ECOLOGY LETTERS

Ecology Letters, (2013) **16**: 106–115 doi: 10.1111/ele.12073

IDEA AND PERSPECTIVE

Biodiversity and ecosystem stability: a synthesis of underlying mechanisms

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Abstract

There is mounting evidence that biodiversity increases the stability of ecosystem processes in changing environments, but the mechanisms that underlie this effect are still controversial and poorly understood. Here, we extend mechanistic theory of ecosystem stability in competitive communities to clarify the mechanisms underlying diversity–stability relationships. We first explain why, contrary to a widely held belief, interspecific competition should generally play a destabilising role. We then explore the stabilising effect of differences in species' intrinsic rates of natural increase and provide a synthesis of various potentially stabilising mechanisms. Three main mechanisms are likely to operate in the stabilising effects of biodiversity on ecosystem properties: (1) asynchrony of species' intrinsic responses to environmental fluctuations, (2) differences in the speed at which species respond to perturbations, (3) reduction in the strength of competition. The first two mechanisms involve temporal complementarity between species, while the third results from functional complementarity. Additional potential mechanisms include selection effects, behavioural changes resulting from species interactions and mechanisms arising from trophic or non-trophic interactions and spatial heterogeneity. We conclude that mechanistic trait-based approaches are key to predicting the effects of diversity on ecosystem stability and to bringing the old diversity–stability debate to a final resolution.

Keywords

Biodiversity, complementarity, ecosystem, fast-slow dynamics, overyielding, stability, synchrony.

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INTRODUCTION

In the past 20 years, remarkable progress has been made towards understanding how the loss of biodiversity affects ecosystem functioning and thereby human societies (Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2012). In particular, there is now unequivocal evidence that biodiversity enhances the efficiency by which ecological communities capture resources, produce biomass and recycle essential nutrients (Cardinale *et al.* 2012). There is also mounting evidence that it increases the stability of ecosystem processes through time (Tilman *et al.* 2006; Griffin *et al.* 2009; Jiang & Pu 2009; Hector *et al.* 2010; Campbell *et al.* 2011). This stabilising effect of biodiversity is of considerable interest for it suggests that biodiversity is critical to the long-term sustainability of ecosystems in the face of environmental changes. Ecosystems are subject to natural variations in climate and other forcing factors, and these variations are increasing currently because of growing anthropogenic impacts on the biosphere. If biodiversity buffers ecosystems against environmental variations, its loss will not only impair ecosystem services on average, it will also make these more variable and less predictable, thus increasing the threat of major ecosystem service failures.

The relationship between diversity and stability has been the subject of a long-standing debate in ecology (May 1973; Pimm 1984; McCann 2000; Loreau *et al.* 2002; Ives & Carpenter 2007; Loreau 2010). A major new insight gained from recent experimental work is that diversity may stabilise aggregate ecosystem or community properties while simultaneously destabilising individual species abundances (Tilman 1996; Tilman *et al.* 2006; Hector *et al.* 2010). Although at first sight this observation might seem to resolve the diversity–stability debate, from a theoretical angle it raises more questions than it provides answers. Traditional theory predicts that diversity and complexity should beget community instability (May 1973). What, then, explains the contrasting effects of diversity at the ecosystem and population levels? How can the stabilising effect of diversity on ecosystem properties be reconciled with existing theory? Although a few early studies started to address these important questions (May 1974; King & Pimm 1983), they did not result in a fully fledged theory able to anticipate and guide recent experimental work.

A number of recent studies of the relationship between diversity and the stability of ecosystem properties have resorted to phenomenological, statistical approaches such as the scaling relationship between the mean and the variance (Doak *et al.* 1998; Tilman *et al.* 1998; Tilman 1999) and the partitioning of the variance of total biomass or abundance into summed species variances and covariances (Tilman 1999; Klug *et al.* 2000; Lehman & Tilman 2000; Ernest & Brown 2001; Houlahan *et al.* 2007). These approaches have the practical advantage of being easily applied to empirical data, but they are very difficult to interpret because the mechanisms underlying the stabilising effect of diversity are hidden. Disentangling these mechanisms is key to building a robust theory that improves our ability to understand and predict the effects of diversity on ecosystem stability (Loreau 2010). Unfortunately, these mechanisms are still controversial and poorly understood.

One popular intuitive hypothesis inspired by traditional competition theory is that competition between species should generate or amplify negative covariations in their abundances, such that these variations compensate for each other, yielding less variation in total abundance or biomass at the aggregate ecosystem or community level (Tilman 1999; Klug *et al.* 2000; Lehman & Tilman 2000; Ernest & Brown 2001; Houlahan *et al.* 2007), a phenomenon called compensatory dynamics (Gonzalez & Loreau 2009). Although some competition models do show compensatory dynamics (Lehman & Tilman 2000), competition as such may not be the factor that generates community stability in these models as they include other potentially stabilising factors, in particular differences in the environmental preferences of the competing species. In general, competition may be expected to increase both the amplitude and the asynchrony of population fluctuations, but these two factors have countervailing effects on the stability of ecosystem properties. As a matter of fact, mechanistic theory that separates the strength of interspecific competition from other factors predicts that it should generally have either no effect or a negative effect on the stability of ecosystem properties (Ives *et al.* 1999; Loreau & de Mazancourt 2008; Loreau 2010).

In contrast, mechanistic models of stochastic community dynamics in fluctuating environments highlight the asynchrony of species' responses to environmental fluctuations as the key factor that drives the stabilising effect of diversity on ecosystem properties (Ives *et al.* 1999; Loreau & de Mazancourt 2008; Loreau 2010), as postulated by the insurance hypothesis (Yachi & Loreau 1999). One limitation of these models, however, is that they have mostly considered symmetrical competitive communities in which all species have identical parameter values except for the degree of synchrony of their environmental responses. Therefore, they do not rule out the possibility that asymmetries between species other than the asynchrony of their environmental responses might also stabilise ecosystem properties. Few theoretical studies have explored this possibility. These studies suggest that asymmetry in the strength of interspecific competition is strongly destabilising at both the population and ecosystem levels (Hughes & Roughgarden 1998), while asymmetry in species intrinsic rates of natural increase can be stabilising under some conditions (Fowler 2009; Fowler *et al.* 2012).

Other factors that may come into play in the stabilising effect of diversity on ecosystem properties include overyielding and observation error. Overyielding occurs when multispecies communities yield more than expected from their constituent species in monoculture (Vandermeer 1981; Loreau 2004), as is commonly found in biodiversity experiments (Loreau & Hector 2001; Cardinale *et al.* 2007). Overyielding means that species have a higher than expected mean biomass or productivity in mixture; when variability is standardised by the mean, as in the traditional coefficient of variation, all else being equal a higher mean tends to decrease variability (Tilman 1999). However, overyielding is generated by processes such as niche differentiation and facilitation that also determine the strength of interspecific competition. How overyielding interacts with the other effects of interspecific competition to influence the stability of ecosystem properties has not been explored so far. Observation error arises from the random effects of uncontrolled factors and appears to play a significant role in the stabilising effect of diversity in some biodiversity experiments (de Mazancourt *et al.*, 2013). We will not consider observation error any further here, as it is strongly context-dependent and lacks an explicit mechanistic basis.

Given the current lack of a comprehensive theory of the mechanisms that underlie the stabilising effect of diversity on ecosystem properties, our present contribution has three related objectives. First, we revisit the controversial role of interspecific competition, and we clarify why it generally does not contribute to ecosystem stability. Second, we extend previous mechanistic theory of ecosystem stability in competitive communities by relaxing the restrictive symmetry assumption to explore potentially new mechanisms and clarify how the various mechanisms interact to stabilise ecosystem properties. Third, we provide a theoretical synthesis of the various mechanisms underlying the relationships between species diversity and ecosystem stability. Here, we focus specifically on the temporal coefficient of variation of total biomass as an inverse measure of ecosystem stability to match recent empirical and experimental studies (Tilman *et al.* 2006; Griffin *et al.* 2009; Hector *et al.* 2010). There are, however, a number of other possible measures of stability (Pimm 1984; Loreau *et al.* 2002; Ives & Carpenter 2007), which we do not consider explicitly here.

To reach our first two objectives above, we use a linear approximation of a general stochastic model of competitive community dynamics in which species are affected by a combination of intra- and interspecific competition, environmental stochasticity and demographic stochasticity. As even this approximation becomes unwieldy when the symmetry assumption is relaxed, we focus on 2-species communities in the second part of the paper to keep the number of parameters limited and thereby explore a wide range of parameter values. We supplement this mathematical analysis with numerical simulations of 2-species and multispecies communities.

MODEL PRESENTATION AND ANALYSIS

Our theoretical model is based on a discrete-time version of the classical Lotka–Volterra competition model that incorporates environmental and demographic stochasticity (Loreau & de Mazancourt 2008; Loreau 2010):

$$\begin{aligned} r_i(t) &= \ln N_i(t+1) - \ln N_i(t) \\ &= r_{mi}\left[1 - \frac{N_i(t)}{K_i} - \sum_{j \neq i} \frac{\beta_{ij} N_j(t)}{K_j}\right] + \sigma_{ei} u_{ei}(t) + \frac{\sigma_{di} u_{di}(t)}{\sqrt{N_i(t)}}. \end{aligned} \quad (1)$$

In this equation, $N_i\ (t)$ is the biomass of species i at time t, $r_i\ (t)$ is its instantaneous mass-specific growth rate at time t, r_{mi} is its intrinsic (maximum) rate of natural increase, K_i is its carrying capacity and β_{ij} is a competition coefficient describing the effect of species j on species i. Note that this coefficient is proportional to the traditional coefficient α_{ij} through the relation $\beta_{ij} = \alpha_{ij} K_j / K_i$. Consequently, any result below that applies to β_{ij} also applies to α_{ij}. We prefer to use β_{ij}, however, because it is more directly related to the conditions for stable coexistence. In particular, stable coexistence requires that $\beta_{ij} < 1$ for all species pairs and that β_{ij}'s be similar enough when they are large (Chesson 2000; Jansen & Kokkoris 2003).

Environmental stochasticity is incorporated through the term $\sigma_{ei} u_{ei}(t)$, where σ_{ei}^2 is the environmental variance of species i, and $u_{ei}(t)$ are normal variables with zero mean and unit variance that are independent through time (white noise), but may be correlated between species (e.g. a good year for one species may be good for another species too). Demographic stochasticity is the last term in eqn (1). It is due to variation in birth and death rates between individuals or independent reproductive units. Here, we incorporate it in the form of the first-order normal approximation that is traditionally used in the theory of stochastic population dynamics (Lande *et al.* 2003) to facilitate mathematical analysis, and we assume that the number of independent reproductive units is proportional to biomass. $\sigma_{di}{}^2$ is the demographic variance of species i, and $u_{di}(t)$ are independent normal variables with zero mean and unit variance.

Model (1) is quite general as it includes the main factors that affect the population dynamics of competing species – that is, intra- and interspecific competition, environmental stochasticity and demographic stochasticity – and it provides a first-order approximation of the effects of these factors on species' per capita population growth rates (Loreau & de Mazancourt 2008). We used this model to derive analytical predictions of the temporal variations and covariations of the biomasses of the various species as well as of the coefficient of variation of total biomass in the community, $N_T(t) = \sum N_i(t)$, in the vicinity of an equilibrium, in two cases: (1) the community has multiple species but is symmetrical (all species have identical parameter values), and (2) the community has only two species but is asymmetric (species have different parameter values). The derivation proceeded as follows (see Appendix A for details). First, we assumed that the system reached a stationary state of small fluctuations and we linearised model (1) around its deterministic equilibrium to describe the dynamics of this stationary state. We then used this first-order approximation to derive an analytical prediction of the variance–covariance matrix of individual species biomasses. Lastly, we obtained the variance and coefficient of variation of total biomass from the variances and covariances of individual species biomasses.

In our derivation, we used the following general equations that link the coefficient of variation, CV_{NT}, variance, σ^2_{NT}, and mean, $\overline{N_T}$, of total biomass and the variances, σ^2_{Ni}, covariances, cov(N_i, N_j), and synchrony, ϕ_N, of individual species biomasses:

$$CV^2_{NT} = \sigma^2_{NT}/\overline{N_T}^2, \tag{2}$$

$$\sigma^2_{NT} = \sum_i \sigma^2_{Ni} + \sum_i \sum_{j \neq i} \mathrm{cov}(N_i, N_j) = \Sigma\mathrm{var} + \Sigma\mathrm{cov}, \tag{3}$$

$$\phi_N = \frac{\sigma^2_{NT}}{\left(\sum_i \sigma_{Ni}\right)^2}. \tag{4}$$

Equation (2) results directly from the definition of the coefficient of variation. Equation (3) expresses the fact that the variance of a sum of variables is the sum of the variances and covariances of all these variables. Equation (4) defines our community-wide measure of population synchrony, which has the major advantage of being standardised between 0 (perfect asynchrony) and 1 (perfect synchrony) irrespective of the number of species (Loreau & de Mazancourt 2008).

WHY COMPETITION IS GENERALLY DESTABILISING

As mentioned above, a widely held belief is that interspecific competition generates compensatory dynamics between species, thereby stabilising aggregate ecosystem properties such as total abundance and total biomass. Closely related to this belief is the assumption that negative summed covariances between species abundances or biomasses are indicative of interspecific competition, in contrast to summed species variances (Tilman 1999; Klug *et al.* 2000; Lehman & Tilman 2000; Ernest & Brown 2001; Houlahan *et al.* 2007). We can use the solution of the first-order approximation of our model to examine these hypotheses explicitly.

As there are $S(S–1)$ competition coefficients in a community of S species, it is impossible to extract a single general measure of the strength of interspecific competition in asymmetric communities. Therefore, we first focus on the special case of symmetrical communities in this section, as in several previous studies (Ives *et al.* 1999; Loreau & de Mazancourt 2008; Loreau 2010) – that is, we assume that all species have identical parameter values, and accordingly we drop the subscripts for all species-specific parameters ($r_{mi} = r_m, K_i = K, \beta_{ij} = \beta, \sigma^2_{ei} = \sigma^2_e, \sigma^2_{di} = \sigma^2_d$ for all i and j). We defer the analysis of asymmetries between species to the next section. Note that, although all species are assumed to have the same environmental variance, their environmental responses differ; the synchrony of their environmental responses, ϕ_e, can vary between 0 (perfectly asynchronous, i.e. opposite responses) and 1 (perfectly synchronised, i.e. identical responses). By definition, demographic stochasticity represents independent stochastic effects on individuals; when species have identical demographic variances, there is no effect of community composition on the strength of demographic stochasticity at the ecosystem level, which only depends on total biomass. We also assume that interspecific competition is weaker than intraspecific competition to ensure stable coexistence ($\beta < 1$).

Substituting the variances and covariances of individual species biomasses derived from the first-order approximation of model (1) into eqns (2)–(4) yields explicit solutions for the various measures of temporal variability in symmetrical multispecies communities (see method in Appendix A):

$$CV^2_{NT} = \frac{\phi_e\sigma^2_e + \sigma^2_d/\overline{N_T}}{r_m(2 - r_m)}, \tag{5}$$

$$\Sigma\mathrm{var} = \frac{\overline{N_T}^2\{[\phi_e + (1 - \phi_e)\theta]\sigma^2_e + [1 + (S - 1)\theta]\sigma^2_d/\overline{N_T}\}}{Sr_m(2 - r_m)}, \tag{6}$$

$$\Sigma\mathrm{cov} = \frac{\overline{N_T}^2\{[(S - 1)\phi_e - (1 - \phi_e)\theta]\sigma^2_e + (S - 1)(1 - \theta)\sigma^2_d/\overline{N_T}\}}{Sr_m(2 - r_m)}, \tag{7}$$

$$\phi_N = \frac{\phi_e\sigma^2_e + \sigma^2_d/\overline{N_T}}{[\phi_e + (1 - \phi_e)\theta]\sigma^2_e + [1 + (S - 1)\theta]\sigma^2_d/\overline{N_T}}, \tag{8}$$

where

$$\overline{N_T} = \frac{SK}{1 + (S - 1)\beta}, \tag{9}$$

$$\phi_e = \frac{\mathrm{var}\left(\sum_i \sigma_e u_{ei}\right)}{S^2\sigma^2_e} = \frac{1 + (S - 1)\bar{\rho}_e}{S}, \tag{10}$$

$$\theta = \frac{(2 - r_m)(1 - \beta + S\beta)}{(1 - \beta)[(2 - r_m)(1 - \beta) + 2S\beta]}. \tag{11}$$

Here, ϕ_e is the synchrony of species environmental responses, and is defined in the same way as ϕ_N, as a community-wide measure standardised between 0 and 1. It is related to the average correlation between species environmental responses, $\bar{\rho}_e$, as shown in eqn (10). The lumped parameter θ does not have a simple biological interpretation; it corresponds to the ratio between the two distinct eigenvalues of the community matrix (one of which has multiplicity $S-1$), and thus it captures the effects of biotic interactions on the dynamical response of the community to perturbations from its equilibrium.

The strength of interspecific competition, β, affects the variability and synchrony of species biomasses, and thereby the variability of total biomass, in two distinct ways: (1) through its effects on parameter θ, and (2) through its effect on mean total biomass, $\overline{N_T}$.

A first, striking feature of eqns (5)–(8) is that θ affects summed species variances, Σvar, summed species covariances, Σcov, and population synchrony, ϕ_N, but it does not affect the coefficient of variation of total biomass, CV_{NT}. Thus, in contrast to population variability, ecosystem variability is unaffected by the way species interactions shape the dynamical response of the community to perturbations in symmetrical communities. As a result, aggregate measures of population variability such as summed species variances, summed species covariances and population synchrony do not provide insights into the mechanisms that govern ecosystem stability, as suggested by previous work (Loreau & de Mazancourt 2008; Loreau 2010).

Furthermore, the dependence of these aggregate measures of population variability on the strength of interspecific competition is complex. Parameter θ generally increases with the strength of interspecific competition ($\partial\theta/\partial\beta > 0$), but it shows an opposite trend ($\partial\theta/\partial\beta < 0$) under some conditions, that is, when the intrinsic rate of natural increase of the various species is large, interspecific competition is weak and species diversity is low (results not shown). As a consequence, summed species variances, summed species covariances and population synchrony can either increase or decrease as interspecific competition gets stronger (eqns 6–8). For many combinations of parameter values, we obtain the results expected from the hypothesis of competition-driven compensatory dynamics at the population level, that is, interspecific competition makes populations more variable but also more asynchronous. Even under those conditions, however, this does not lead to stabilisation of ecosystem properties: decreased population synchrony due to stronger interspecific competition is exactly compensated by increased population variability, such that ecosystem stability is unaffected.

Interspecific competition also has a negative effect on mean total biomass (eqn 9). This in turn decreases the magnitude of summed species variances and covariances (eqns 6–7), but it increases the strength of the effects of demographic stochasticity, thereby increasing the variability of total biomass (eqn 5).

Combining these various indirect effects of competition, we see that interspecific competition is expected to (1) often (though not always) increase summed species variances, (2) often (though not always) decrease summed species covariances, (3) often (though not always) decrease population synchrony and (4) increase the variability of total biomass. Thus, our analysis does not support the intuitive hypothesis that interspecific competition stabilises aggregate ecosystem properties through compensatory dynamics between species in symmetrical communities. Competition does often increase the asynchrony of population fluctuations but it also destabilises populations. Increased asynchrony of population fluctuations is not sufficient to compensate for their increased amplitude, such that ecosystem stability is decreased (Fig. 1).

If competition does not stabilise aggregate ecosystem properties in symmetrical communities, what, then, are the factors that contribute to the stabilising effect of biodiversity? Two factors stand out from eqn (5).

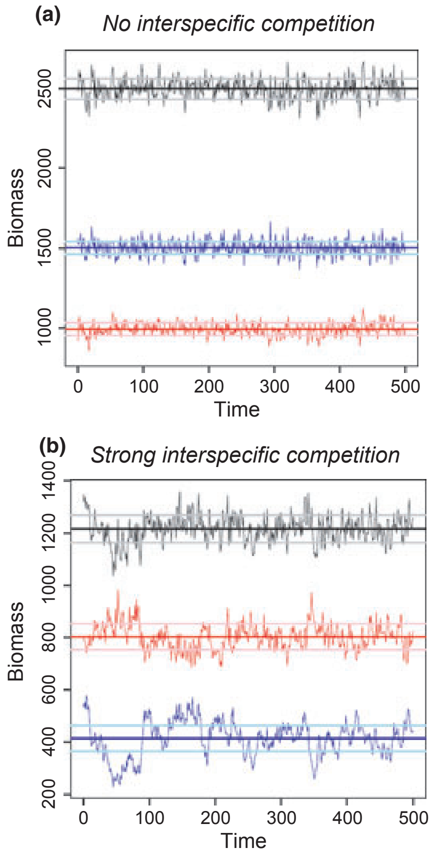


Figure 1 Effects of the strength of interspecific competition on the temporal fluctuations of the biomasses of two species (1 – red and 2 – blue) and their total biomass (black) predicted by model (1). Interspecific competition increases the asynchrony of population fluctuations (the temporal correlation between the biomasses of the two species is 0.02 in (a) and –0.74 in (b)) but this increased asynchrony is not sufficient to compensate for the increased amplitude of these fluctuations, such that ecosystem stability is decreased (the coefficient of variation of total biomass is 0.028 in (a) and 0.043 in (b)). Horizontal lines show means and standard deviations. Parameter values: $r_{m1} = 0.5$; $r_{m2} = 0.8$; $K_1 = 1000$; $K_2 = 1500$; $\phi_e = 0.5$; $\sigma_{e1} = \sigma_{e2} = 0.02$; $\sigma_{d1} = \sigma_{d2} = 1$; $\beta_{12} = \beta_{21} = 0$ in A; $\beta_{12} = 0.7$ and $\beta_{21} = 0.9$ in B.

The first is asynchrony of species environmental responses. As the number of species increases, the synchrony of their environmental responses, ϕ_e, decreases. In the special case when species environmental responses are independent, their synchrony decreases as $1/S$, but even positively correlated environmental responses result in a decreased synchrony as species diversity increases, except in the unlikely limiting case where they are perfectly synchronous (Loreau 2010). This decreased synchrony contributes to decrease the variability of total biomass due to environmental fluctuations (eqn 5). To understand the role of the synchrony of species environmental responses, it is important to distinguish it from the synchrony of species abundances or biomasses, ϕ_N. A species' environmental response describes the immediate response of its per capita population growth rate to exogenous environmental fluctuations. Thus, it is an expression of that species' fundamental niche, and as such it can be regarded as a lower-level property when it comes to explain ecosystem stability. In contrast, a species' abundance or biomass is the result of its past abundance or biomass and of all the forces that affect its dynamics in the community. The longer the temporal window considered, the wider the fluctuations in abundance because of ecological drift (Loreau & de Mazancourt 2008). Thus, fluctuations in abundance or biomass are only distantly related to a species' fundamental niche and are affected by community dynamics.

The second factor that contributes to the stabilising effect of biodiversity in symmetrical communities is the mirror image of the destabilising role of competition: a *reduction* in the strength of competition contributes to increasing mean total biomass, thereby decreasing the variability of total biomass due to demographic stochasticity (eqn 5). When interspecific competition is weaker than intraspecific competition ($\beta < 1$), not only is coexistence promoted, mean total biomass also increases. The weaker interspecific competition and the larger the number of species, the stronger this effect (eqn 9). The stabilising role of increased mean total biomass is known as the 'overyielding effect' (Tilman 1999). This effect, however, lacked a mechanistic basis and was conceived as distinct from the supposedly stabilising effect of competition through compensatory dynamics. Here, we see that the overyielding effect acts through a reduction in the strength of demographic stochasticity, and that, counter-intuitively, it occurs precisely because competition is destabilising and thus reduced competition is stabilising.

STABILISING AND DESTABILISING EFFECTS OF ASYMMETRIES BETWEEN SPECIES

The range of mechanisms through which biodiversity can stabilise ecosystem properties in symmetrical communities is necessarily limited by the symmetry assumption. In particular, the only difference between species that symmetrical models have allowed so far is in their environmental responses (because these are incorporated in the form of the functions $u_{ei}(t)$, not as fixed parameters). Therefore, one might wonder whether the key role played by the asynchrony of species environmental responses in existing theory is simply due to the fact that other differences between species have been ignored. Do other stabilising mechanisms emerge when the symmetry assumption is relaxed? Here, we first explore this question using the linear approximation of our model in 2-species communities. Even with only two species, however, the linear approximation yields mathematical expressions that are too complex to be presented in the main text; accordingly, we focus on the most salient results in graphical form.

Because of the properties of the linear approximation, the squared coefficient of variation of total biomass can always be expressed as a sum of two terms, one that captures the effects of environmental stochasticity, and the other the effects of demographic stochasticity, as in eqn (5). Assuming, for the sake of simplicity, that the environmental and demographic variances of the two species are equal, this yields an equation of the form:

$$CV_{NT}^2 = A\sigma_e^2 + B\sigma_d^2, \tag{12}$$

where A and B are complex functions of model parameters as well as of the covariance between the normalised environmental responses of the two species, $u_{e1}(t)$ and $u_{e2}(t)$. Note that when the environmental and demographic variances of the two species are not equal, each of the terms in eqn (12) becomes a sum of effects due to each species. This makes selection effects possible, that is, effects due to dominance by species with either high or low environmental or demographic variance (see Discussion), but no qualitatively new mechanism of stabilisation of ecosystem properties arises from differences in environmental or demographic variances. Here, we use eqn (12) to examine the effects of asymmetries in other parameters on the environmental (A) and demographic (B) components of the variability of total biomass separately.

We have seen in the previous section that interspecific competition is generally destabilising at both the population and ecosystem levels. When keeping other parameters symmetrical, asymmetry in the strength of interspecific competition is even more destabilising than is average strength. Asymmetry in interspecific competition coefficients increases both the environmental and demographic components of the variability of total biomass (Fig. 2a, b, d, e). Its effect on the environmental component is strongest when species environmental responses are asynchronous (Fig. 2d, e), and vanishes in the limiting case when species environmental responses are completely synchronous (Fig. 2g, h). This confirms previous work showing that differences in interspecific competition coefficients destabilise aggregate ecosystem properties (Hughes & Roughgarden 1998) just as they destabilise individual populations, thereby limiting coexistence (Kokkoris *et al.* 2002; Jansen & Kokkoris 2003). The same conclusion holds for differences in species' carrying capacities (results not shown).

Note that the two components of variability are lowest when the intrinsic rates of natural increase of the two species approach 1 (Fig. 2, middle panels). This is because the resilience of either a single-species population or a symmetrical multispecies community is maximum when $r_m = 1$ and decreases steadily as r_m approaches its critical values leading to either extinction ($r_m = 0$) or the onset of limit cycles ($r_m = 2$), resulting in a *U*-shaped dependence of the variability of total biomass on r_m (Fig. 3). Although the linear approximation does not hold beyond these critical values, variability continues to increase as r_m further increases beyond 2.

Asymmetry in species' intrinsic rates of natural increase can alter these predictions qualitatively. When the intrinsic rates of natural increase of the two species differ, both the demographic and environmental components of the variability of total biomass are generally lowest when competition coefficients are moderately asymmetric (Fig. 2c, f). Furthermore, strong interspecific competition can now have a stabilising effect on total biomass, especially when species environmental responses are strongly synchronised (Fig. 2i). In this case, a strong competitive effect (β_{21}) of the more stable species 1 ($r_{m1} = 1$) on the less stable species 2 ($r_{m2} = 0.15$) is stabilising because it promotes dominance by the more stable species. In contrast, when species have asynchronous responses (e.g. independent responses for the demographic component in Fig. 2c, or perfectly asynchronous environmental responses for the environmental component in Fig. 2f), highest ecosystem stability is generally found when the slower species 2 has a relatively stronger competitive effect on the faster species 1 (stability tends to be highest slightly below the 1 : 1 diagonal line, where $\beta_{12} > \beta_{21}$). Although asymmetry in intrinsic rates of natural increase stabilises total biomass compared with a system in which both rates are either high (i.e. close to 2 or higher) or low (i.e. close to 0: compare right panels with left panels in Fig. 2), it generally yields lower ecosystem stability than does a system in which both rates are intermediate (i.e. close to 1: compare right panels with middle panels in Fig. 2, although this result does not hold for all parameter values). Thus, the stabilising potential of asymmetry in intrinsic rates of natural increase is generally more reduced than that of asynchrony of species environmental responses (compare Fig. 2d–f with g–i).

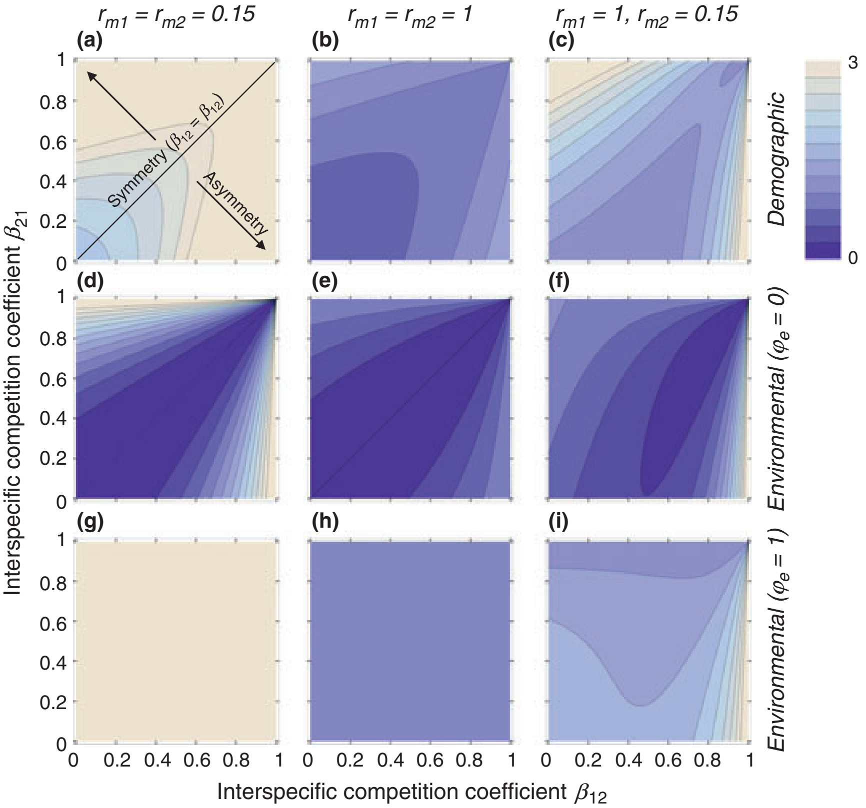


Figure 2 Effect of asymmetry in the strength of competition between two species on ecosystem stability for different values of intrinsic rates of natural increase. Other parameters are kept symmetrical ($K_1 = K_2 = K$; $\sigma_{e1} = \sigma_{e2}$; $\sigma_{d1} = \sigma_{d2}$). Top (a–c): demographic component of CV_{NT}^2 ($B \times K$ in eqn 12). Middle (d–f): environmental component of CV_{NT}^2 (A in eqn 12) when environmental responses are perfectly asynchronous. Bottom (g–i): same when environmental responses are perfectly synchronous. Contour lines and colours show values from 0 (dark) to 3 (light) with a 0.25 increment. Thus, darker means higher ecosystem stability. Symmetry in the strength of interspecific competition occurs along the 1 : 1 diagonal; asymmetry increases as one moves away from this diagonal (see panel (a)).

To examine more thoroughly the role of asymmetry in the intrinsic speed of population dynamics of the two species, including beyond the threshold $r_m = 2$ where the linear approximation is no longer valid, we performed extensive numerical simulations of model (1) in a 2-species system with symmetrical competition in which one species has a low intrinsic rate of natural increase ($r_{m1} = 0.1$) and the other has an intrinsic rate of natural increase that varies from low ($r_{m2} = 0.1$) to high ($r_{m2} = 3.5$) (see Appendix B for methods). When intrinsic rates of natural increase differ and competition is symmetrical, interspecific competition should decrease the variability of the environmental component of total biomass (variability decreases along the 1 : 1 diagonal in Fig. 2f, i). Numerical simulations show that increasing the strength of interspecific competition does generally decrease the variability of total biomass provided demographic and environmental variances are small (Fig. 4a). The decrease is particularly marked for high values of r_{m2}. When $r_{m2} > 2$, species 2 has cyclic or chaotic dynamics in the absence of competition; interspecific competition then stabilises its dynamics by coupling it to a species with slow dynamics (Fowler 2009). Maximum ecosystem stability is achieved when r_{m2} is relatively large but below the critical value of 2. Note, however, that interspecific competition becomes destabilising when the strength of interspecific competition approaches its maximum value of 1 (Fig. 4a). This pattern is exacerbated when demographic and/or environmental variances are high; interspecific competition then becomes destabilising even when it has moderate strength, thus deviating qualitatively from the pattern predicted by the linear approximation (Fig. 4b).

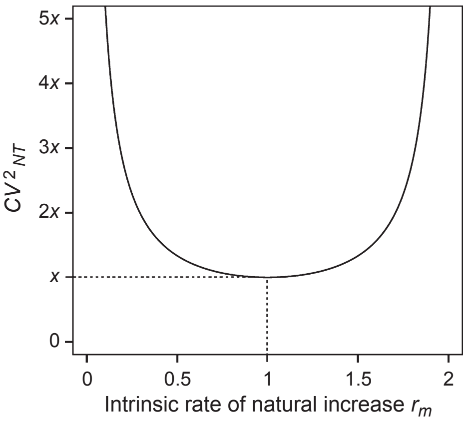


Figure 3 Variability of total biomass (measured by CV_{NT}^2) as a function of the intrinsic rate of natural increase in either a single-species population or a symmetrical multispecies community. $x = \phi_e \sigma_e^2 + \sigma_d^2 / \overline{N_T}$ from eqn (5), where $\phi_e = 1$ in the case of a single species.

Thus, our analysis shows that differences in intrinsic rates of natural increase can contribute to stabilising ecosystem properties, especially when these differences are large and interspecific competition is moderate or strong. The combination of fast and slow dynamics in response to perturbations is thought to play an important part in the stability of food webs (Rooney *et al.* 2006). Our analysis confirms that this mechanism can also stabilise aggregate ecosystem properties in competitive communities (Fowler 2009), but it suggests that both the conditions under which it operates and its effects on ecosystem stability are more limited than previously thought. Asymmetry in intrinsic rates of natural increase can be strongly stabilising compared with a system in which both species have either low or high intrinsic rates of natural increase, but it seldom increases ecosystem stability compared with a system in which both species have intermediate intrinsic rates of natural increase. The most striking feature of asymmetry in intrinsic rates of natural increase is probably the fact that it can generate situations where both the strength and asymmetry of interspecific competition have stabilising effects on ecosystem properties.

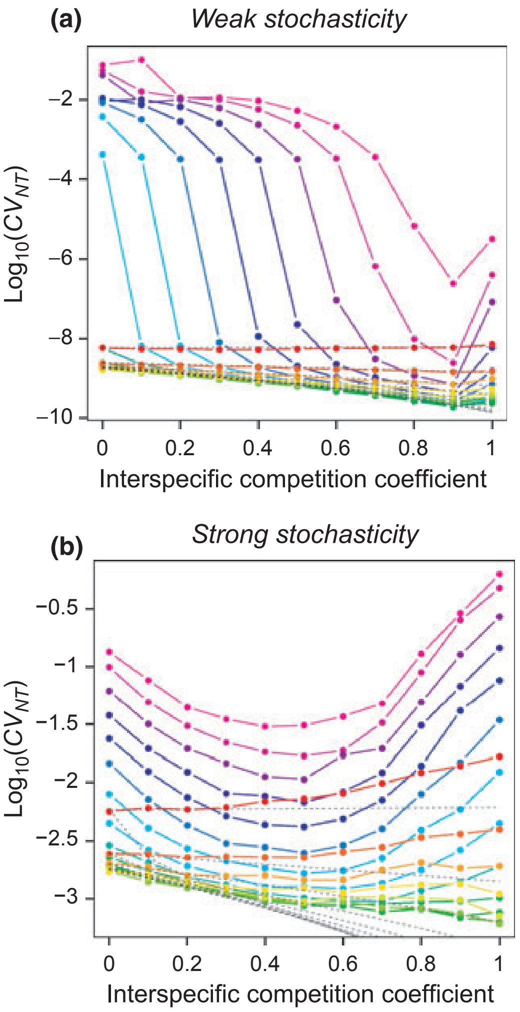


Figure 4 Effect of the strength of competition between two species on ecosystem stability when competition is symmetrical, one species has a very low intrinsic rate of natural increase ($r_{m1} = 0.1$), and the intrinsic rate of natural increase of the other species is varied from very low to very high. Both environmental stochasticity and demographic stochasticity are weak in (a) ($\sigma_{e1} = \sigma_{e2} = 0.01$; $\sigma_{d1} = \sigma_{d2} = 0.2$), and strong in (b) ($\sigma_{e1} = \sigma_{e2} = 0.2$; $\sigma_{d1} = \sigma_{d2} = 4$). Solid curves show means from numerical simulations for r_{m2} that varies from 0.1 (red) to 3.5 (pink) with a 0.2 interval. Highest stability (lowest CV_{NT}) is achieved for $r_{m2} = 1.9$ (green). Black dashed lines show the corresponding linear approximations for $r_{m2} < 2$. Other parameter values: $K_1 = K_2 = 20\,000$; $\phi_e = 0.5$.

Given this feature, we performed another set of numerical simulations to assess the net stabilising or destabilising effect of interspecific competition in multispecies communities where all parameters are asymmetric (see Appendix B for methods). The proportion of feasible and stable communities in which the variability of total biomass was higher in the presence than in the absence of interspecific competition was lower than the null expectation of 0.5 when both the number of species and the mean strength of interspecific competition were low, but it increased steadily as either the number of species or the mean strength of interspecific competition increased (Fig. 5). Thus, although interspecific competition does appear to often have a net stabilising effect on total biomass when it is weak and species richness is low, it has a marked destabilising effect as it gets stronger and species richness increases.

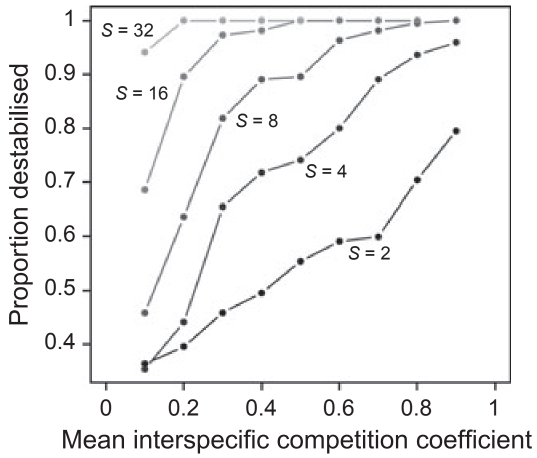
A SYNTHESIS OF MECHANISMS UNDERLYING THE RELATIONSHIP BETWEEN DIVERSITY AND ECOSYSTEM STABILITY

Unveiling the mechanistic basis of the relationship between biodiversity and ecosystem stability is critical for understanding and predicting the effects of environmental changes on ecosystem functioning. We have shown above that some of the mechanisms traditionally invoked to account for this relationship do not work as originally conceived, while other potential mechanisms have received little attention. In particular, we have shown that, contrary to a popular belief, interspecific competition generally destabilises aggregate ecosystem properties, just as it destabilises the population dynamics of component species (Kokkoris *et al.* 2002; Jansen & Kokkoris 2003; Allesina & Tang 2012). Its effects on ecosystem stability, however, are complex. By disentangling the various mechanisms through which biodiversity can affect ecosystem stability, we have also identified specific conditions under which it can have a stabilising effect when coupled with differences in species' intrinsic rates of natural increase.

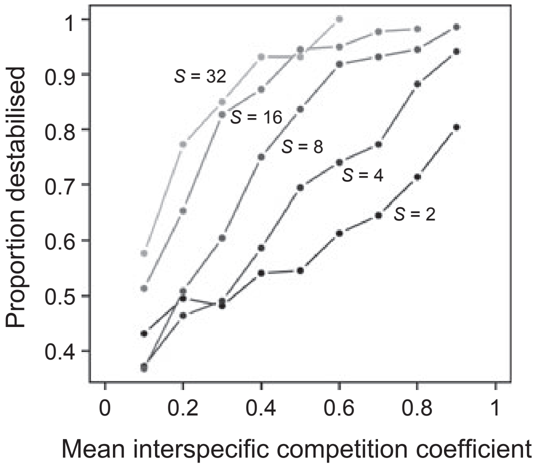
Given the variety of potential mechanisms involved in the relationship between diversity and ecosystem stability, a synthesis of these mechanisms and of their outcomes is needed to guide future empirical and experimental studies. When and how can biodiversity be expected to enhance ecosystem stability? Our theoretical analysis highlights three main mechanisms through which biodiversity can stabilise aggregate ecosystem properties:

(1) asynchrony of species responses to environmental fluctuations;
(2) differences in the speed at which species respond to perturbations;
(3) reduction in the strength of competition.

The first two mechanisms provide two complementary ways in which species may differ in their responses to internal or external perturbations. In the first mechanism, different species have different preferences for abiotic or biotic environmental factors such as temperature, rainfall and resources. These differences in the fundamental niches of the various species generate asynchronous responses to environmental fluctuations, which in turn tend to generate asynchronous population dynamics, ultimately yielding more stable aggregate ecosystem properties (Loreau 2010). Asynchrony of species environmental responses is always stabilising, and thus, it is expected to be a major factor causing compensatory dynamics between species. This



(a) Demographic >> Environmental



(b) Environmental >> Demographic

Figure 5 Effect of the mean strength of interspecific competition on the proportion of feasible and stable ecosystems that are destabilised by interspecific competition (i.e. in which CV_{NT} if higher than in the absence of interspecific competition) for different values of species richness *S*, when either demographic stochasticity is stronger than environmental stochasticity (a) or vice versa (b). Results from numerical simulations; see Appendix B for methods and parameter values.

mechanism has been shown to partly explain the stabilising effect of species diversity in a number of experimental and empirical studies (Leary & Petchey 2009; Hector *et al.* 2010; Thibaut *et al.* 2012; de Mazancourt *et al.*, 2013). Most biodiversity experiments, however, have not run long enough to fully reveal the role of this factor, which requires long time series to be detected.

In the second mechanism, different species have different intrinsic rates of natural increase that allow them to respond at different speeds to perturbations due to factors that may be either internal or external to the community. These differences in the speed of their responses also tend to generate asynchronous population dynamics and thereby promote ecosystem stability (Rooney *et al.* 2006; Fowler 2009). This mechanism, however, operates under more restrictive conditions and has less stabilising potential than the first since it seldom increases ecosystem stability compared with a system in which all species have the same speed of response that minimises the variability of their population dynamics. However, it has special properties; in particular, it seems to be the only scenario in which strong interspecific competition can generate compensatory dynamics as initially envisaged. To our knowledge, this mechanism has never been studied so far in biodiversity experiments and provides an interesting alternative hypothesis to be tested.

Both these mechanisms can be viewed as forms of temporal complementarity between species, in contrast to the third mechanism, that is, reduction in the strength of competition. Reduced competition is stabilising under most conditions – except when the second mechanism above operates – , in particular through the ‘overyielding effect’, that is, increased mean total biomass in mixtures. Overyielding results from functional complementarity between species, a non-temporal form of complementarity that captures the short-term effects of such diverse species interactions as resource partitioning, enemy partitioning, facilitation and interference (Loreau *et al.* 2012). In principle, overyielding does not affect the environmental component of the variability of total biomass when variability is scaled by the mean as in the coefficient of variation (eqn 5). However, it does affect its demographic component because increased abundance or biomass reduces the strength of demographic stochasticity in population dynamics (Lande *et al.* 2003). Therefore, the overyielding effect is expected to be especially important in small plots or populations, which is typically the case in recent biodiversity experiments. Increase in mean total biomass has also been shown to partly explain the stabilising effect of species diversity in several experiments (Hector *et al.* 2010; de Mazancourt *et al.* 2013).

In addition to the above three mechanisms, other mechanisms can influence the relationship between biodiversity and ecosystem stability. Theory has identified two broad classes of effects of biodiversity on ecosystem functioning: complementarity and selection (Loreau & Hector 2001). The three mechanisms that we considered in our analysis arise from different forms of complementarity between species. However, as mentioned earlier, selection effects are also present in our model. The reason why we did not analyse them in detail is that they are variable and quite intuitive. If species that have a higher than average environmental variance or a higher than average demographic variance tend to dominate multispecies communities, this will generate a positive selection effect of diversity on the variability of total biomass or, equivalently, a negative selection effect on ecosystem stability. Conversely, if species that have a lower than average environmental or demographic variance tend to dominate multispecies communities, this will generate a positive selection effect on ecosystem stability. Several experiments have revealed such selection effects on the stability of aggregate ecosystem properties (Gonzalez & Descamps-Julien 2004; Steiner *et al.* 2006; Grman *et al.* 2010).

Lastly, additional mechanisms can arise from processes not included in our model. In particular, our model describes only competitive interactions between species and ignores other types of interactions such as trophic and non-trophic interactions between multiple trophic levels. These interactions are likely to be present in any natural system, including in field biodiversity experiments that manipulate a single trophic level such as plants. Other forms of complementarity between species arise from trophic and non-trophic interactions (Loreau 2010). Biodiversity can stabilise ecosystem properties through asynchrony of species environmental responses in food webs as it does in competitive communities, but an additional factor that governs the stabilising or destabilising effect of species diversity when multiple trophic levels are considered is consumers’ combined interaction strength, as measured by the total per capita effect of all resources combined on the population growth rate of consumers (Ives *et al.* 2000). For species diversity to stabilise ecosystem properties, a trade-off between the niche breadth of consumers and their predation efficiency on each prey is required (Thébault & Loreau 2005; Loreau 2010). Such a trade-off can arise when prey diversity forces predators to spend more time on information processing, thereby reducing their consumption efficiency (Kratina *et al.* 2007). Although the stabilising effect of coupled fast–slow dynamics was first suggested in food webs (Rooney *et al.* 2006), the dynamics of consumer–resource interactions at multiple trophic levels is also complex enough to generate counterintuitive effects on ecosystem stability. For instance, environmentally induced fluctuations in the mortality rates of intermediate consumers can contribute to synchronise their dynamics, which in turn can paradoxically promote food-web stability because of the transient responses of basal resources and top predators (Vasseur & Fox 2007). Another factor that our model ignores is spatial heterogeneity, which itself can be affected by interactions with other trophic levels. Spatial heterogeneity is present even in controlled experiments, and is likely to partly explain the significant role of observation error in ecosystem stability detected in some long-term grassland biodiversity experiments (de Mazancourt *et al.* 2013).

Ives & Hughes (2002) showed that the stabilising or destabilising role of species diversity also hinges on whether and how species diversity affects environmental variance in model competitive communities. Our model incorporates environmental stochasticity in the form of an additive, density-independent term in a species' per capita population growth rate (eqn 1), in agreement with existing knowledge (Lande *et al.* 2003). This essentially assumes that environmental fluctuations affect individuals irrespective of density or diversity – a reasonable assumption in the absence of evidence to the contrary. If, however, the effect of environmental fluctuations on per capita population growth rates were to change systematically with diversity because of changes in individual behaviour as a result of species interactions, this would obviously alter our prediction. Specifically, if environmental fluctuations were to affect individuals relatively less in species-rich (species-poor) communities, this would act as an additional mechanism contributing to the stabilising (destabilising) effect of diversity on aggregate ecosystem properties. Fowler *et al.* (2012) recently explored a scenario where environmental variance decreased with species diversity, although they did not provide a biological rationale for this assumption.

Our work suggests that studies of compensatory dynamics in natural communities may need to be refocused. Historically, interest in functional compensatory changes between species arose from their putative role in ecosystem stability. McNaughton (1977) was probably the first author to clearly argue for the role of functional compensatory changes in ecosystem stability, and many of the examples he discussed concerned differences in species functional responses to environmental changes, not so much changes in species abundances. In contrast, recent studies of compensatory dynamics have typically focussed on fluctuations in species abundances (Frost *et al.* 1995; Klug *et al.* 2000; Ernest & Brown 2001; Houlahan *et al.* 2007). These fluctuations are easy to measure but they are only distantly related to issues of functional compensation and ecosystem stability, as we have shown here. As a result, they provide limited insights into the mechanisms that underlie ecosystem stability. Focussing on key species-specific or individual-level traits such as species' responses to environmental fluctuations and the speed at which they respond to perturbations would greatly help to enhance our ability to understand and predict the effects of diversity on ecosystem stability in changing environments. Long-term experiments that manipulate the diversity of such traits rather than species richness are feasible; some experiments have begun to do this by imposing temperature fluctuations and selecting combinations of species with different responses to temperature in aquatic laboratory microcosms (Gonzalez & Descamps-Julien 2004; Leary & Petchey 2009). A critical unknown that limits the predictive ability of current theory on ecosystem stability, however, is the potential dependence of individual-level environmental variance on species diversity. Experiments that explore or manipulate the diversity dependence of components of per capita population growth rates are rare (Kratina *et al.* 2007); yet, this is potentially one of the most important factors that govern ecosystem stability in both competitive communities (Ives & Hughes 2002) and food webs (Thébault & Loreau 2005; Loreau 2010).

Probably the greatest future challenge for both theoretical and empirical work will be to extend the mechanistic trait-based approach advocated here to complex food webs and ecosystems. Because of the myriad trophic and non-trophic interactions between multiple trophic levels and functional groups, ecosystems typically have much more complex structure and dynamics than do competitive communities. Despite recent theoretical advances (Ives *et al.* 2000; Thébault & Loreau 2005), we still have limited understanding of the links between population- and ecosystem-level stability and of the effects of biodiversity on stability in complex ecosystems because of the strong dependence of stability on the diversity, topology and strength of trophic and non-trophic interactions (de Ruiter *et al.* 1995; Rooney *et al.* 2006; Mougi & Kondoh 2012). Therefore, uncovering the general structural properties of ecosystems might be a key to making further progress in this area and bringing the old diversity–stability debate to a final resolution (Rooney & McCann 2012).

ACKNOWLEDGEMENTS

We thank Andy Hector, Mark Emmerson and two anonymous referees for providing helpful comments on the manuscript. This study was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

AUTHORSHIP

Both authors conceived the study and designed and analysed the model. CdM performed the simulations. ML wrote the first draft of the manuscript.

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Editor, Emmett Duffy
Manuscript received 24 September 2012
First decision made 27 October 2012
Manuscript accepted 13 December 2012