LETTER

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 stabilising effects for regional ecosystems, through local and spatial insurance effects respectively. We further show that at the regional scale, the stabilising 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 homogenisation) and biodiversity loss on ecosystem sustainability at large scales.

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 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 homogenised across space (McKinney & Lockwood 1999; Olden *et al.* 2004; Solar *et al.* 2015). Such biotic homogenisation, 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 synchronise 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; France & Duffy 2006). Despite these experimental insights, theory has yet to be developed to understand the effects of biotic homogenisation on the dynamics and stability of ecosystems at landscape to regional scales.

In addition to biotic homogenisation, the abiotic environment itself is also undergoing increased homogenisation 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 stabilising effects of diversity in local ecosystems (Romanuk *et al.* 2006; Hautier *et al.* 2014). Yet, it is unclear how environmental homogenisation 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 homogenisation. 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 stabilising effects of alpha diversity on alpha variability. Here, we explore how the local stabilising 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 stabilises local ecosystem properties, gamma diversity can either stabilise or destabilise regional ecosystem properties, although the scenarios that yield destabilising effects may be uncommon in natural ecosystems. Our model also shows that the stabilising 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 homogenisation 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 used to analyse 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:

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

$$(1)$$

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 eqn 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:

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

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), eqn 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 summarise 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

Table 1 Symbols and parameter values used in the simulation. Note that due to mathematical constrains, 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
$N_{il}(t)$	Biomass of species i in patch l at time t	Specified by eqn 1
m	Number of patches within a metacommunity.	$m = 2$
r_{il}	Intrinsic growth rate of species i in patch l	$r_{il} \sim runif\ [0.5, 1.5]$
K_{il}	Carrying capacity of species i in patch l	$K_{il} \sim runif\ [0.5, 1.5]$
c_{ijl}	Competition coefficient of species j on species i in patch l	$c_{ijl} \sim runif\ [0.25, 0.75]$
d_i	Dispersal rate of species i	$d_i = 0$ for specialists, and $d_i \sim runif\ [0.05, 0.15]$ for generalists
E_{il}	Response of species i's population growth rate to environmental fluctuations in patch l	Specified by eqn 2
η_l	Patch-specific environmental response in patch l	$\eta_l \sim rnorm(0, \sigma_\eta^2)$, $cor(\eta_l, \eta_k) = \rho_\eta$
ε_i	Species-specific environmental response of species i	$\varepsilon_i \sim rnorm(0, \sigma_\varepsilon^2)$, $cor(\varepsilon_i, \varepsilon_j) = \rho_\varepsilon$
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	$\kappa = 0, 8$

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 S1). In our study, we define beta diversity (β_D) in a multiplicative way, i.e. as the ratio of gamma diversity to alpha diversity: $\beta_D = \gamma_D/\alpha_D$. 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 ($\alpha_{D'}$) is the mean species richness across local communities, and richness-based gamma diversity ($\gamma_{D'}$) is the species richness of the whole metacommunity. Again, richness-based beta diversity ($\beta_{D'}$) 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 eqn 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_{il}). 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_{il}).

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 and Appendix S2). 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: $\alpha_D = 1 \Big/ \sum_i \left(\frac{K_{il}}{\sum_i K_{il}} \right)^2$ and $\gamma_D = 1 \Big/ \sum_i \left(\frac{\sum_l K_{il}}{\sum_{i,l} K_{il}} \right)^2$, respectively (see Appendix S2), 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 S3).

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 five species are generalists, which are shared and disperse between the two patches; the other 10 species (five 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 S4). 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 eqn 1 (see details in Appendix S4). 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 5000 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 1000 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 S2):

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

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

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

Note that in these equations, beta diversity (β_D) always lies between 1 and m (see Appendix S1). Also, note 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 S2).

Equations (3–5) predict explicit links between diversity and ecosystem variability across scales, which are summarised in Fig. 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 S3). 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 (Fig. 1 and Fig. 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 (Fig. 1 and Fig. 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, high beta diversity can contribute to weakening the desynchronising 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 stabilising effect at the local scale (Fig. 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 (Fig. 2). Furthermore, the stabilising 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) (Fig. 2). Here, the stabilising 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 S3).

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 (Fig. 1 and Fig. S1). Similarly, the stabilising
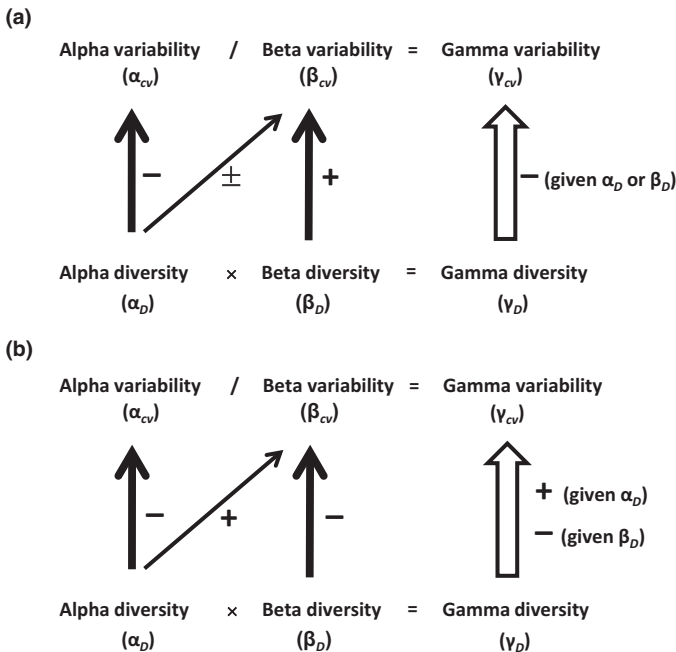

Figure 1 Diversity-variability relationships across scales predicted by the analytic solutions: (a) when $1 + \kappa^2\sigma_\eta^2\rho_\eta > 0$ (i.e. $\rho_\eta > 0$ or κ is small), and (b) when $1 + \kappa^2\sigma_\eta^2\rho_\eta < 0$ (i.e. $\rho_\eta < 0$ and κ is large). Except for the alpha scale, 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.
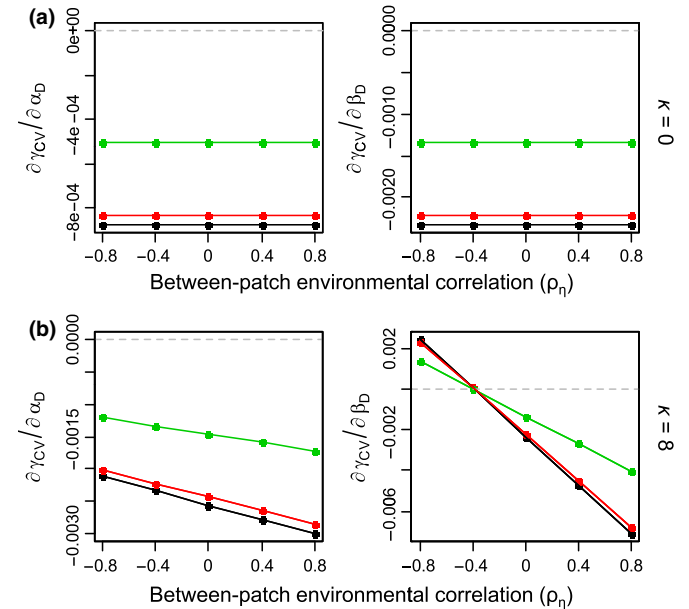
Figure 2 Effects of between-patch environmental correlation (ρ_η), between-species environmental correlation (ρ_ε) and the strength of the interaction between patch- and species-specific environmental responses (κ) on the derivative of gamma variability to diversity from the analytic solutions: (a) $\kappa = 0$, (b) $\kappa = 8$. Minus the derivative represents the strength of the stabilising effect of diversity. Parameters: $m = 2$, $r = 1$, $\sigma_\eta^2 = 0.04$, $\sigma_\varepsilon^2 = 0.04$, and $\rho_\varepsilon = -0.05$ (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.

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 S3).

Finally, the analytical solutions (i.e. eqn 5) also predict that under a given gamma diversity, gamma variability is influenced by the spatial pattern of biodiversity (Appendix S3). 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) (Fig. 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 (Fig. 3 and Fig. S5).

Overall, the simulated diversity–variability relationships were generally consistent with predictions from the analytically tractable limiting case (compare Fig. 4 vs. Fig. 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 (ρ_ε, ρ_η, κ), exhibited qualitatively similar patterns as the analytic predictions in Fig. 1. Moreover, just as predicted by the analytic

solutions, the stabilising 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 $\kappa > 0$ (Fig. 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 (Fig. 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
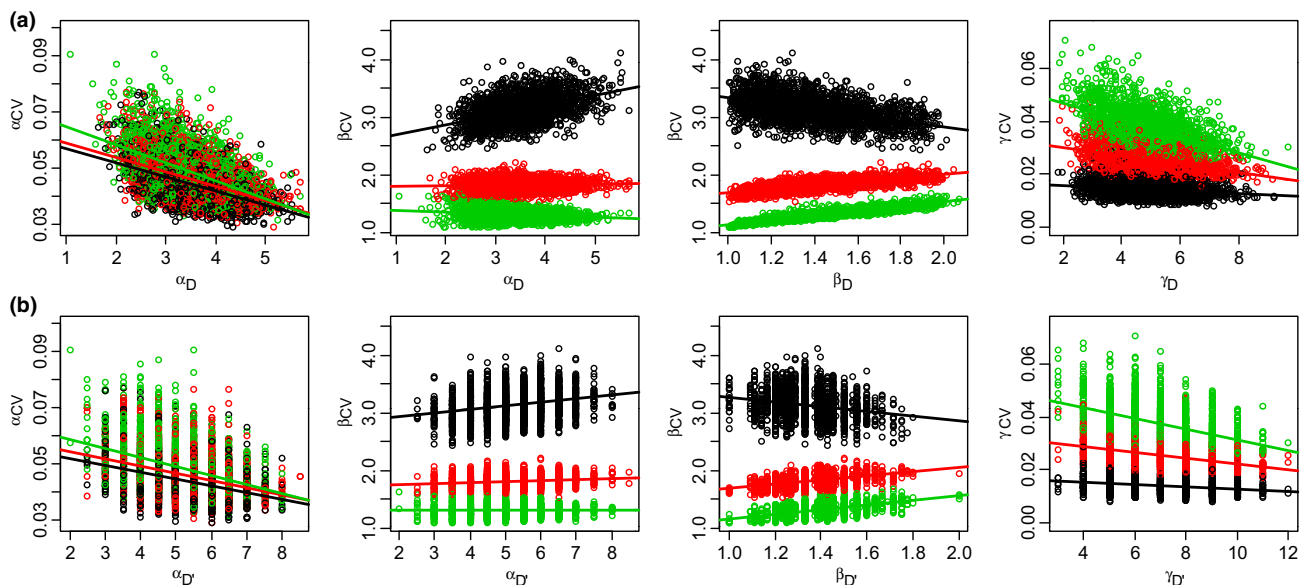

Figure 3 Diversity–variability relationships across scales in simulated metacommunities: (a) ENS-based diversity; (b) richness-based diversity. Parameters: $\kappa = 8$, $\rho_\varepsilon = 0$, $\rho_\eta = -0.8$ (black), 0 (red), and 0.8 (green), and others in Table 1. Lines represent least-square fits under respective scenarios. See Figure S3 for parallel results under $\kappa = 0$.
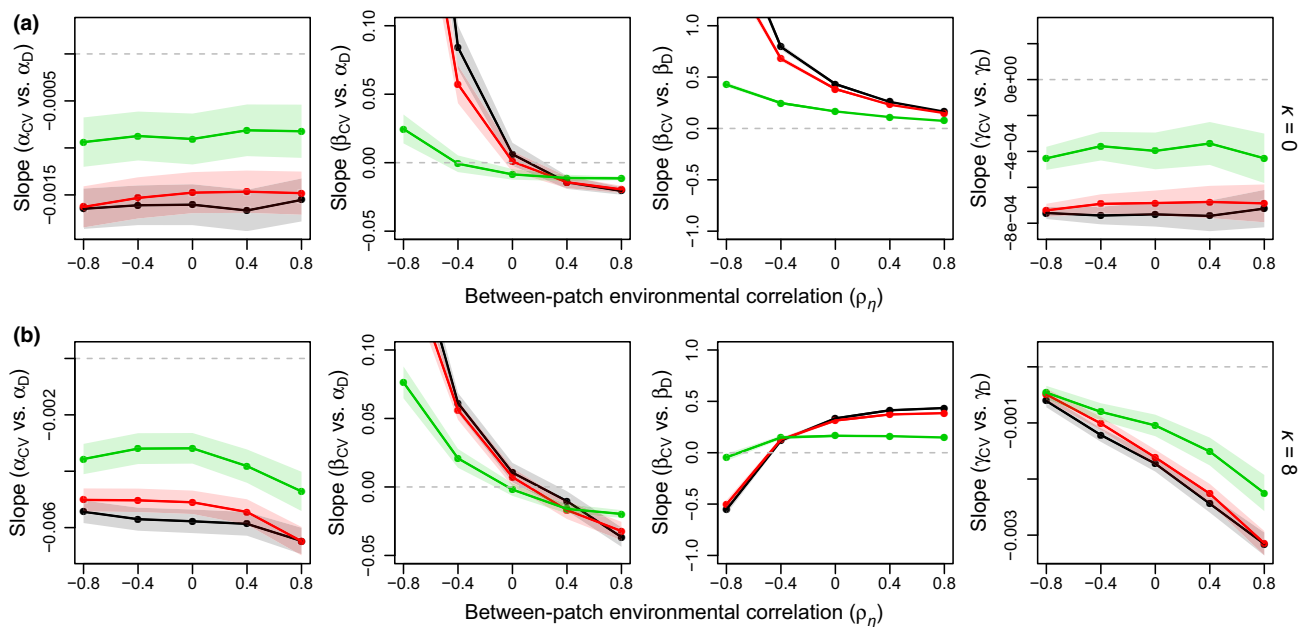
Figure 4 Effects of between-patch environmental correlation (ρ_η), between-species environmental correlation (ρ_ε) and the strength of the interaction between patch- and species-specific environmental responses (κ) on the regression slopes between variability and diversity in simulated metacommunities: (a) $\kappa = 0$, (b) $\kappa = 8$. Each point represents a regression slope between respective variables calculated from 2000 simulated metacommunities (e.g. scatters shown in Figure 3). Polygons represent the 95% confidence intervals. Parameters: $\rho_\varepsilon = -0.05$ (black), 0 (red), and 0.4 (green), and others in Table 1. The results shown here correspond to ENS-based diversity; see Figures S4 for parallel results for richness-based diversity.

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 constrains (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 (Fig. 1a). This is consistent with recent experimental results that a larger compositional dissimilarity among local communities can increase spatial asynchrony (France & Duffy 2006).

The effects of diversity on alpha and beta variability determine their effects on gamma variability (Wang & Loreau 2014). While stabilising 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 (Fig. 2 and Fig. S6), implying that the local stabilising (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 stabilising effects on regional ecosystem properties. As a consequence, both local biodiversity loss and biotic homogenisation impair the stability of large-scale ecosystem properties.

Although alpha and beta diversity provide stabilising effects through similar mechanisms (i.e. local and spatial insurance, respectively), these mechanisms operate at different scales and differ in the strength of their stabilising 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) (Fig. S8). Therefore, the stability of regional ecosystems is not solely determined by the richness and abundance distribution of species (i.e. gamma diversity), but also by their spatial distribution (i.e. 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 stabilising effects of alpha and beta diversity on gamma variability increases with between-patch environmental correlation (Fig. 2 and Fig. 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. desynchronising) 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 synchronising effects (Moran
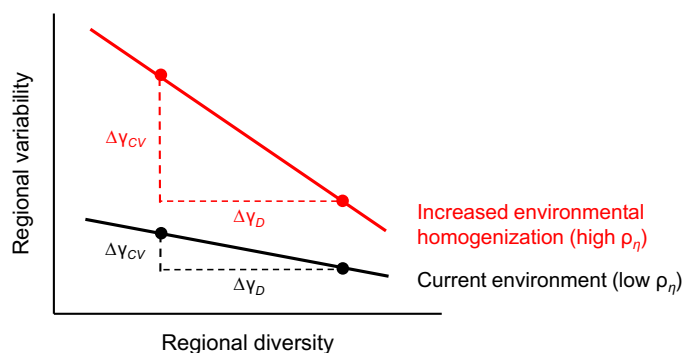
Figure 5 Effect of biodiversity loss on ecosystem stability at the regional scale, under different scenarios of positive spatial environmental correlations. Global environmental changes may increase environmental homogenisation and thus spatial environmental correlation (ρ_η). Under a higher ρ_η, the same amount of biodiversity loss ($\Delta\gamma_D$) can cause a higher increase of ecosystem variability ($\Delta\gamma_{CV}$).

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 (Fig. 5). Therefore, if global changes such as climate warming and nitrogen deposition cause increased environmental homogenisation (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 destabilising effects of biodiversity loss when it occurs (Fig. 5).

Our results also suggest that ENS-based diversity measures provide better predictions on the effects of diversity on ecosystem stability than richness-based ones (Fig. 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 stabilise 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 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 multiscale framework and makes new predictions on the consequences of large-scale biodiversity loss and environmental homogenisation. Our results demonstrate that biodiversity loss, both in the form of local diversity declines and in the form of biotic homogenisation, impair the stability of natural ecosystems at large scales. Moreover, the destabilising effect of biodiversity loss can be more pronounced when the environment is homogenised. 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.

AUTHORSHIP

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

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