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## The relationship between biodiversity and ecosystem functioning in food webs

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**Abstract** Recent theoretical and experimental work provides clear evidence that biodiversity loss can have profound impacts on functioning of natural and managed ecosystems and the ability of ecosystems to deliver ecological services to human societies. Work on simplified ecosystems in which the diversity of a single trophic level is manipulated shows that diversity can enhance ecosystem processes such as primary productivity and nutrient retention. Theory also strongly suggests that biodiversity can act as biological insurance against potential disruptions caused by environmental changes. However, these studies generally concern a single trophic level, primary producers for the most part. Changes in biodiversity also affect ecosystem functioning through trophic interactions. Here we review, through the analysis of a simple ecosystem model, several key aspects inherent in multitrophic systems that may strongly affect the relationship between diversity and ecosystem processes. Our analysis shows that trophic interactions have a strong impact on the relationships between diversity and ecosystem functioning, whether the ecosystem property considered is total biomass or temporal variability of biomass at the various trophic levels. In both cases, food-web structure and trade-offs that affect interaction strength have major effects on these relationships. Multitrophic interactions are expected to make biodiversity–ecosystem functioning relationships more complex and non-linear, in contrast to the monotonic changes predicted for simplified systems with a single trophic level.

**Keywords** Biodiversity · Ecosystem functioning · Stability · Trophic interactions · Top-down control

### Introduction

The role that biodiversity plays in ecosystem functioning has attracted much attention during the last decade (see syntheses in Kinzig et al. 2002; Loreau et al. 2002; Hooper et al. 2005) due to the current erosion of biodiversity (Pimm et al. 1995). The central question of this research area focuses on the potential consequences of biodiversity loss on ecosystem services (e.g. primary and secondary production, plant pollination, maintenance of soil fertility, etc.), and more generally on ecosystem processes.

Ecological experiments show that ecosystem properties depend greatly on biodiversity. It is generally found that plant diversity increases primary production (Hector et al. 1999; Tilman et al. 2001), and several empirical studies have found decreased variability of primary production as diversity increases (Tilman et al. 1996; McGrady-Steed et al. 1997). These latter results are still debated because of potential confounding factors. Theoretical developments and debates that have arisen from these studies propose several mechanisms to explain the positive effects of diversity. The impact of biodiversity on productivity has been explained by two mechanisms: first, a complementarity effect generated by niche differentiation and facilitation and second, a selection effect that can cause dominance of the most productive species (Tilman et al. 1997; Loreau 1998; Loreau and Hector 2001). Other theoretical studies have considered the effects of diversity under changing conditions and focused mainly on variability of ecosystem processes. If different species respond differently to environmental changes, theory predicts that community variability should decline with increasing species richness. Thus biodiversity can also provide an ‘insurance’ or a buffer against environmental fluctuations, leading to more predictable aggregate community or ecosystem properties (Yachi and Loreau 1999; Doak et al. 1998; Lehman and Tilman 2000).

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While experiments and theories have mainly concentrated on single trophic level systems, for the most part, primary producers, (see for example Hector et al. 1999; Tilman et al. 1997, 2001; Dimitrakopoulos and Schmid 2004; van Ruijven and Berendse 2005; Loreau 1998), relatively few theoretical and experimental studies have examined effects of species richness on ecosystem properties in multitrophic systems (Mulder et al. 1999; Downing and Leibold 2002; Duffy et al. 2003, 2005; Fox 2004; Ives et al. 2005). This bias towards single trophic level systems is true for both the relationship between diversity and the magnitude of ecosystem processes and for the relationship between diversity and the variability of these processes. Furthermore, the complementarity and selection effects on one hand and the insurance hypothesis on the other hand virtually concern single trophic levels. Theory is then insufficient to predict multitrophic effects of diversity changes that can be mediated through trophic interactions and their indirect effects on ecosystem processes (Naeem 2002).

Studying biodiversity impact on ecosystem functioning in multitrophic systems is important for several reasons: (1) multiple trophic levels are common in ecosystems, and extinction threats appear to be higher for species at higher trophic levels (Petchey et al. 1999); (2) changes in consumer richness can have effects on ecosystem functioning that are as large as, or even larger than, comparable changes in primary producers' richness (Duffy 2003). Recent analyses have shown that consumers may modify the relationship between diversity and primary production (Mulder et al. 1999; Paine 2002; Duffy et al. 2003, 2005). As multitrophic diversity increases, average ecosystem properties could increase, decrease, stay the same or follow more complex non-linear patterns. A broad research tradition has studied how trophic interactions can affect biomass and productivity at various trophic levels (Abrams 1993; Chapin et al. 1997; Shurin et al. 2002; Schmitz 2003) as well as at various measures of stability (MacArthur 1955; May 1972; Pimm 1984). However, this research area has considered the importance of functional diversity across trophic levels and not how diversity within trophic levels affects ecosystem processes. Merging these theories with the study of the relationship between diversity and ecosystem functioning may help to provide new mechanisms to explain how diversity affects ecosystem processes in multitrophic systems. Only a few studies have recently begun to build a bridge between these two approaches to build a broader theoretical framework that has greater relevance to natural ecosystems (Duffy 2002; Thébault and Loreau 2003; Ives et al. 2005).

Here we review, through the analysis of a simple ecosystem model, several key aspects inherent in multitrophic systems that may strongly affect the relationship between diversity and ecosystem processes.

## Underlying model

We have developed an ecosystem model that allows us to analyse the impacts of food-web structure on both the relationship between species diversity and total biomass at the various trophic levels and the relationship between species diversity and the temporal variability of these biomasses (Thébault and Loreau 2003, 2005). This model is an extension of the model proposed by Loreau (1996) for a nutrient-limited ecosystem containing an arbitrary number of plants and specialised herbivores in a heterogeneous environment. In this model, plant nutrient uptake is assumed to decrease the soil concentration of a limiting nutrient in the immediate vicinity of the rooting system, thus creating a local resource depletion zone around each plant and allowing plant coexistence under some conditions. Here we generalise it by allowing herbivores to be generalists, but for simplicity we do not consider food-web configurations that include carnivores. The model is described by the differential equations:

$$\left\{ \begin{array}{l} \frac{dP_j}{dt} = a_j V_j N_j P_j - m_p(t) P_j - \alpha \sum_{i \neq j} c_i H_i P_j - c_j H_j P_j \\ \frac{dH_i}{dt} = e c_i H_i P_i + e \alpha \sum_{j \neq i} c_j H_i P_j - m_h(t) H_i \\ \frac{dD_p}{dt} = \sum_j m_p(t) P_j - (l_p + q) D_p \\ \frac{dD_h}{dt} = \sum_i m_h(t) H_i + (1 - e) \sum_i [c_i H_i P_i + \sum_{j \neq i} \alpha c_i H_i P_j] \\ \quad - (l_h + q) D_h \\ \frac{dN_j V_j}{dt} = V_j k (R - N_j) - a_j(t) V_j N_j P_j \\ \frac{dR V_R}{dt} = q V_R (R_0 - R) - k \sum_j V_j (R - N_j) + l_h D_h + l_p D_p \end{array} \right. \quad (1)$$

where  $R$  is the nutrient concentration in the regional soil pool with volume  $V_R$ ;  $N_i$  is the nutrient concentration in the set of local resource depletion zones, with total volume  $V_i$ , of plants from species  $i$ ;  $D_p$  and  $D_h$  are the nutrient stocks of plant and herbivore dead organic matter; and  $P_i$  and  $H_i$  are the biomasses (measured as nutrient stocks) of plant and herbivore species  $i$  respectively. Nutrients are transported between local and regional pools at a rate  $k$  per unit time. Plant species  $i$  has a growth rate  $a_i$ , herbivore species  $i$  consumes plant species  $i$  at a rate  $c_i$ , and  $l_p$  and  $l_h$  are decomposition rates of plant and herbivore detritus, respectively.  $\alpha$  is the degree of generalisation of herbivores. The death rates  $m_{pi}$  and  $m_{hi}$  of plants and herbivores respectively will be considered to be identical in our analysis for the sake of simplicity. Lastly,  $q$  is the rate of nutrient loss from the ecosystem in inorganic form, and  $R_0$  is nutrient supply concentration.

We present results for total plant and herbivore biomasses as ecosystem properties for comparison with experimental studies. Stability is assessed here as the ability to reduce temporal variability of these properties in a fluctuating environment. Environmental fluctuations were included in the form of sinusoidal variations in temperature or other abiotic variables on which plant and herbivore mortality rates depend. We assume that these rates have a Gaussian dependence on temperature with identical standard deviations.

We examine how changes in species richness influence ecosystem properties (1) for different food-web configurations: either herbivores are specialist or generalist, and either all plants are edible or not; (2) for different scenarios of biodiversity changes: either plant species richness and herbivore species richness vary in parallel, or herbivore species richness varies alone. For each scenario and configuration, we compare six levels of species richness, with 1, 2, 4, 8, 12 or 16 species per trophic level. At each diversity level, the community is a random assemblage of the species present at the highest diversity level. We report the results from numerical simulations of the model for the average value and the coefficient of temporal variation (CV)—a common standardised measure of variability (e.g. Doak et al. 1998; Lehman and Tilman 2000)—of the total biomass at each trophic level. Analytical studies and more extensive results (such as the calculation of complementarity and selection effects; Loreau and Hector 2001) are presented elsewhere for both the relationship between diversity and total biomass at equilibrium (Thébault and Loreau 2003) and the relationship between diversity and ecosystem stability (Thébault and Loreau 2005).

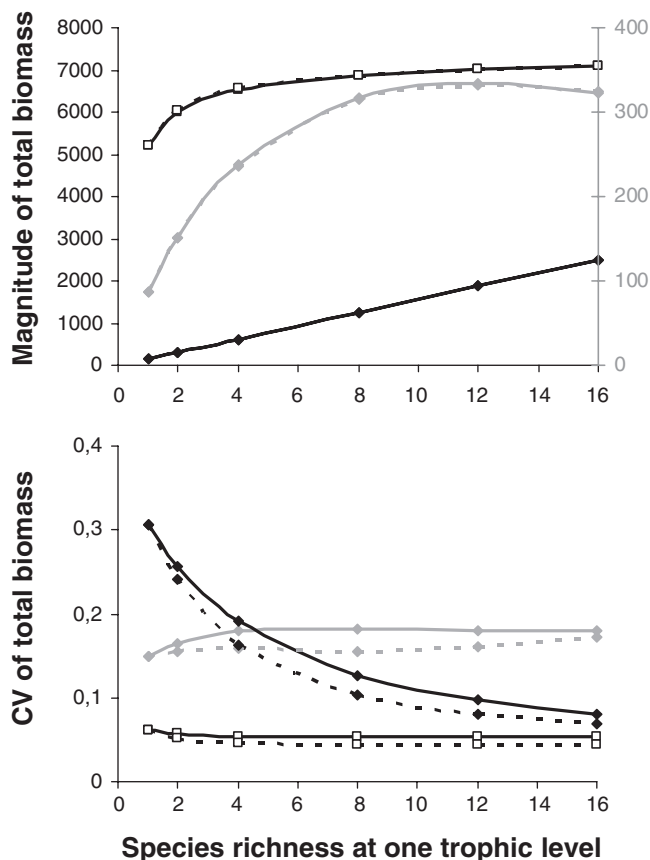
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### Top-down control and destabilising effect: two mechanisms by which consumers affect the relationship of diversity–ecosystem functioning

Many studies have demonstrated a strong top-down effect in various systems (Shurin et al. 2002), but they have considered only the importance of ‘vertical’ diversity, i.e. functional diversity across trophic levels along the food chain. Identically, the study of predator effects on stability has mainly focused on the impact of this ‘vertical’ diversity and not on how diversity within trophic levels affects ecosystem stability. A destabilising effect of consumers on prey stability has generally been found in this case (Pimm and Lawton 1977; Halpern et al. 2005). Here we compare the relationship between diversity and ecosystem properties in the absence or presence of consumers when plant species richness and consumer species richness (when present) vary in parallel. We take an example where all herbivores are specialists for simplicity. In this case, changes in diversity in the absence of herbivores (Fig. 1, squares) can have different effects than when herbivores are present (Fig. 1, diamonds), whether the ecosystem property is

total biomass or temporal variability of biomass at the various trophic levels.

In both systems, total plant biomass increased with species richness while CV of total plant biomass decreased (Figs. 1, 2). A higher degree of asynchrony of individual species responses to environmental fluctuations had identical effects on these relationships: it generally reduced CV of total biomass and this reduction



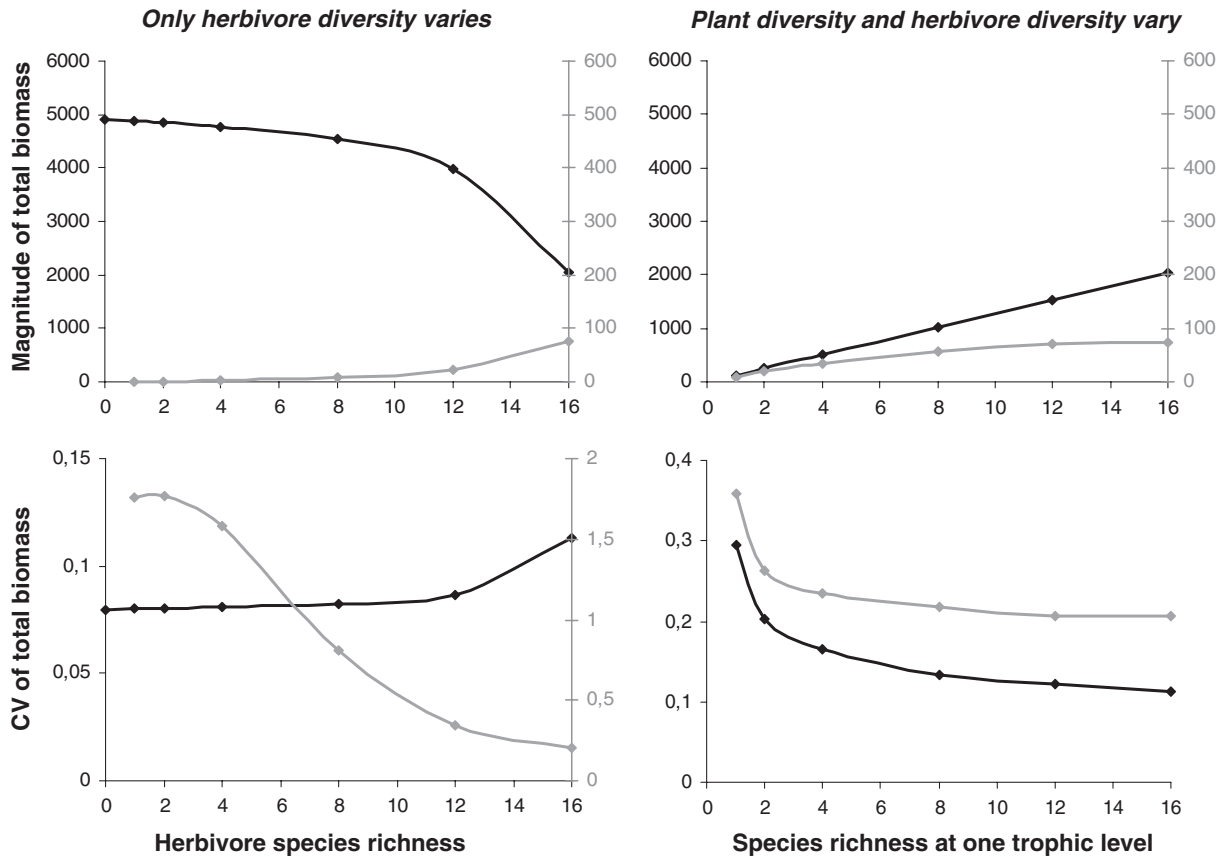
**Fig. 1** Magnitude and coefficients of variation (CV) of total plant and herbivore biomass as functions of species diversity for a single trophic level system and a two trophic level system with specialist herbivores. Two scenarios of species response to environmental fluctuations are considered. *Solid lines* correspond to identical responses of species to environmental fluctuations, and *dotted lines* to different responses of species. In each panel, *black lines* correspond to producer properties, while *grey lines* correspond to consumer properties. *Empty squares* correspond to the single trophic level system, while *full diamonds* correspond to the two trophic level system. Magnitude and coefficients of variation were calculated from data sets generated by integrating Eq. 1 with the Runge-Kutta method. For each of 200 simulations, values of  $l_p$ ,  $l_h$ ,  $q$ ,  $k$ ,  $V_R$ ,  $V_i$ ,  $R_0$ ,  $c_i$  and  $a_i$  were selected using a random number generator from uniform distributions with means 0.5, 0.5, 0.2, 45, 350, 15.5, 3.5, 0.084 and 0.016, and standard deviations 0.04, 0.04, 0.08, 10, 850, 0.25, 1.25, 0.0015 and 0.0003 respectively. The minimum mortality rates  $m_{pi}$  and  $m_{hi}$  were selected using a random number generator from uniform distributions with means 0.09 and 0.09 and standard deviations 0.003 and 0.003. Simulations at the various diversity levels used the same set of selected parameters values; species present at a lower diversity level were a sample of species present at the higher diversity levels

was stronger at higher diversities. However, the shape of these relationships, as well as the strength of diversity effects, depends on consumer presence. When each plant is consumed by a specialist herbivore, total plant biomass increases linearly with species richness whereas in the absence of herbivores, total plant biomass saturates at high diversity levels as has often been shown previously (Tilman et al. 1997; Loreau 1998). In the presence of specialist herbivores, each plant is controlled by its own herbivore and is unaffected by the addition of other species, which leads to this linear increase. This also results in a positive complementarity effect, as has been shown by Thébault and Loreau (2003). Complementarity is then generated by a different mechanism than in the simple competitive system: it does not arise from resource partitioning but from top-down control by the upper trophic level. In parallel, whereas CV of total plant biomass in the presence of herbivores is higher than in their absence, the positive impact of diversity is stronger in the multitrophic system (Fig. 1, bottom). This greater decrease in CV of total plant biomass in the presence of herbivores is explained by a reduction of the destabilising effect of plant biomass by herbivores since individual herbivore biomass and net herbivore

consumption on each plant species decreases as species richness increases (e.g. Thébault and Loreau 2005).

In the multitrophic system, the relationship between diversity and properties of total trophic level biomass are not always similar at both trophic levels. At the herbivore level, total herbivore biomass saturates at high diversity and can even decrease in some cases (Fig. 1). This saturation and potential decrease is explained by a decrease in the biomass of each herbivore with the addition of plant species: herbivore biomass depends on soil nutrient concentration, which decreases as more plants compete for the limiting nutrient. CV of total herbivore biomass is also complex and can either increase or decrease as diversity increases (Figs. 1, 2).

Thus, the nature of population controls (top-down vs. bottom-up) and the potential destabilising effect of consumers in an ecosystem can profoundly affect ecosystem responses to changes in species richness. The trophic position of species loss and various food-web properties such as connectivity, interaction strength or presence of inedible species are important to consider as they modify trophic cascades and top-down control (Leibold 1989; Abrams 1993) as well as various stability measures (Pimm 1984; McCann 2000) in food webs.



**Fig. 2** Magnitude and coefficients of variation (CV) of total plant and herbivore biomass as functions of species diversity for two scenarios of diversity changes, either species richness varies only at herbivore level or species richness varies at both trophic levels in parallel. In each panel, *black lines* correspond to producer

properties, while *grey lines* correspond to consumer properties. Parameter values as in Fig. 1, except for  $R_0$ ,  $V_i$  and  $c_i$  which were selected using a random number generator from uniform distributions with means 4.5, 2.5 and 0.1, and standard deviations 1.25, 0.25 and 0.0016 respectively

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## Impact of trophic position of species loss

Recent theory and experiments predict potentially opposing influences of diversity on primary productivity at adjacent trophic levels (Worm and Duffy 2003; Duffy et al. 2003). While producer biomass generally increases with plant richness (Hooper et al. 2005 for overview), algal biomass has been found to decrease with herbivore richness (Duffy et al. 2003, 2005). Here, we analyse two feasible scenarios of biodiversity changes: either plant richness and herbivore richness vary in parallel, or only herbivore richness changes. Changing plant richness alone leads to unfeasible food-web configurations in our model, because herbivore species cannot be more numerous than plant species at equilibrium. We take again an example where all herbivores are specialists and where all species respond identically to environmental fluctuations for simplicity.

Changes in diversity at the consumer trophic level alone (Fig. 2, left column) have very different effects than do simultaneous changes at both plant and herbivore trophic levels (Fig. 2, right column) whether the ecosystem property considered is total biomass or temporal variability of biomass at the various trophic levels. Mean total plant biomass decreases upon herbivore addition while it increases in the other scenario of biodiversity changes. These results are consistent with recent experiments on the effects of consumer diversity (Duffy et al. 2003). More surprisingly, countervailing effects of autotroph diversity and heterotroph diversity can also exist on total plant biomass variability: CV of total plant biomass increases upon herbivore addition while it generally decreases when both plants and herbivores are added.

At the herbivore level, secondary production is increased with herbivore addition, which can be explained by complementarity in resource use of specialist herbivores (Thébault and Loreau 2003). In parallel, CV of total herbivore biomass decreases. As found previously, the relationship between diversity and properties of trophic level biomass is not always similar at the two trophic levels and can even be opposite.

Thus, the relationship between diversity and ecosystem functioning depends strongly on the trophic position of species loss because consumers have particular effects on population control and stability.

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## Impacts of food-web properties

### Effect of the presence of inedible species

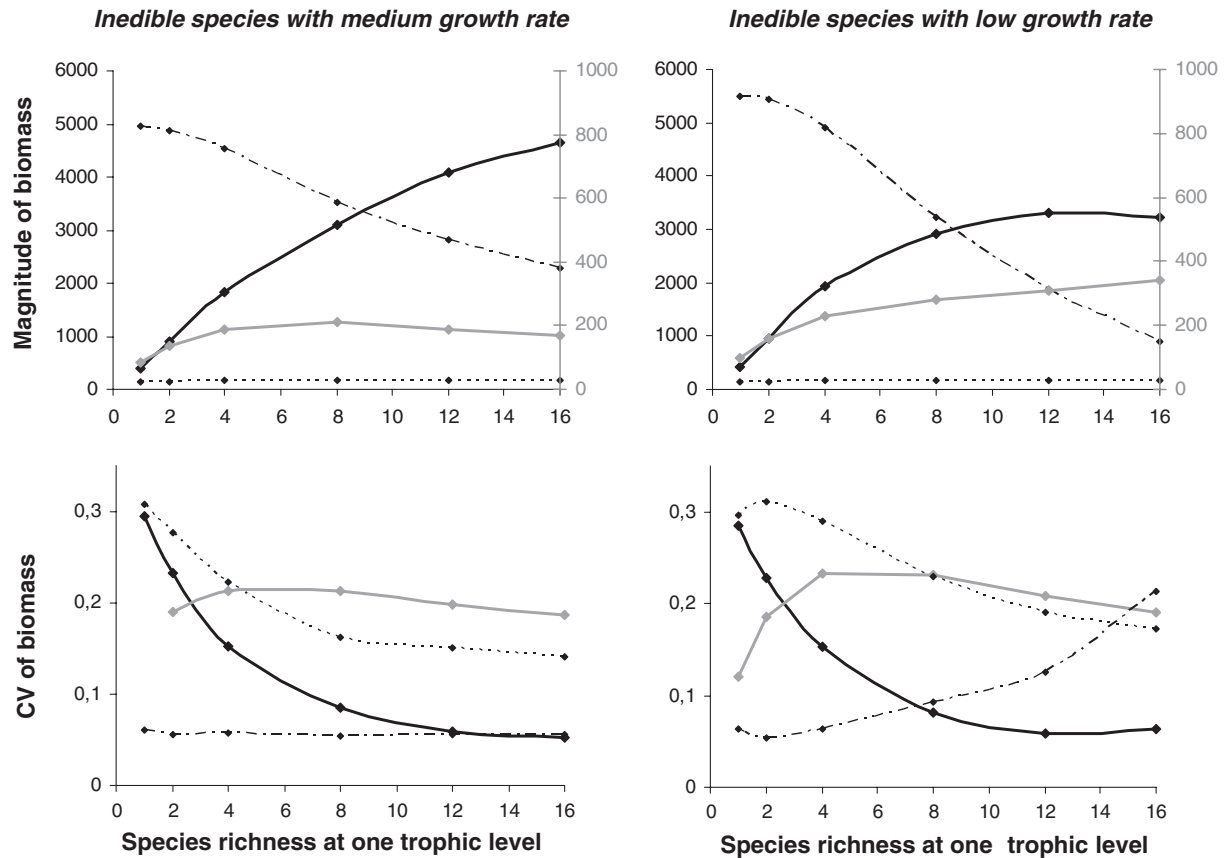
The presence of less edible species in the food-web has been shown to have a strong impact on ecosystem properties and particularly to dampen trophic cascades (Hulot et al. 2000). Heterogeneity can also strongly affect the relationship between diversity and magnitude of ecosystem functioning (Thébault and Loreau 2003). If

we compare two food-web configurations, a food-web where all species are edible and a food-web that comprises an inedible plant, the predicted relationships between diversity and ecosystem processes are qualitatively different both for the magnitude and the variability of these processes (compare Figs. 1, 3).

As shown previously, when all species are consumed by specialist herbivores, total plant biomass increases linearly with species richness (Figs. 1, 2). In contrast, when the same food-web comprises an inedible plant, total plant biomass does not increase linearly and can even decrease at high diversity (Fig. 3). In the latter case, the biomass of the inedible plant is controlled by resource availability, which decreases as plant richness increases (Fig. 3). The relationship between diversity and total plant biomass depends on the dominance of the inedible species and on its competitive ability. If the inedible species is dominant and does not suffer strongly from competition (case with high growth rate), total plant biomass increases with diversity due to complementarity between edible species and to a higher probability of the presence of the dominant species at higher diversity levels. If the inedible species is dominant but suffers strongly from competition (low competitive ability), total plant biomass decreases at high levels of diversity because the inedible species decreases strongly as diversity increases. This can also lead to a negative selection effect (Thébault and Loreau 2003): the dominant species at low diversity, the inedible species, is highly affected by an increase in diversity and it is no longer dominant at high diversity. In contrast, there is a positive selection effect when the most productive species is dominant at high diversity.

Changes in CV of total biomass also depend strongly on the presence of inedible species (Fig. 3, bottom). CV of total plant biomass decreases as diversity increases but it can also increase at higher diversity levels. This relationship between diversity and CV of total plant biomass also depends on the dominance of the inedible species and on its competitive ability. If the inedible species is dominant and does not suffer strongly from competition (case with high growth rate), CV of the inedible plant is not affected by diversity and is always lower than CV of edible plants. CV of total plant biomass then decreases as diversity increases due to a higher probability of the presence of the dominant species and also, as previously, to a lower destabilising impact of herbivores. If the inedible species is dominant but suffers strongly from competition (low competitive ability), CV of total plant biomass increases at high levels of diversity because the CV of the edible species is higher and the CV of the inedible species increases strongly as diversity increases. Competition between edible and inedible species might explain the latter result: the variability of the inedible species might be strongly affected by the high variability of edible species through resource competition.

Thus, in the context of a multitrophic level system, species edibility is an important factor to consider as



**Fig. 3** Magnitude and coefficients of variation (CV) of total plant and herbivore biomass as functions of species diversity for two cases of inedible plant species, either the inedible species has a medium growth rate or the inedible species has a slow growth rate. In each panel, *black lines* correspond to producer properties, while *grey lines* correspond to consumer properties. *Semi-dotted lines*

correspond to properties of the inedible species while *dotted lines* correspond to the properties of the edible species. Parameter values as in Fig. 1, except for the case where the inedible species has a slow growth rate:  $R_0$ ,  $k$  and  $a_i$  for the inedible species were selected from uniform distributions with means 4, 145 and 0.0064, and standard deviations 1.25, 10 and 0.0001

diversity can lead to strong shifts in dominance, which can strongly affect ecosystem properties.

#### Effect of herbivore generalism and strength of consumption

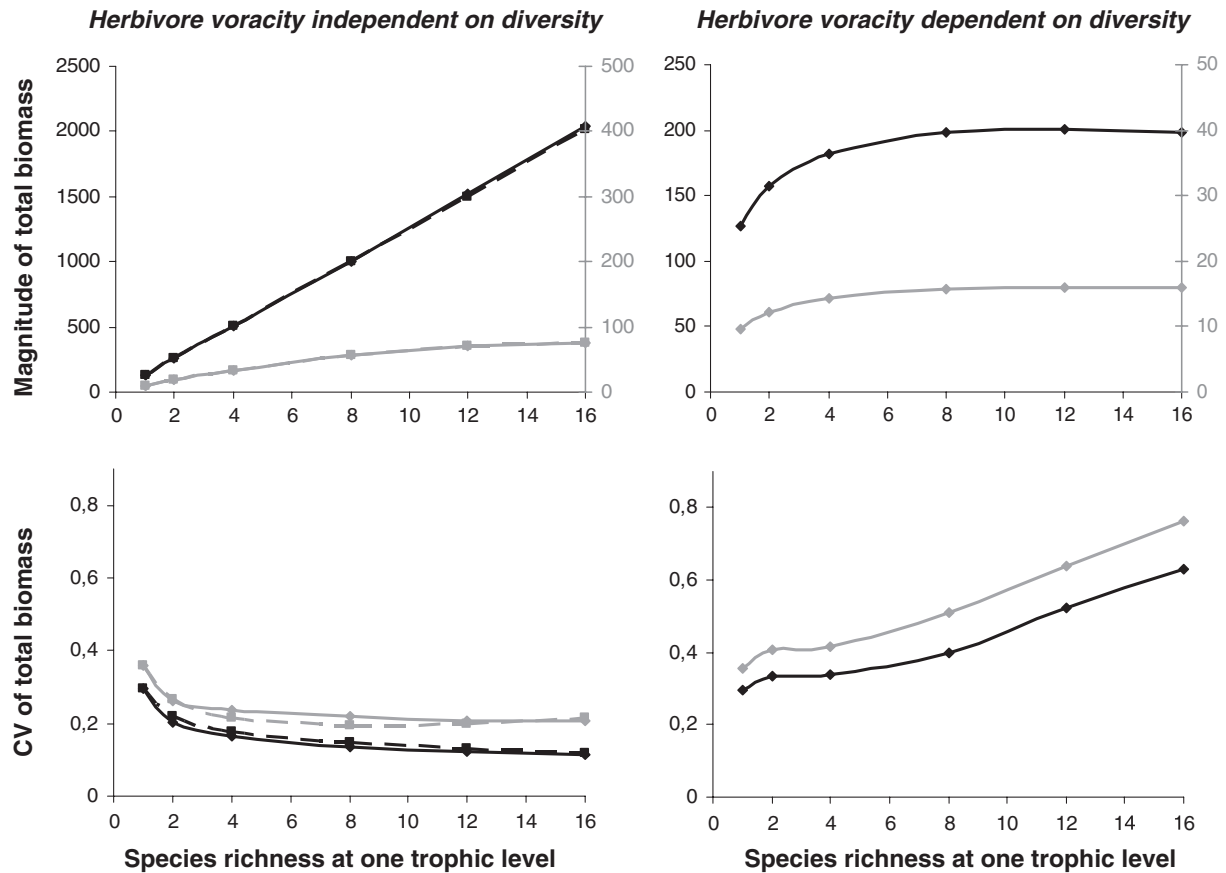
Complementarity between consumers may depend strongly on their degree of generalism and their differences in diet. The plasticity of consumer diet and interaction strength may strongly impact the diversity effects on both the magnitude and variation of ecosystem processes, as already suggested for species richness effects on biomass and productivity (Duffy 2002). Two cases of herbivore generalism are studied here: (1) herbivores compensate for plant species loss by increasing their consumption on other species, their voracity is then independent of their prey diversity; (2) herbivore consumption rates on the various plant species do not depend on plant diversity, their voracity increases as their prey diversity increases.

The degree of generalisation or specialisation of herbivores has a strong impact on the relationship

between diversity and ecosystem processes and depends mainly on how consumption strength changes with prey diversity (Fig. 4).

When total consumption of plants by herbivores is independent of species richness, total plant biomass increases linearly with species richness; when consumption increases with diversity, total plant biomass saturates and can even decrease at high diversity (Fig. 4). In this case, the biomass of each plant species is still controlled by herbivores but it decreases with the addition of other herbivore species because plant consumption increases. This in turn can result in a decrease in total plant biomass. In parallel, total herbivore biomass can also saturate and even decrease at high diversity. Competition between generalist herbivores is important and resource-use complementarity is then lower (Thébault and Loreau 2003).

Changes in CV of total biomass also depend strongly on how consumption by herbivores varies with diversity: CV of total biomass at both trophic levels can increase with diversity when herbivore voracity increases with diversity. In contrast, CV of total biomass decreases upon plant and herbivore addition when herbivores are



**Fig. 4** Magnitude and coefficients of variation (CV) of total plant and herbivore biomass as functions of species diversity for three food-web configurations. In each panel, *black lines* correspond to producer properties, while *grey lines* correspond to consumer properties. For the graphs in which herbivore voracity is

independent of diversity, *solid lines* correspond to a case where herbivores are specialist while *dotted lines* correspond to the case where herbivores are generalist. Parameter values as in Fig. 2. When herbivores are generalist, we set  $\alpha=0.6$  while when herbivores are specialist,  $\alpha=0$

specialists or when their voracity is independent of diversity.

These results confirm the classical result that stability requires low interaction strength (Kokkoris et al. 2002). Herbivore generalism and interaction strength may have a strong impact on the relationship between diversity and ecosystem processes as they modify plant biomass and stability.

It should be noted that the absence of differences between the case where herbivores are specialist and the case where herbivores are generalist with constant voracity can be explained by the very similar values of herbivore consumption rates and plant absorption rates in the model. These small differences in plant and herbivore parameters are due to constraints on coexistence in the model. Greater asymmetry and the presence of a trade-off between plant edibility and plant competitive ability, however, may affect these results.

## Conclusions and perspectives

Recent theoretical and experimental work provides clear evidence that biodiversity loss can have profound

impacts on functioning of ecosystems. Work on simplified ecosystems in which the diversity of a single trophic level is manipulated shows that taxonomic and functional diversity can enhance ecosystem processes such as primary productivity and nutrient retention. Theory also strongly suggests that biodiversity can act as biological insurance against potential disruptions caused by environmental changes.

One of the current challenges, however, is to extend this study to multitrophic systems that more closely mimic complex natural ecosystems. This requires merging biodiversity–ecosystem functioning and food-web theory (Ives et al. 2005). A growing number of studies have begun to analyse the effects of diversity changes on food webs (Duffy 2002; Raffaelli et al. 2002; Duffy et al. 2003, 2005; Fox 2004; Hillebrand and Cardinale 2004).

Multitrophic interactions are expected to make biodiversity–ecosystem functioning relationships more complex and non-linear, in contrast to the monotonic changes predicted for simplified systems with a single trophic level. Recent studies show that trophic interactions can have a strong impact on the relationships between diversity and the magnitude of ecosystem processes (Mulder et al. 1999; Downing and Leibold

2002; Duffy et al. 2003, 2005; Thébault and Loreau 2003; Finke and Denno 2004). The impact of trophic interactions on the relationship between diversity and the variability of ecosystem processes has been studied far less (but see Ives et al. 2000). The recent review by Hooper et al. (2005) has no section about consumers in 'Variability in ecosystem properties' while heterotroph impacts are considered in two sections under 'Magnitude of ecosystem properties'.

Several aspects of the relationship between diversity and both the magnitude and variability of ecosystem processes arise from the analyses of the present ecosystem model. First, the different mechanisms which affect diversity effects in simple competitive systems can also operate in multitrophic systems. If different species respond differently to environmental fluctuations, total biomass variability decreases more or increases less as diversity increases. Biodiversity can still provide an 'insurance' or a buffer against environmental fluctuations as long as species differ sufficiently in their response to environmental changes and consumption rates do not increase too much with diversity. Complementarity and selection effects at both trophic levels can still affect the relationship between diversity and ecosystem functioning in food webs (Ives et al. 2005; Thébault and Loreau 2003). For example, when herbivores differ in their resources, total herbivore biomass increases with herbivore addition. However, even though complementarity and selection effects can be calculated in most cases in multitrophic systems (Thébault and Loreau 2003), the values of these effects do not necessarily indicate which mechanisms are responsible for the patterns observed. An increase in total plant biomass with a positive complementarity effect can arise from plant control by herbivores, and not only from resource partitioning or from facilitation between plants. Positive or negative selection effects can also arise from the dominance of inedible species, and not only from the dominance of the most competitive species. The detailed mechanisms that drive the biodiversity–ecosystem functioning relationship are thus difficult to disentangle in multitrophic systems. Considering top-down control and the destabilising effect of herbivores might help to understand the impact of diversity changes in one trophic level on processes that occur at other trophic levels. Although our model considers only two trophic levels, several impacts of additional trophic levels can be predicted. For example, if we add a third trophic level, trophic cascades result in herbivores being controlled by carnivores, which leads to a linear increase in total herbivore biomass with diversity. At the same time, plants are no longer controlled by herbivores and total plant biomass no longer increases linearly (Thébault and Loreau 2003). CV of total plant and herbivore biomass might also be higher in the presence of carnivores due to the destabilising effects of predators on their prey. Thus, this study begins to build a bridge connecting the broad range of studies on top-down effects and trophic cascades (Shurin et al. 2002; Schmitz 2003; Hillebrand and

Cardinale 2004) and stability in food webs (Pimm and Lawton 1977; McCann 2000; Halpern et al. 2005).

Several key factors are predicted to affect strongly the relationships between diversity and ecosystem processes.

First, trophic position of species gained or loss has a strong impact on these relationships due to different effects of producers and consumers on stability and biomass at various trophic levels. The functional differences between species are thus essential to consider in order to improve our knowledge of the consequence of species loss. Impacts of consumers may also depend on ecosystem types: top-down effects of predators are generally stronger in aquatic systems than in terrestrial systems (Shurin et al. 2002) and destabilising effects of predators have been found to be stronger in lake ecosystems (Halpern et al. 2005).

Second, the presence of inedible species and of a trade-off between plant competitive ability and resistance to herbivory also strongly affects the relationships between diversity and ecosystem processes. If prey diversity increases the probability of resistance to grazing as suggested by a recent study (Hillebrand and Cardinale 2004), changes in diversity might lead to shifts in the dominance of producers that have a strong impact on ecosystem functioning (Duffy et al. 2005).

Third, the relationships between diversity and ecosystem properties also depend on herbivore generalisation and on how consumption strength changes with prey diversity. If prey density is high, the total consumption by each predator might be limited and this total consumption is then diluted among more prey species (e.g. Ives et al. 2000). However, it has also been found that increasing prey diversity can enhance consumer growth by providing a more balanced diet (DeMott 1998). The question of how grazer consumption is affected by species richness of available prey is important for further research on the relationship between diversity and ecosystem functioning in multitrophic systems.

These different aspects deserve to be analysed experimentally to gain better knowledge of the impacts of biodiversity changes on ecosystem functioning in multitrophic systems.

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## References

- Abrams PA (1993) Effects of increased productivity on the abundances of trophic levels. *Am Nat* 141:351–371
- Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. *Science* 277:500–504
- DeMott WR (1998) Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology* 79:2463–2481
- Dimitrakopoulos PG, Schmid B (2004) Biodiversity effects increase linearly with biotope space. *Ecol Lett* 7:574–583



- Doak DF, Bigger D, Harding EK, Marvier MA, O'Malley RE, Thomson D (1998) The statistical inevitability of stability–diversity relationships in community ecology. *Am Nat* 151:264–276
- Downing AL, Leibold MA (2002) Ecosystem consequences of species richness and composition in pond food webs. *Nature* 416:837–841
- Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–219
- Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecol Lett* 6:680–687
- Duffy JE, Richardson JP, Canuel EA (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol Lett* 6:637–645
- Duffy JE, Richardson JP, France KE (2005) Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol Lett* 8:301–309
- Finke DL, Denno RF (2004) Predator diversity dampens trophic cascades. *Nature* 429:407–410
- Fox JW (2004) Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology* 85:549–559
- Halpern BS, Borer ET, Seabloom EW, Shurin JB (2005) Predator effects on herbivore and plant stability. *Ecol Lett* 8:189–194
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Korner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read D, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127
- Hillebrand H, Cardinale BJ (2004) Consumer effects decline with prey diversity. *Ecol Lett* 7:192–201
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–25
- Hulot FD, Lacroix G, Lescher-Moutoué FO, Loreau M (2000) Functional diversity governs ecosystem response to nutrient enrichment. *Nature* 405:340–344
- Ives AR, Klug JL, Gross K (2000) Stability and species richness in complex communities. *Ecol Lett* 3:399–411
- Ives AR, Cardinale BJ, Snyder WE (2005) A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecol Lett* 8:102–116
- Kinzig AP, Pacala SW, Tilman D (2002) The functional consequences of biodiversity: empirical progress and theoretical extensions. Princeton University Press, Princeton
- Kokkoris GD, Jansen VAA, Loreau M, Troumbis AY (2002) Variability in interaction strength and implications for biodiversity. *J Anim Ecol* 71:362–371
- Lehman C, Tilman D (2000) Biodiversity, stability, and productivity in competitive communities. *Am Nat* 156:534–552
- Leibold MA (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am Nat* 134:922–949
- Loreau M (1996) Coexistence of multiple food chains in a heterogeneous environment: interactions among community structure, ecosystem functioning, and nutrient dynamics. *Math Biosci* 134(2):153–188
- Loreau M (1998) Biodiversity and ecosystem functioning: a mechanistic model. *Proc Natl Acad Sci USA* 95:5632–5636
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Loreau M, Naem S, Inchausti P (2002) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford
- MacArthur R (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533–536
- May RM (1972) Will a large complex system be stable? *Nature* 238:413–414
- McCann K (2000) The diversity–stability debate. *Nature* 405:228–233
- McGrady-Steed J, Harris PM, Morin PJ (1997) Biodiversity regulates ecosystem predictability. *Nature* 390:162–165
- Mulder CPH, 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
- Naem S (2002) Autotrophic–heterotrophic interactions and their impacts on biodiversity and ecosystem functioning. In: Kinzig A, Pacala SW, Tilman D (eds) Functional consequences of biodiversity: empirical progress and theoretical extensions. Princeton University Press, Princeton, pp 96–119
- Paine R (2002) Trophic control of production in a rocky intertidal community. *Science* 296:736–739
- Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72
- Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307:321–326
- Pimm SL, Lawton JH (1977) Number of trophic levels in ecological communities. *Nature* 268:329–331
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. *Science* 269:347–350
- Raffaelli D, van der Putten WH, Persson L, Wardle DA, Petchey OL, Koricheva J, van der Heijden MGA, Mikola J, Kennedy T (2002) Multi-trophic dynamics and ecosystem processes. In: Loreau M, Naem S, Inchausti P (eds) Biodiversity and ecosystem functioning synthesis and perspectives. Oxford University Press, Oxford, pp 147–154
- van Ruijven J, Berendse F (2005) Diversity–productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proc Natl Acad Sci USA* 102:695–700
- Schmitz O (2003) Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett* 6:156–163
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecol Lett* 5:785–791
- Thébault E, Loreau M (2003) Food-web constraints on biodiversity–ecosystem functioning relationships. *Proc Natl Acad Sci USA* 100:14949–14954
- Thébault E, Loreau M (2005) Trophic interactions and the relationship between species diversity and ecosystem stability. *Am Nat* 166(4):E95–E114
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proc Natl Acad Sci USA* 94:1857–1861
- Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845
- Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. *Trends Ecol Evol* 18:628–632
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci USA* 96:1463–1468