Published in final edited form as:

Ecol Lett. 2016 May ; 19(5): 510–518. doi:10.1111/ele.12582.

Biodiversity and ecosystem stability across scales in metacommunities

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Abstract

Although diversity-stability relationships have been extensively studied in local ecosystems, the global biodiversity crisis calls for an improved understanding of these relationships in a spatial context. Here we use a dynamical model of competitive metacommunities to study the relationships between species diversity and ecosystem variability across scales. We derive analytic relationships under a limiting case; these results are extended to more general cases with numerical simulations. Our model shows that, while alpha diversity decreases local ecosystem variability, beta diversity generally contributes to increasing spatial asynchrony among local ecosystems. Consequently, both alpha and beta diversity provide stabilizing effects for regional ecosystems, through local and spatial insurance effects, respectively. We further show that at the regional scale, the stabilizing effect of biodiversity increases as spatial environmental correlation increases. Our findings have important implications for understanding the interactive effects of global environmental changes (e.g. environmental homogenization) and biodiversity loss on ecosystem sustainability at large scales.

Keywords

Biodiversity loss; biotic homogenization; diversity-stability relationship; effective number of species (ENS); environmental homogenization; metacommunity; scale; variability

INTRODUCTION

The earth's ecosystems are undergoing significant changes in their biotic components (e.g. species extinction) and abiotic environment (Vitousek et al. 1997; Tilman & Lehman 2001; Western 2001). A critical task is to understand how these changes may alter ecosystem functioning, stability and services (Loreau et al. 2001; Cardinale et al. 2012). The past two

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Author contributions: SW and ML designed the study, SW performed the research, and SW and ML wrote the manuscript.

decades have seen a growing interest and major advances in understanding the relationship between biodiversity and the stability of ecological systems (McCann 2000; Ives & Carpenter 2007). A general consensus from recent studies is that a higher biodiversity can enhance the temporal stability of aggregate ecosystem properties (e.g. biomass, productivity, etc.), although its effect on population stability remains controversial (reviewed in Hooper et al. 2005; Loreau 2010). These findings provide significant insights for understanding the consequences of local biodiversity loss for ecosystem stability (Cardinale et al. 2012; Newbold et al. 2015; but see Vellend et al. 2013).

Biodiversity is not only declining in many local ecosystems, but is also becoming increasingly homogenized across space (McKinney & Lockwood 1999; Olden et al. 2004; Solar et al. 2015). Such biotic homogenization, captured by an increased spatial similarity in community composition, might affect ecosystem stability at larger scales. At the population level, spatial correlation in the environment can synchronize population dynamics and thereby decrease the stability of large-scale population dynamics (Moran 1953; Hudson & Cattadori 1999; Gouhier et al. 2010). A few recent experiments suggest that spatial similarity in community composition may similarly increase the spatial synchrony of ecosystem dynamics and impair the stability of regional ecosystems (Olden et al. 2004; Duffy & France 2006). Despite these experimental insights, theory has yet to be developed to understand the effects of biotic homogenization on the dynamics and stability of ecosystems at landscape to regional scales.

In addition to biotic homogenization, the abiotic environment itself is also undergoing increased homogenization due to large-scale perturbations, such as global warming and nitrogen deposition (Vitousek et al. 1997). These large-scale perturbations tend to reduce spatial heterogeneity and increase the spatial correlation of environmental fluctuations (Western 2001). Such changes can affect ecosystem stability directly, by increasing spatial correlation in the environment (Moran 1953; Hudson & Cattadori 1999), and indirectly, through their impacts on biodiversity (Western 2001; Hautier et al. 2015). Furthermore, they may alter diversity-stability relationships. Recent experiments showed that nitrogen addition can weaken the stabilizing effects of diversity in local ecosystems (Romanuk et al. 2006; Hautier et al. 2014). Yet, it is unclear how environmental homogenization may affect diversity-stability relationships at large scales.

In this paper, we study diversity-stability relationships in a spatial context and examine how they are influenced by environmental homogenization. A useful framework to study biodiversity in space is given by the concepts of alpha, beta, and gamma diversity (Whittaker 1972; Lande 1996). Alpha and gamma diversity represent diversity at local and regional scales, respectively, while beta diversity is a measure of dissimilarity among local communities. Parallel to this framework, we have recently developed a spatial partitioning framework for ecosystem stability or variability (Wang & Loreau 2014). Alpha and gamma variability are defined as the temporal variability of some aggregate ecosystem property at local and regional scales, respectively, and beta variability measures the spatial asynchrony of this ecosystem property among local ecosystems. Gamma variability (of regional ecosystems) then equals the ratio between mean alpha variability (of local ecosystems) and beta variability. Thus, beta variability quantifies how much ecosystem variability is reduced

from local to regional scales, and any factor contributing to increasing beta variability provides spatial insurance for regional ecosystems (Loreau et al. 2003; Wang & Loreau 2014).

Previous studies have mostly focused on the local stabilizing effects of alpha diversity on alpha variability. Here, we explore how the local stabilizing effect of diversity scales up to the regional scale and, more importantly, how alpha and beta diversity affect beta variability and thereby provide or impair spatial insurance effects for regional ecosystems. For example, we show that alpha diversity affects both alpha and beta variability; therefore its net effect on large-scale (gamma) variability is unclear. We use a dynamical metacommunity model to explore these issues. Our model describes a competitive metacommunity, in which population dynamics are regulated by competition, dispersal, and environmental stochasticity. Species diversity is an outcome of these interacting factors. Our interest, however, is not in the mechanisms that promote species diversity in metacommunities, which have been well documented in previous studies, both theoretically (Leibold et al. 2004; Holyoak et al. 2005; Haegeman & Loreau 2014) and empirically (Cadotte 2006; Carrara et al. 2014). Instead, we take advantage of the spatial framework provided by the metacommunity model to explore how the resulting patterns of species diversity affect ecosystem stability across scales. We investigate the model analytically under a limiting case and numerically in general cases. Our results establish explicit links between diversity and ecosystem variability across scales. They show that the scaling of diversity-variability relationships from local to regional scales is far from trivial. While alpha diversity always stabilizes local ecosystem properties, gamma diversity can either stabilize or destabilize regional ecosystem properties, although the scenarios that yield destabilizing effects may be uncommon in natural ecosystems. Our model also shows that the stabilizing effect of diversity on regional ecosystem properties becomes stronger as the spatial environmental correlation increases. We discuss the implications of these results for predicting the consequences of biotic and environmental homogenization for ecosystem stability at large spatial scales.

METHODS

Our approach is to develop a dynamical model of competitive metacommunities and study the relationships between species diversity and ecosystem variability across scales. In this section, we first describe our metacommunity model and the way to calculate diversity and ecosystem variability at multiple scales within a metacommunity. We then describe the analytical and simulation methods we use to analyze our model. Our analytical work is based on a limiting case, in which the metacommunity behaves as an assembly of independent populations in the absence of any local or spatial interaction (i.e. no competition and no dispersal). This limiting case provides important analytical insights that allow us to predict and interpret the numerical results. Lastly, we perform numerical simulations to extend these analytical results to more general cases.

The model

Our model is a simple extension of the Lotka-Volterra competition model in a patchy, stochastic environment. We consider a metacommunity that consists of m patches or local communities. Local population growth is regulated by intra- and interspecific density dependence and environmental stochasticity, and populations disperse among patches. Here, for simplicity, we model dispersal as a random passive process, which is assumed to be patch and density independent. So, emigrants from patch i have equal probabilities to reach any of the other $m-1$ patches. Our model thus reads:

$$\frac{dN_{il}(t)}{dt} = r_{il}N_{il}(t) \cdot \left(1 - \frac{N_{il}(t) + c_{ijl} \cdot \sum_{j \neq i} N_{jl}(t)}{K_{il}} \right) + \left(-d_i \cdot N_{il}(t) + \sum_{p \neq l} N_{ip}(t) \cdot \frac{d_i}{m-1} \right) + N_{il}(t) \cdot E_{il}(t) \quad (1)$$

where $N_{il}(t)$ is the biomass of species i in patch l at time t . The first term in the right-hand side of equation (1) shows the effects of intra- and interspecific competition in patch l , with r_{il} and K_{il} denoting the intrinsic growth rate and carrying capacity of species i in patch l , respectively, and c_{ijl} denoting the competition coefficient of species j on species i in patch l . The second term shows the effect of dispersal among patches, with d_i denoting the per capita emigration rate of species i . The third term shows the impact of environmental stochasticity on the population growth rate, where $E_{il}(t)$ is the response of species i 's population growth rate to environmental fluctuations in patch l .

In our model, we formulate this environmental response as follows:

$$E_{il}(t) = \eta_l(t) + \varepsilon_i(t) + \kappa \cdot \eta_l(t) \cdot \varepsilon_i(t) \quad (2)$$

where η_l and ε_i represent the patch-specific and species-specific environmental responses of species i in patch l , respectively, and $\eta_l \varepsilon_i$ represents the interaction between them. Parameter κ determines the relative strength of this interaction. We assume that η and ε are normal variables (with zero mean, and variances of σ_η^2 and σ_ε^2 , respectively) that are independent through time (i.e. white noise) and from each other. Between patches, patch-specific environmental responses can be correlated (ρ_η) due to spatial environmental correlation; between species, species-specific environmental responses can be correlated (ρ_ε) due to interspecific niche overlap. These two types of correlations will be called between-patch and between-species environmental correlations, respectively (Ruokolainen 2013). While species responses to environmental fluctuations may be complex and nonlinear (Chesson 2000), equation (2) may be regarded as a first approximation of a more general class of models.

In our study, we assume that the metacommunity has a stable equilibrium in the absence of environmental fluctuations; but due to environmental stochasticity, populations fluctuate

permanently around their equilibria. This assumption allows us to use linear approximations to investigate our model under some limiting cases. In Table 1, we summarize the key symbols used throughout the paper.

Alpha, beta and gamma diversity and variability

Within a metacommunity, both diversity and ecosystem variability can be defined at alpha, beta and gamma scales. At each of these scales, we quantify species diversity by a measure of the “effective number of species” (ENS for short hereafter), which takes both species richness and evenness into account (Hill 1973). More specifically, we use the inverse Simpson index, i.e. $D = 1 / \sum p_i^2$ (Simpson 1949), as our diversity measure, where p_i is the relative biomass of species i in a community or metacommunity. Alpha diversity (α_D) is then defined as the inverse of the biomass-weighted average of local Simpson indices, and gamma diversity (γ_D) is defined as the inverse Simpson index over the whole metacommunity (Olszewski 2004; see Appendix 1). In our study, we define beta diversity (β_D) in a multiplicative way, i.e., as the ratio of gamma diversity to alpha diversity, i.e.: $\beta_D = \gamma_D / \alpha_D$. As we will show, these ENS-based diversity measures are linked directly to ecosystem variability in our model. In our simulation studies, in addition to the ENS-based measures, we have also investigated the relationships between ecosystem variability and richness-based diversity measures. Similarly, richness-based alpha diversity (α_D') is the mean species richness across local communities, and richness-based gamma diversity (γ_D') is the species richness of the whole metacommunity. Again, richness-based beta diversity (β_D') is defined as the ratio between gamma and alpha diversity, i.e. $\beta_D' = \gamma_D' / \alpha_D'$.

Just as with biodiversity, ecosystem variability (of biomass) can be defined at alpha, beta and gamma scales. Alpha variability (α_{CV}) represents the mean temporal variability at the local community scale. Specifically, for each local community, the coefficient of variation (CV , i.e. the ratio of the standard deviation to the mean) of total biomass is computed. The average CV , weighted by local community biomass, is then calculated, and α_{CV} is defined as the square of this average CV . Gamma variability (γ_{CV}) represents the temporal variability at the metacommunity scale, which is measured as the square of the CV of total biomass in the whole metacommunity. Beta variability (β_{CV}) represents the spatial asynchrony in biomass dynamics among local patches. Mathematically, β_{CV} is defined as the reciprocal of a metacommunity-wide measure of spatial synchrony, which is calculated as the ratio between total metacommunity variance and its maximum value when all local patches have perfectly correlated dynamics (Loreau & de Mazancourt 2008). Beta variability, as such defined, equals the ratio of alpha variability to gamma variability, i.e. $\beta_{CV} = \alpha_{CV} / \gamma_{CV}$ (Wang & Loreau 2014). In other words, β_{CV} measures how much ecosystem variability is reduced from local (alpha) to regional (gamma) scales.

Analytical investigations under a limiting case

We consider a limiting case of equation (1) that allows analytical investigations. This limiting case presents a non-interacting metacommunity, which ignores competition among species within a patch and dispersal between patches, i.e. $c_{ijl} = 0$ and $d_i = 0$. Thus, the metacommunity is an assembly of independent populations. We assume all species have the same intrinsic growth rate ($r_{il} = r$) but differ in their carrying capacities (K_{ij}). Note that a

species i may have a zero carrying capacity in some patches and non-zero ones in others. Because each species fluctuates independently from all other species within a patch and from all conspecific populations in other patches, its equilibrium biomass (in the absence of environmental stochasticity) corresponds to its local carrying capacity (K_{ij}). In this limiting case, diversity is effectively an independent variable (since species richness and abundances can be manipulated by changing species' carrying capacities), which allows us to study the direct effects of diversity on ecosystem stability.

Under this limiting case, we derive analytical solutions for alpha, beta and gamma variability, which are functions of the ENS-based measures of alpha, beta and gamma diversity and other parameters (see Results & Appendix 2). To simplify the analytical solutions, we further assume that all local communities have identical total biomass and ENS. In such a metacommunity, the ENS-based alpha and gamma diversity are:

$$\alpha_D = 1 / \sum_i \left(\frac{K_{il}}{\sum_i K_{il}} \right)^2 \quad \text{and} \quad \gamma_D = 1 / \sum_i \left(\frac{\sum_l K_{il}}{\sum_{i,l} K_{il}} \right)^2, \text{ respectively (see Appendix 2), and}$$

beta diversity is given by the equation: $\beta_D = \gamma_D / \alpha_D$. Based on these solutions, we investigate analytically the relationships between species diversity and ecosystem variability at the multiple scales, and how these relationships are shaped by the parameters of species environmental responses, i.e. between-patch environmental correlation (ρ_η), between-species environmental correlation (ρ_ϵ) and the strength of the interaction between patch- and species-specific environmental responses (κ) (see Appendix 3).

Numerical simulations

We performed numerical simulations to investigate diversity-variability relationships across scales in the general case, when species interact locally and spatially with varying parameters. We used both ENS- and richness-based diversity measures in these simulations. In each simulation, we started with a two-patch metacommunity comprising 10 species in each patch. We assumed that 5 species are generalists, which are shared and disperse between the two patches; the other 10 species (5 from each patch) are specialists, which occur only in one patch (i.e. zero carrying capacity in the other patch) and do not disperse. A zero dispersal rate can happen if the dispersal rates for specialist species are so low that species sorting makes it impossible for dispersers to establish in other patches (Mouquet & Loreau 2003; Leibold et al. 2004). This assumption is made simply to generate nontrivial richness-based beta diversity (if all species can disperse freely, they will occur in all patches and the richness-based beta diversity will always be 1). Note that relaxing the assumption to let all species have non-zero dispersal rates and carrying capacities does not qualitatively alter the results for ENS-based diversity measures (see Appendix 4). For each species, parameters were randomly sampled from uniform distributions: $r_{il} \sim [0.5, 1.5]$, $K_{il} \sim [0.5, 1.5]$, $c_{ijl} \sim [0.25, 0.75]$, $d_i = 0$ (for specialists) or $\sim [0.05, 0.15]$ (for generalists).

We examined the relationships between diversity and ecosystem variability in simulated metacommunities and explored how these relationships depended on the parameters of species environmental responses (i.e. ρ_η , ρ_ϵ and κ ; see Table 1 for parameter values). Under each of the 30 combinations of these parameters (i.e. five levels of ρ_η , three levels of ρ_ϵ and

two levels of κ), we constructed 2000 metacommunities following the above procedure and simulated their dynamics following equation (1) (see details in Appendix 4). In each simulation, to facilitate the convergence towards the stationary state, the initial species biomasses were given around their equilibria in the absence of environmental stochasticity. The metacommunity dynamics were then simulated for 5,000 time steps (each time step was divided into 10 finer time steps, i.e. $\Delta t = 0.1$), during which some species went extinct due to competition and/or dispersal (and potentially, environmental fluctuations). We then used the last 1,000 time steps to calculate diversity and ecosystem variability at the multiple scales. Note that in these simulations, diversity is an intermediate variable that is determined by lower-level processes (e.g. competition, dispersal, etc.) and that in turn, in combination with these processes, affects ecosystem stability. This is a typical situation in empirical studies. Therefore these simulations also allow us to check whether the effects of diversity on ecosystem stability that we predict under the limiting case can be detected in a more realistic setting, in which diversity is not a completely independent variable.

RESULTS

Analytical insights from the limiting case

The limiting case provides analytical solutions for alpha, beta and gamma variability (Appendix 2):

$$\alpha_{CV} = \frac{1}{2r} \left[\sigma_\varepsilon^2 (1 + \kappa^2 \sigma_\eta^2) \left(\rho_\varepsilon + \frac{1 - \rho_\varepsilon}{\alpha_D} \right) + \sigma_\eta^2 \right] \quad (3)$$

$$\beta_{CV} = \frac{m [\sigma_\varepsilon^2 \rho_\varepsilon + \sigma_\eta^2 (1 + \kappa^2 \sigma_\varepsilon^2 \rho_\varepsilon)] \alpha_D + m \sigma_\varepsilon^2 (1 - \rho_\varepsilon) (1 + \kappa^2 \sigma_\eta^2)}{[m \sigma_\varepsilon^2 \rho_\varepsilon + (1 + (m - 1) \rho_\eta) (1 + \kappa^2 \sigma_\varepsilon^2 \rho_\varepsilon) \sigma_\eta^2] \alpha_D + (1 - \rho_\varepsilon) \sigma_\varepsilon^2 \cdot \left(1 + \kappa^2 \sigma_\eta^2 + \left(\frac{m}{\beta_D} - 1 \right) (1 + \kappa^2 \sigma_\eta^2 \rho_\eta) \right)} \quad (4)$$

$$\gamma_{CV} = \frac{1}{2rm} \left[m \sigma_\varepsilon^2 \rho_\varepsilon + (1 + (m - 1) \rho_\eta) \cdot (1 + \kappa^2 \sigma_\varepsilon^2 \rho_\varepsilon) \sigma_\eta^2 + (1 - \rho_\varepsilon) \sigma_\varepsilon^2 \cdot \frac{1 + \kappa^2 \sigma_\eta^2 + (m/\beta_D - 1) (1 + \kappa^2 \sigma_\eta^2 \rho_\eta)}{\alpha_D} \right] \quad (5)$$

Note that in these equations, beta diversity (β_D) always lies between 1 and m (see Appendix 1). Note also that similar analytical solutions can be obtained under another limiting case that incorporates competition and dispersal but assumes strong symmetry among species and local communities (Appendix 2).

Equations (3-5) predict explicit links between diversity and ecosystem variability across scales, which are summarized in Figure 1. They show that alpha variability is affected only by, and decreases with, alpha diversity. In contrast, beta variability is affected by both alpha and beta diversity; these effects depend on the parameters of species environmental responses (i.e. ρ_η , ρ_ε and κ) (Appendix 3). When ρ_η is negative, alpha diversity generally increases beta variability; when ρ_η is positive, alpha diversity either increases or decreases beta variability, depending on the values of ρ_ε and κ (Figures 1&S1). The effect of beta diversity on beta variability is also context dependent. When ρ_η is positive or κ is small, beta diversity increases beta variability. However, when ρ_η is negative and κ is large, beta diversity can decrease beta variability (Figures 1&S1). To understand the latter result, consider two patches A and B with strongly asynchronous environments ($\rho_\eta \approx -1$; e.g. alternating flood and drought). When the two patches have a very similar species composition (i.e. low beta diversity), they should exhibit strongly asynchronous dynamics in response to their asynchronous environments. In contrast, a high beta diversity can contribute to weakening the desynchronizing effects of the asynchronous environments, for instance, if species in patch A are flood-resistant while those in patch B are drought-resistant (Baruch 1994).

Through their effects on alpha and beta variability, alpha and beta diversity both influence gamma variability. Although alpha diversity may either decrease or increase beta variability, it always decreases gamma variability because of its strong stabilizing effect at the local scale (Figure 2). Since beta diversity has no effect on alpha variability, its effect on gamma variability is mainly determined by its effect on beta variability. Thus, beta diversity decreases gamma variability when $\rho_\eta > 0$ or κ is small, and the opposite occurs when $\rho_\eta < 0$ and κ is large (Figure 2). Furthermore, the stabilizing effects of alpha and beta diversity on gamma variability decrease with ρ_ε and increase with ρ_η (unless $\kappa = 0$, when there is no dependence) (Figure 2). Here, the stabilizing effect of diversity is measured by the magnitude of the decrease in variability with a unit increase in diversity, i.e. minus the derivative of variability with respect to diversity (see Appendix 3).

As a consequence, if gamma diversity is mainly determined by alpha diversity (e.g. beta diversity is fixed), gamma diversity always decreases gamma variability; if gamma diversity is mainly determined by beta diversity (e.g. alpha diversity is fixed), gamma diversity decreases gamma variability when $\rho_\eta > 0$ or κ is small, and the opposite occurs when $\rho_\eta < 0$ and κ is large (Figures 1&S1). Similarly, the stabilizing effect of gamma diversity, through either alpha or beta diversity, decreases with ρ_ε and increases with ρ_η (unless $\kappa = 0$, when there is no dependence) (see Appendix 3).

Finally, the analytical solutions (i.e. equation 5) also predict that under a given gamma diversity, gamma variability is influenced by the spatial pattern of biodiversity (Appendix 3). In the above analyses, alpha and beta diversity were considered as independent variables; however, in reality, they can be correlated with each other. Under the special case where gamma diversity is constant, alpha and beta diversity are inversely related. In this case, gamma variability tends to decrease with alpha diversity or increase with beta diversity (unless $\kappa = 0$, when there is no dependence) (Figure S2).

Diversity-variability relationships across scales in simulated metacommunities

We investigated diversity-variability relationships across scales in general cases using numerical simulations. Figure 3 shows the resulting patterns of diversity and ecosystem variability in simulated metacommunities under three sets of parameters (i.e. $\rho_\eta = -0.8, 0, 0.8$; $\rho_\varepsilon = 0$; $\kappa = 8$). The ENS- and richness-based diversity measures generated qualitatively similar diversity-variability relationships; however, the former generally provided a better explanation (higher R^2) for ecosystem variability at all scales (Figures 3 & S5).

Overall, the simulated diversity-variability relationships were generally consistent with predictions from the analytically tractable limiting case (compare Figures 4 vs. S1). More specifically, the effects of alpha and beta diversity on alpha and beta variability, and their dependence on the parameters of species environmental responses ($\rho_\varepsilon, \rho_\eta, \kappa$), exhibited qualitatively similar patterns as the analytic predictions in Figure 1. Moreover, just as predicted by the analytic solutions, the stabilizing effects of diversity (at alpha, beta, and gamma scales) on gamma variability, decreased with between-species environmental correlation (ρ_ε) and increased with between-patch environmental correlation (ρ_η) when $\kappa > 0$ (Figure S6). Note that in the analytically tractable case, these predictions were derived under the assumption that alpha and beta diversity are independent. In our simulations, alpha and beta diversity were weakly, but negatively correlated (Fig. S7); however, the results still exhibited patterns that agreed with the analytic predictions. Finally, we examined the effects of beta diversity on gamma variability under a given gamma diversity. This was done by investigating the correlation between the residuals of the regression of gamma variability on gamma diversity and those of the regression of beta diversity on gamma diversity. In agreement with the analytic predictions, the correlation was positive when $\kappa > 0$ (Fig. S8).

DISCUSSION

In this paper, we have developed new theory based on a metacommunity model to predict diversity-stability relationships at multiple spatial scales. Our results establish explicit links between species diversity and ecosystem variability across scales (Figure 1). At the local scale, our model predicts a negative relationship between alpha diversity and alpha variability, in agreement with previous studies (Hooper et al. 2005; Cardinale et al. 2012). More interestingly, our model clarifies how species diversity affects beta variability, which is a critical step to understand diversity-stability relationships at large scales (Wang & Loreau 2014). The relationships between diversity and beta variability depend on the sign of between-patch environmental correlation (ρ_η). A positive between-patch environmental correlation, however, seems most relevant in reality. Although a negative between-patch environmental correlation can sometimes occur in simple experiments (Steiner et al. 2011), in natural ecosystems the environment is usually positively correlated across space (Moran 1953; Hudson & Cattadori 1999; Gouhier et al. 2010). In addition, a negative between-patch environmental correlation is unlikely to occur in large landscapes that consist of a large number of patches, simply due to mathematical constraints (Loreau & de Mazancourt 2008). Therefore, in the following we consider the scenario where $\rho_\eta > 0$ unless specified otherwise. Under this scenario, beta variability always increases with beta diversity, and it either increases or decreases with alpha diversity (Figures 1a). This is consistent with recent

experimental results that a larger compositional dissimilarity among local communities can increase spatial asynchrony (Duffy & France 2006).

The effects of diversity on alpha and beta variability determine their effects on gamma variability (Wang & Loreau 2014). While stabilizing local ecosystems, alpha diversity may either increase or decrease beta variability, which have contrasting consequences for regional ecosystem stability. However, our analytic and simulation results show that gamma variability always decreases with alpha diversity (Figures 2 & S6), implying that the local stabilizing (or local insurance) effect of alpha diversity is stronger than its negative effect on beta variability when this negative effect occurs. On the other hand, beta diversity generally increases beta variability and thereby provides spatial insurance effects for ecosystems at large spatial scales. Thus, these results show that both alpha and beta diversity provide stabilizing effects on regional ecosystem properties. As a consequence, both local biodiversity loss and biotic homogenization impair the stability of large-scale ecosystem properties.

Although alpha and beta diversity provide stabilizing effects through similar mechanisms (i.e. local and spatial insurance, respectively), these mechanisms operate at different scales and differ in the strength of their stabilizing effects on regional ecosystem properties. The local insurance effect of alpha diversity results from the fact that species with different functional traits exhibit asynchronous responses to their shared local environment (Yachi & Loreau 1999). In contrast, the spatial insurance effect of beta diversity results from the fact that communities with different species compositions exhibit asynchronous responses to a spatially correlated environment. Our results show that, under a fixed gamma diversity, a metacommunity with a higher alpha diversity (or lower beta diversity) is generally more stable than one with a lower alpha diversity (or higher beta diversity) (Figure S8). Therefore, the stability of regional ecosystems is not solely determined by the richness and abundance distribution of species (gamma diversity), but also by their spatial distribution (alpha and beta diversity). In order to maintain ecosystem stability at large scales, conservation efforts should preserve biodiversity not only at the regional scale, but also at the local scale.

Our model further predicts that the strength of the stabilizing effects of alpha and beta diversity on gamma variability increases with between-patch environmental correlation (Figures 2 & S6). Such dependence is particularly strong for beta diversity. This can be understood as follows. When between-patch environmental correlation is low, the environment provides strong spatial insurance (i.e., desynchronizing) effects, which results in low spatial synchrony in community dynamics regardless of the dissimilarity among local communities. When between-patch environmental correlation is high, the synchronous environment provides synchronizing effects (Moran 1953), and the dissimilarity among local communities becomes important in providing spatial insurance. This result has important implications for predicting the consequences of biodiversity loss in the context of global environmental changes. The same amount of biodiversity loss can cause a higher loss of ecosystem stability in a more correlated environment (Figure 5). Therefore, if global changes such as climate warming and nitrogen deposition cause increased environmental homogenization (Vitousek et al. 1997; Western 2001), we predict that these changes will not

only decrease the stability of regional ecosystems directly, but will also increase the destabilizing effects of biodiversity loss when it occurs (Figure 4).

Our results also suggest that ENS-based diversity measures provide better predictions on the effects of diversity on ecosystem stability than richness-based ones (Figure S5). This is because ENS takes into account both species richness and evenness (Hill 1973). For a given species richness, a higher species evenness can decrease community-wide species synchrony and thereby stabilize ecosystem properties (de Mazancourt et al. 2013; Thibaut & Connolly 2013); the same holds for metacommunities. Such a result is consistent with previous findings that species composition can be as important as species richness for ecosystem functioning and stability (Hooper et al. 2005). Note, however, that this result may be altered if biomass is correlated with population-level stability across species. More specifically, if common species have a higher temporal stability, unevenness induced by the dominance of such stable species can contribute to a higher ecosystem stability (Loreau & de Mazancourt 2013). Such an effect has been called a selection effect in the studies of biodiversity and ecosystem functioning (Loreau et al. 2001). In our model, this selection effect was weak because species parameters were assigned randomly; but in practice, selection effects can be strong. Our model also assumes that metacommunity dynamics are in a stationary regime, in which populations fluctuate moderately around their average biomass. In reality, ecosystem dynamics may not be stationary (Crone & Taylor 1996), and temporal records may not be long enough to reach stationary dynamics. These factors can affect the predictability of the ENS-based diversity measures on ecosystem stability.

In conclusion, our study extends the theory of diversity-stability relationships to a multi-scale framework and makes new predictions on the consequences of large-scale biodiversity loss and environmental homogenization. Our results demonstrate that biodiversity loss, both in the form of local diversity declines and in the form of biotic homogenization, impairs the stability of natural ecosystems at large scales. Moreover, the destabilizing effect of biodiversity loss can be more pronounced when the environment is homogenized. Although these predictions were obtained using metacommunity theory, they should apply more generally to spatial competition systems, for instance to continuous landscapes with local or global dispersal. One limitation of our model is the assumption that the metacommunity reaches a stable equilibrium in the absence of environmental stochasticity. Future studies are needed to explore whether our results still hold if the metacommunity exhibits complex dynamics (e.g. cycles, chaos, etc.; Fowler et al. 2012). Finally, our results could be easily tested by experiments, for instance with microbial communities (Steiner et al. 2011; Altermatt et al. 2015). While previous metacommunity experiments have mostly focused on the effect of dispersal on species diversity and ecosystem dynamics, few have manipulated the spatial pattern of biodiversity and examined its consequence for ecosystem stability. Future experimental efforts in this direction should provide exciting new insights into diversity-stability relationships in a spatial context.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

ACKNOWLEDGEMENTS

We thank Bart Haegeman for stimulating discussions and technical assistance, and Florian Altermatt, Jean-François Arnoldi, Wanlu Deng, Bart Haegeman, Vincent A.A. Jansen and three anonymous referees for helpful comments on earlier versions of the manuscript. This work was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41) and by the BIOSTASES Advanced Grant, funded by the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement No 666971).

References

- Altermatt F, Fronhofer EA, Garnier A, Giometto A, Hammes F, Klecka J, Legrand D, Mächler E, Massie TM, Pennekamp F, Plebani M, et al. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. *Methods in Ecology and Evolution*. 2015; 6:218–231.
- Baruch Z. Responses to drought and flooding in tropical forage grasses. *Plant and Soil*. 1994; 164:87–96.
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA. Biodiversity loss and its impact on humanity. *Nature*. 2012; 486:59–67. [PubMed: 22678280]
- Carrara F, Rinaldo A, Giometto A, Altermatt F. Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. *The American Naturalist*. 2014; 183:13–25.
- Chesson P. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*. 2000; 31:343–366.
- Crone EE, Taylor DR. Complex dynamics in experimental populations of an annual plant, *Cardamine pensylvanica*. *Ecology*. 1996; 77:289–299.
- de Mazancourt C, Isbell F, Larocque A, Berendse F, Luca E, Grace JB, Haegeman B, Wayne Polley H, Roscher C, Schmid B, Tilman D, et al. Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*. 2013; 16:617–625. [PubMed: 23438189]
- Fowler MS, Laakso J, Kaitala V, Ruokolainen L, Ranta E. Species dynamics alter community diversity–biomass stability relationships. *Ecology Letters*. 2012; 15:1387–1396. [PubMed: 22931046]
- France KE, Duffy JE. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*. 2006; 441:1139–1143. [PubMed: 16810254]
- Gouhier TC, Guichard F, Gonzalez A. Synchrony and stability of food webs in metacommunities. *The American Naturalist*. 2010; 175:E16–E34.
- Haegeman B, Loreau M. General relationships between consumer dispersal, resource dispersal and metacommunity diversity. *Ecology Letters*. 2014; 17:175–184. [PubMed: 24304725]
- Hautier Y, Seabloom EW, Borer ET, Adler PB, Harpole WS, Hillebrand H, Lind EM, MacDougall AS, Stevens CJ, Bakker JD. Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*. 2014; 508:521–525. [PubMed: 24531763]
- Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*. 2015; 348:336–340. [PubMed: 25883357]
- Hill MO. Diversity and evenness: a unifying notation and its consequences. *Ecology*. 1973; 54:27–432.
- Holyoak, M.; Leibold, MA.; Holt, RD. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press; 2005.
- Hooper D, Chapin III F, Ewel J, Hector A, Inchausti P, Lavorel S, Lawton J, Lodge D, Loreau M, Naeem S. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*. 2005; 75:3–35.
- Hudson PJ, Cattadori IM. The Moran effect: a cause of population synchrony. *Trends in Ecology & Evolution*. 1999; 14:1–2. [PubMed: 10234236]
- Ives A, Gross K, Klug J. Stability and variability in competitive communities. *Science*. 1999; 286:542–544. [PubMed: 10521351]

- Ives AR, Carpenter SR. Stability and diversity of ecosystems. *Science*. 2007; 317:58–62. [PubMed: 17615333]
- Lande R. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*. 1996:5–13.
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase J, Hoopes M, Holt R, Shurin J, Law R, Tilman D, Loreau M, et al. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*. 2004; 7:601–613.
- Loreau M. *From populations to ecosystems: Theoretical foundations for a new ecological synthesis* (MPB-46). Princeton University Press; 2010.
- Loreau M, de Mazancourt C. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*. 2008; 172:E48–E66.
- Loreau M, de Mazancourt C. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*. 2013; 16:106–115. [PubMed: 23346947]
- Loreau M, Mouquet N, Gonzalez A. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*. 2003; 100:12765–12770.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime J, Hector A, Hooper D, Huston M, Raffaelli D, Schmid B, Tilman D, et al. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*. 2001; 294:804–808. [PubMed: 11679658]
- McCann KS. The diversity–stability debate. *Nature*. 2000; 405:228–233. [PubMed: 10821283]
- McKinney ML, Lockwood JL. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*. 1999; 14:450–453. [PubMed: 10511724]
- Moran P. The statistical analysis of the Canadian Lynx cycle. *Australian Journal of Zoology*. 1953; 1:291–298.
- Mouquet N, Loreau M. Community patterns in source-sink metacommunities. *The American Naturalist*. 2003; 162:544–557.
- Newbold T, Hudson LN, Hill SL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B. Global effects of land use on local terrestrial biodiversity. *Nature*. 2015; 520:45–50. [PubMed: 25832402]
- Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*. 2004; 19:18–24. [PubMed: 16701221]
- Olszewski TD. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos*. 2004; 104:377–387.
- Romanuk TN, Vogt RJ, Kolasa J. Nutrient enrichment weakens the stabilizing effect of species richness. *Oikos*. 2006; 114:291–302.
- Ruokolainen L. Spatio-temporal environmental correlation and population variability in simple metacommunities. *PloS one*. 2013; 8(8):e72325. [PubMed: 24023615]
- Simpson EH. Measurement of diversity. *Nature*. 1949; 163:688.
- Solar, RRdC; Barlow, J.; Ferreira, J.; Berenguer, E.; Lees, AC.; Thomson, JR.; Louzada, J.; Maués, M.; Moura, NG.; Oliveira, VHF.; Chaul, JCM., et al. How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*. 2015; 18:1108–1118. [PubMed: 26299405]
- Steiner CF, Stockwell RD, Kalaimani V, Aqel Z. Dispersal promotes compensatory dynamics and stability in forced metacommunities. *The American naturalist*. 2011; 178:159–170.
- Thibaut LM, Connolly SR. Understanding diversity–stability relationships: towards a unified model of portfolio effects. *Ecology Letters*. 2013; 16:140–150. [PubMed: 23095077]
- Tilman D, Lehman C. Human-caused environmental change: impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences*. 2001; 98:5433–5440.
- Vellend M, Baeten L, Myers-Smith IH, Elmendorf SC, Beauséjour R, Brown CD, De Frenne P, Verheyen K, Wipf S. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*. 2013; 110:19456–19459.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. Human domination of Earth's ecosystems. *Science*. 1997; 277:494–499.

- Wang S, Loreau M. Ecosystem stability in space: α , β and γ variability. *Ecology Letters*. 2014; 17:891–901. [PubMed: 24811401]
- Western D. Human-modified ecosystems and future evolution. *Proceedings of the National Academy of Sciences*. 2001; 98:5458–5465.
- Whittaker RH. Evolution and measurement of species diversity. *Taxon*. 1972; 21:213–251.
- Yachi S, Loreau M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences*. 1999; 96:1463–1468.

(a) $1 + \kappa^2 \rho_\eta \sigma_\eta^2 > 0$ (i.e. $\rho_\eta > 0$ or κ is small)

(b) $1 + \kappa^2 \rho_\eta \sigma_\eta^2 < 0$ (i.e. $\rho_\eta < 0$ and κ is large)

Figure 1.

Diversity-variability relationships across scales predicted by the analytic solutions: (a) $\rho_\eta > 0$ or κ is small, and (b) $\rho_\eta < 0$ and κ is large. Except for the alpha scale, diversity-variability relationships are context dependent of between-patch environmental correlation (ρ_η), between-species environmental correlation (ρ_ϵ), and the strength of the interaction between patch- and species-specific environmental responses (κ). In particular, in the scenario (a), beta variability can either increase or decrease with alpha diversity, depending on ρ_ϵ and κ

(see Appendix 3). Note that in natural ecosystems, spatial environmental correlation (ρ_η) is usually positive and hence scenario (a) is most relevant in reality.

Figure 2.

Effects of between-patch environmental correlation (ρ_η), between-species environmental correlation (ρ_ϵ) and the strength of the interaction between patch- and species-specific environmental responses (κ) on the derivative of gamma variability to diversity from the analytic solutions: (a) $\kappa = 0$, (b) $\kappa = 8$. Minus the derivative represents the strength of the stabilizing effect of diversity. Parameters: $m = 2$, $r = 1$, $\sigma_\eta^2 = 0.04$, $\sigma_\epsilon^2 = 0.04$, and $\rho_\epsilon = -0.05$ (black), 0 (red), and 0.4 (green). While these derivatives depend also on the alpha and beta diversity, we set $\alpha_D = 4$ and $\beta_D = 1.5$, which correspond to the median values of the simulation data.

Figure 3.

Diversity-variability relationships across scales in simulated metacommunities: (a) ENS-based diversity; (b) richness-based diversity. Parameters: $\kappa = 8$, $\rho_{\varepsilon} = 0$, $\rho_{\eta} = -0.8$ (black), 0 (red), and 0.8 (green), and others in Table 1. Lines represent least-square fits under respective scenarios. See Figure S3 for parallel results under $\kappa = 0$.

Figure 4.

Effects of between-patch environmental correlation (ρ_η), between-species environmental correlation (ρ_ϵ) and the strength of the interaction between patch- and species-specific environmental responses (κ) on the regression slopes between variability and diversity in simulated metacommunities: (a) $\kappa = 0$, (b) $\kappa = 8$. Each point represents a regression slope between respective variables calculated from 2,000 simulated metacommunities (e.g. scatters shown in Figure 3). Polygons represent the 95% confidence intervals. Parameters: $\rho_\epsilon = -0.05$ (black), 0 (red), and 0.4 (green), and others in Table 1. The results shown here correspond to ENS-based diversity measures; see Figures S4 for parallel results for richness-based diversity.

Figure 5.

Effect of biodiversity loss on ecosystem stability at the regional scale, under different scenarios of positive spatial environmental correlations. Global environmental changes may increase environmental homogenization and thus spatial environmental correlation (ρ_η). Under a higher ρ_η the same amount of biodiversity loss (γ_D) can cause a higher increase of ecosystem variability (γ_{CV}).

Table 1

Symbols and parameter values used in the simulation. Note that due to mathematical constraints, the between-species environmental correlation need satisfy: $\rho_\varepsilon > -1/(S-1)$, where S is species richness and was initially set to 15 in our simulations.

Symbol	Explanation	Values in the simulation
$N_{ik}(t)$	Biomass of species i in patch I at time t	Specified by equation (1)
m	Number of patches within a metacommunity.	$m = 2$
r_{ij}	Intrinsic growth rate of species i in patch I	$r_{ij} \sim \text{runif}[0.5, 1.5]$
k_{ij}	Carrying capacity of species i in patch I	$k_{ij} \sim \text{runif}[0.5, 1.5]$
c_{ijl}	Competition coefficient of species j on species i in patch I	$c_{ijl} \sim \text{runif}[0.25, 0.75]$
d_i	Dispersal rate of species i	$d_i = 0$ (for specialists), and $d_i \sim \text{runif}[0.05, 0.15]$ (for generalists)
E_{ij}	Response of species i 's population growth rate to environmental fluctuations in patch I	Specified by equation (2)
η_l	Patch-specific environmental response in patch I	$\eta_l \sim \text{norm}(0, \sigma_\eta^2)$, $\text{cor}(\eta_k, \eta_l) = \rho_\eta$
ε_i	Species-specific environmental response of species i	$\varepsilon_i \sim \text{norm}(0, \sigma_\varepsilon^2)$, $\text{cor}(\varepsilon_i, \varepsilon_j) = \rho_\varepsilon$
σ_η^2	Variance of patch-specific environmental response	$\sigma_\eta^2 = 0.04$
σ_ε^2	Variance of species-specific environmental response	$\sigma_\varepsilon^2 = 0.04$
ρ_η	Between-patch correlation of patch-specific environmental responses (between-patch environmental correlation for short)	$\rho_\eta = -0.8, -0.4, 0, 0.4, 0.8$
ρ_ε	Between-species correlation of species-specific environmental responses (between-species environmental correlation for short)	$\rho_\varepsilon = -0.05, 0, 0.4$
κ	Strength of the interaction between patch- and species-specific environmental responses.	$\kappa = 0, 8$