. plants assimilating inorganic resources, detritivores feeding on dead organic matter, etc.). One of the key questions as we extend BEF theory to multi-trophic systems is whether this same set of simple relationships holds true for systems where the resources are themselves dynamic. Interestingly, several authors have analyzed Lotka–Volterra models for both dynamic and non-dynamic resources and found that the effects of species diversity on community biomass are often qualitatively similar between one and two trophic-level systems (Thebault and Loreau 2003, Thebault and Loreau 2006, Ives *et al.* 2005, Fox 2004b). There seems to be just two general instances where new behaviors emerge in a multi-trophic system. The first occurs when dynamic resources, which have the potential to be overexploited in a multi-trophic system, are brought to extinction by their consumers. Overexploitation or extinction of resources by a diverse group of generalist consumers can yield humped-shaped diversity–biomass relationships in both predators and prey, which is a BEF relationship that is not found in single trophic-level systems (Thebault and Loreau 2003, Thebault and Loreau 2006, Ives *et al.* 2005). Second, there are certain types of life-history tradeoffs that can alter the shape and magnitude of a diversity–biomass relationship (Thebault and Loreau 2003, Thebault and Loreau 2006). For example, when resource species exhibit a tradeoff between their competitive abilities and their ability to

resist or recover from consumption, this can moderate coexistence among prey (Holt *et al.* 1994) and dictate whether prey biomass increases or decreases with diversity (Holt and Loreau 2002, Thebault and Loreau 2003). Similarly, the tradeoff between the degree of resource specialization and assimilation efficiency of consumers has important implications for the BEF relationship. The diversity of consumers that pay no cost to generalism, i.e. that do not trade off their ability to consume a wide diversity of resources against their efficiency at consuming each of these resources, typically has a strong destabilizing effect on both population- and ecosystem-level fluctuations, whereas species diversity has a stabilizing effect on ecosystem-level fluctuations when consumers do have such tradeoffs (Thebault and Loreau 2005).

So are the consequences of extinction the same in single versus multi-trophic systems? Theory predicts that the answer entirely depends on the form of tradeoffs that mediate the coexistence of both consumers and their resources, and whether or not resources exhibit density dependent dynamics and overexploitation by consumers. What we need now are innovative experiments that manipulate the strength of consumer–resource interactions and/or the existence of tradeoffs that are presumed to underlie diversity effects in multi-trophic systems. Although such innovative experiments will no doubt be challenging, they have the potential to yield some of the most important new insights into the functioning of food webs.

8.4.2 Realistic scenarios of extinction

It is well established that species extinction is a non-random processes. Throughout both geological and modern time, certain biological traits such as dispersal ability, generation time, body size, geographic range, and local density have proven to be correlated with extinction risk (McKinney 1997, Lawton and May 1995, Purvis *et al.* 2000a). Trophic position also appears to be correlated with extinction risk. In marine systems, extinction of fish species generally proceeds from the top of food webs downward (Pauly *et al.* 1998), which is partly due to human preferences for large-bodied fish, and partly because such fish have low resilience due to late maturity and slow growth (Myers and Worm

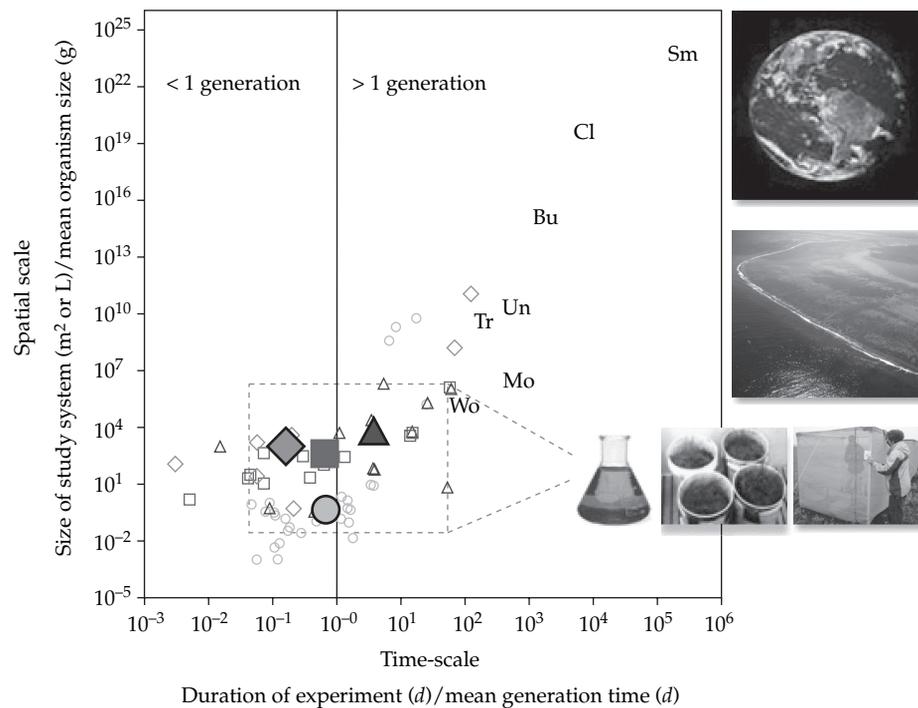


Figure 8.5 The spatial and temporal scale of biodiversity-ecosystem functioning experiments. The experimental duration (in days) and spatial scale (in m^2 or L) of experiments reviewed by Cardinale *et al.* (2006) were standardized to the mean generation time and body sizes of the focal organisms. Data were divided into four trophic groups: Plants = green circles, Herbivores = blue triangles, Predators = red squares, Detritivores = brown diamonds. The scale of each individual study is given by smaller symbols while the medians for each trophic group are shown as larger symbols. The box denoted by the dashed line gives the 10th and 90th percentiles for the scale of all experiments. For comparative purposes we show the scale of several natural extinctions: Wo = wolves from Yellowstone National Park, USA; Mo = Moa from New Zealand; Tr = Trout from Lake Superior, USA; Un = Unionid mussels from the lower Mississippi River, USA; Bu = Various species of butterflies in Europe; Cl = Loss of certain cladoceran zooplankton from Lake Superior, USA; Sm = Global eradication of the small pox virus.

2005). In terrestrial systems, studies similarly report higher extinction probabilities for predators than their prey (Kruess and Tscharntke 1994, Didham *et al.* 1998b).

Non-random patterns of extinction can affect diversity–function relationships in at least two ways: via the functional traits lost, and via changes in community interactions. Initially, ecosystem function may be most affected by the functional traits of the species that preferentially go extinct (Srivastava and Vellend 2005, Lavorel and Garnier 2002). Positive covariance between extinction risk and the magnitude (Gross and Cardinale 2005) or uniqueness (Petchey and Gaston 2002b) of a species functional effects can exacerbate the impacts of species loss on ecosystem function (i.e. diversity–function effects are initially stronger for realistic extinctions than

random extinctions). Predators may have high functional importance in food webs, first because of the strength of top-down processes in food webs (Duffy 2003), and second because predators may have traits that are additionally correlated with high functional impact (e.g. body size – Solan *et al.* 2004).

Following extinction of a species, diversity–function relationships are additionally influenced by the response of the surviving species to loss of a community member. Gross and Cardinale (2005) showed that the effect of species interactions amongst survivors depends critically on the mechanisms that underlie diversity–function relationships: niche partitioning, facilitation or the sampling effect each make very different predictions about how biased extinction scenarios differ from random extinction scenarios. In food web simulations, Ives and Cardinale (2004)

showed that the coupling of directional extinction with species interactions can lead to unexpected changes in the functional importance of species. Although it is clear that non-random patterns of extinction can have very different implications than the random extinctions that commonly simulated in experiments, our ability to predict the functional changes that stem from non-random extinction – particularly the top-down effects of species loss on ecosystem function – is still in its infancy. After our need to characterize interaction strengths and inter-specific tradeoffs (Section 8.4.1), our single biggest gap of knowledge stems from a lack of information about levels of covariance between extinction risk and species-specific impacts on rates of ecological processes at various trophic levels.

8.4.3 Environmental heterogeneity, patch dynamics, and scale

The typical biodiversity experiment performed to date has taken place in experimental units slightly larger than a five-gallon bucket, and has run for less than one generation of the focal organisms (Fig. 8.5). While there are noteworthy exceptions (Tilman *et al.* 2001, Hector *et al.* 1999), it seems safe to say that most of our inferences about biodiversity stem from experiments performed at spatial scales much smaller, and temporal scales much shorter than those at which species extinctions actually matter (also see Naeem 2001a for a more complete review). Overcoming this mismatch in scale is a daunting task, and the difficulties of performing large-scale, long-term experiments are why ecologists use simplified model systems in the first place (Srivastava *et al.* 2004). Nevertheless, ecologists have begun to make progress on these issues by incorporating the important ecological factors that co-vary with scale into their experimental designs (Cardinale and Palmer 2002, Dimitrakopoulos and Schmid 2004, Mulder *et al.* 2001) and accounting for them in meta-analyses of experiments performed at different scales (Cardinale *et al.* 2007).

The issue of scale is by no means unique to BEF research, nor is it specific to multi-trophic systems. There are, however, certain characteristics of multi-trophic systems that make it especially important that we deal more directly with the issue. Namely, dis-

persal as a process affecting species coexistence becomes particularly prominent at higher trophic levels where organisms are typically more mobile (at least, on the shorter time-scales of most experiments) and, therefore, have the ability to integrate information across a landscape and aggregate in response to the density of their prey. This is important because dispersal and aggregation across spatially distinct patches or habitat boundaries can translate into various forms of niche partitioning that stabilize competitive interactions and consumer–resource dynamics (Armstrong 1976, McCann *et al.* 2005). As it modifies coexistence, dispersal across patches or habitat boundaries can also qualitatively alter the BEF relationship (Mouquet *et al.* 2002).

Although most of the work that has examined how dispersal affects BEF relationships has focused on single trophic level systems, it is useful to quickly review here and then consider how these predictions might be extended to systems with dynamics resources. A wide variety of ecological models have highlighted the important role that dispersal plays in maintaining the diversity of communities (e.g. Island Biogeography Theory – MacArthur and Wilson 1967, ‘mass’ effects – Shmida and Wilson 1985, ‘rescue’ effects – Brown and Kodricbrown 1977). Historically, models of dispersal have been phenomenological, meaning they did not explain the existence of diversity based on first principles. Instead, these models assumed there was some ‘magical’ pool of species that coexisted at large scales via some unknown mechanism(s), and these species generated propagules that could subsidize local populations. The emergence of meta-community theory (Leibold *et al.* 2004) represented a major advance because these models acknowledged that everything in a propagule pool must ultimately come from the collection of patches or habitats that span a species range. Based on first principles, meta-community models predict both the causes and consequences of diversity at ‘local’ (organisms interacting as communities within patches) and ‘regional’ scales (patches of communities connected by dispersal).

One common form of meta-community models assumes that species coexist through tradeoffs in their abilities to compete in patches that have differing types or supply rates of resources (i.e. what Leibold *et al.* 2004 call ‘species-sorting’ models).

These models predict that at the scale of any local community, increasing the number of species in the meta-community serves only to ensure that species best adapted to a given patch will colonize and dominate that patch. This is the typical ‘selection effect’ of diversity (Loreau and Hector 2001, Huston 1997), which has been formalized as follows: assume that species can be ranked by their carrying capacities such that $K_{(m)}$ represents the species having the highest carrying capacity in any single patch, $K_{(m-1)}$ is the next highest, and so on. If competition among species is strong ($\alpha = 1$ in Eqn 8.1), only one species will be present in a patch at equilibrium, and the biomass in a patch will be

$$B(\infty) = \frac{N_{col}}{\gamma} K_{(m)} + \left(1 - \frac{N_{col}}{\gamma}\right) \left(\frac{N_{col}}{\gamma-1}\right) K_{(m-1)} + \left(1 - \frac{N_{col}}{\gamma}\right) \left(1 - \frac{N_{col}}{\gamma-1}\right) \left(\frac{N_{col}}{\gamma-2}\right) K_{(m-2)} + \dots \quad (8.4)$$

Equation (8.4) says that the amount of biomass produced in a patch at equilibrium is proportional to the probability, N_{col}/γ , that the species with the highest carrying capacity, $K_{(m)}$, will colonize the patch. If a patch is not colonized by the most productive species, then the probability that the second most productive species, $K_{(m-1)}$, will colonize and dominate the patch is $\left(1 - \frac{N_{col}}{\gamma}\right) \left(\frac{N_{col}}{\gamma-1}\right)$. Note that as the number of species colonizing a patch increases, the probability that a patch becomes dominated by the most productive species in the regional species pool approaches unity. However, one key point is that for the selection effect to operate in the first place, species diversity must first exist in the regional colonist pool (i.e. γ must exist at the scale of a meta-community). But in order for diversity to be maintained in the regional colonist pool, species must exhibit some form of tradeoff that ensures they use resources in ways that are complementary across patches. This suggests that the same mechanisms that ensure complementary use of resources across patches in a region also produce species-specific selection effects at the scale of a local community (Cardinale *et al.* 2004).

Loreau *et al.* (2003) similarly showed that coexistence of species at a regional scale could maximize biological production at a local scale, and called this the ‘spatial insurance’ hypothesis of diversity (also see Chapter 10, where Gonzalez treats the issue exten-

sively). The general idea of the spatial insurance hypothesis is that while one species may be sufficient to maximize production in any local community, the maximization of productivity across all patches in any heterogeneous landscape requires that a diversity of species exhibit niche differences at a regional scale. Meta-community models like that used to generate the spatial insurance hypothesis are important because they serve as a springboard from which we can address more pressing issues within the field of BEF research. From the perspective of basic theory, we need to extend meta-community models to consider how species diversity impacts the production of community biomass when consumers and their resources both move across a spatially heterogeneous landscape. We need to know what happens to BEF relationships when (1) resources have a spatial refuge from their consumers, (2) consumers and resources disperse at similar versus different rates, or (3) species exhibit spatially mediated tradeoffs, such as in their dispersal versus competitive abilities, or dispersal versus ability to resist consumption. At the same time, we need experiments that explicitly mimic the assumptions of different meta-community models, and then examine how diversity impacts the production of local and regional biomass for various mechanisms that allow consumer–resource coexistence. These advances are essential if we expect to predict the ecological consequences of extinction from real food webs where the norm is that species move across habitat boundaries and make choices about where to spend their time in order to maximize fitness.

8.4.4 Socio-economic impacts of food web diversity

After several decades of research, it has become apparent that loss of diversity from an ecosystem can have impacts on ecological processes that rival, if not exceed, many other forms of environmental change. Ecologists are now in a position to estimate the number of species required to maximize the removal of greenhouses gasses like CO_2 from the atmosphere, remove nutrient pollutants from streams and lakes that serve as drinking water, or to produce crops and fisheries. Indeed, it is now possible to make reasonably educated estimates of how diversity loss

Box 8.1 Socioeconomic impacts of predator diversity

One of the primary services that ecosystems provide to society is the biological control of insect pests. This service is estimated to be worth US\$400 billion per year globally (Costanza *et al.* 1997). Although it has long been assumed that effective pest management requires a diversity of predators, parasites, and pathogens (collectively called 'natural enemies'), experiments designed to explicitly test this hypothesis have only recently begun. Two case studies highlight the range of results observed thus far.



AQ: Please provide caption for this figure.

Case study 1: Predator diversity decreases pest populations

In a field experiment performed in Wisconsin, USA, Cardinale *et al.* (2003) manipulated the richness of three natural enemies of aphids (pea and cowpea) that are herbivorous pests of alfalfa. Two of the enemies – a ladybeetle and an assassin bug – were generalist predators that fed on both aphid species. The third was a specialist parasitoid wasp that attacks only pea aphids. They found that as generalist predators reduced the density of both

aphids, the parasitoid wasp became more efficient at attacking the pea aphid. As a result, when all three enemies were together they reduced aphid populations to one-half of that achieved by any enemy species alone. This translated to a 51 per cent increase in the yield of alfalfa. Alfalfa is the fourth most widely grown crop in the USA with an estimated annual value of US\$11.7 billion (source: US Department of Agriculture). In 2003 when this study was performed, alfalfa was selling for \$150 per acre. The state of Wisconsin dedicates 3.5 million acres to the production of alfalfa. Assuming the results of this experiment can be generalized to Wisconsin, the economic benefit of predator diversity would be roughly US \$525 million during a single harvesting cycle. In a typical year in the midwestern USA, alfalfa is harvested 3× per summer.

Case study 2: Predator diversity increases pest populations

In a second field experiment, Cardinale *et al.* (2006) manipulated the diversity of a different group of aphid predators, this time focusing on three species of ladybeetles that are all generalist predators. When the ladybeetles were placed together in field enclosures, they tended to compete with each other in a way that reduced their individual ability to capture prey. As a result, more diverse predator assemblages were roughly 60 per cent less efficient at controlling aphid populations than expected based on how each ladybeetle performed when alone. In this case, the antagonistic interactions among the predators led to a 17 per cent decrease in alfalfa yield. This result emphasizes that predator species can interact in ways that may have economic costs. A key challenge for ecologists is to determine the frequency of positive and negative interactions among predators that might help us evaluate the costs versus benefits of biodiversity.

translates into societally meaningful units – whether that be in dollars, health risks, carbon credits, or otherwise.

The socio-economic implications of biodiversity are perhaps most obvious from studies of higher-trophic levels, including those of pollinators, and of natural enemies that control pest populations.

Invertebrate predators, parasitoids, and pathogens can be important promoters of top-down control in terrestrial food webs, helping to keep pests below economically damaging levels. This natural biological control of pests represents a valuable ecosystem service that is essential to sustainable production of food and fibre. Recent economic

valuation of the services provided by insects suggests the value of biological control of native pests by natural enemies is \$4.49 billion per year in the USA alone (Losey and Vaughan 2006), and > US \$400 billion per year at a global scale (Costanza *et al.* 1997). While classical biological control tends to focus on the contribution of individual species of natural enemies, a growing number of studies suggest that the efficiency of biocontrol is often a function of non-additive interactions among multiple predators, parasitoids, and pathogens (Rosenheim 2007, Losey and Denno 1998, Snyder and Ives 2003, Snyder *et al.* 2006, Finke and Denno 2005, Cardinale *et al.* 2003, Cardinale *et al.* 2006b). Although it is not yet clear whether these interactions among enemies generally increase or decrease prey populations, it is clear that the economic impacts of natural enemy diversity can be substantial (Box 8.1).

Crop pollination is another ecosystem service centred on interactions across trophic levels. The global value of pollination services have been estimated at US\$117 billion per year (Costanza *et al.* 1997) and in a recent review, Klein *et al.* (2007) concluded that fruit, vegetable, or seed biodiversity (i.e. richness, abundance, and distribution of multiple species of pollinators) in delivering this ecosystem service are often poorly quantified. Similar to evaluations of classical biocontrol, where the focus is on the action of one or few natural enemies rather than diversity *per se*, many of the economic valuations of pollination services consider the contribution of honey bees alone. Klein *et al.* (2007) report case studies for nine crops on four continents implicating a diversity of pollinators and revealing that agricultural intensification jeopardizes wild bee communities and their stabilizing effect on pollination services at the landscape scale. At the individual farm level, such natural pollination services can contribute significantly to annual income; a study from a coffee plantation in Costa Rica, for example, indicated native bee species account for \$62,000, or 7 per cent of the farm's annual income

(Ricketts *et al.* 2004). At a more regional level, Losey and Vaughan (2006) calculate that native pollinators (mostly bees) may be responsible for > \$3 billion of fruit and vegetables produced in the USA.

Although often less direct, changes in biodiversity and associated trophic structure have major implications for issues such as disease risk, with associated impacts on economics and human well being. For example, top predators are often the first species to disappear as habitat is destroyed and fragmented. As elaborated in Chapter 15, when predators are lost to ecosystems, their prey may increase in abundance, leading to increased transmission efficiency of zoonotic diseases such as Lyme disease (Ostfeld and Holt 2004, Dobson *et al.* 2006). While quantifying the benefit of biodiversity in terms of disease regulation and infected cases averted is clearly complex, many diseases such as malaria, tick-borne encephalitis, and West Nile fever have been shown to increase as biodiversity falls (Dobson *et al.* 2006, and Chapter 15).

8.5 Summary

The emerging paradigm of Biodiversity Effects on Ecosystem Functioning has shown great potential to augment ecology's historical focus on the causes of biodiversity with a much more contemporary understanding of its ecological consequences. Even so, BEF studies have, thus far, been limited to highly simplified 'model' communities that are nowhere near the trophic complexity of real communities. To overcome this limitation, it is now imperative that ecologists begin to merge the BEF paradigm with more classic ideas in food web ecology that detail how interactions among trophic levels that play out in space and time can constrain fluxes of energy and matter. Most hypotheses about the functional role of diversity within and across trophic levels are in their infancy, and they represent a rich opportunity for new work during the second generation of BEF experiments.