

## IDEA AND PERSPECTIVE

### Ecosystem stability in space: $\alpha$ , $\beta$ and $\gamma$ variability

Shaopeng Wang\* and Michel Loreau

Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du CNRS, 09200, Moulis, France

\*Correspondence: E-mail: shaopeng.wang@ecoex-moulis.cnrs.fr

#### Abstract

The past two decades have seen great progress in understanding the mechanisms of ecosystem stability in local ecological systems. There is, however, an urgent need to extend existing knowledge to larger spatial scales to match the scale of management and conservation. Here, we develop a general theoretical framework to study the stability and variability of ecosystems at multiple scales. Analogously to the partitioning of biodiversity, we propose the concepts of alpha, beta and gamma variability. Gamma variability at regional (metacommunity) scale can be partitioned into local alpha variability and spatial beta variability, either multiplicatively or additively. On average, variability decreases from local to regional scales, which creates a negative variability–area relationship. Our partitioning framework suggests that mechanisms of regional ecosystem stability can be understood by investigating the influence of ecological factors on alpha and beta variability. Diversity can provide insurance effects at the various levels of variability, thus generating alpha, beta and gamma diversity–stability relationships. As a consequence, the loss of biodiversity and habitat impairs ecosystem stability at the regional scale. Overall, our framework enables a synthetic understanding of ecosystem stability at multiple scales and has practical implications for landscape management.

#### Keywords

Diversity partitioning, diversity–stability relationship, hierarchical theory, insurance hypothesis, metacommunity, spatial synchrony, species synchrony, variability partitioning, variability–area relationship.

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#### INTRODUCTION

Understanding the mechanisms governing ecosystem stability is essential for predicting the consequences of global environmental changes on ecosystem functioning and sustainability. During the past two decades, substantial efforts have been devoted to exploring the relationship between biodiversity and ecosystem functioning, stability and services (Loreau *et al.* 2001, 2002; Kinzig *et al.* 2002; Naeem *et al.* 2009). There is mounting evidence from experimental studies that biodiversity loss impairs and destabilises ecosystem functioning (Hector *et al.* 1999, 2010; Tilman 1999; Tilman *et al.* 2006; Cardinale *et al.* 2012). New theories have been developed to understand the stabilising effect of biodiversity on aggregate ecosystem properties (Doak *et al.* 1998; Tilman *et al.* 1998; Ives *et al.* 1999; Yachi & Loreau 1999; McCann 2000; Ives & Carpenter 2007; Loreau & de Mazancourt 2008, 2013; Thibaut & Connolly 2013). These theories generated hypotheses such as the portfolio effect (Doak *et al.* 1998; Tilman *et al.* 1998) and the insurance hypothesis (Yachi & Loreau 1999), which both borrow metaphors from financial management and make similar predictions (Loreau 2010). Underlying the stabilising effect of biodiversity in most theories and hypotheses is the fact that different species exhibit asynchronous dynamics due to their differential responses to environmental fluctuations and/or other forms of stochasticity (Ives *et al.* 1999; Bai *et al.* 2004; Loreau & de Mazancourt 2008, 2013; Hautier *et al.* 2014), although other mechanisms are also possible (de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013). These findings have greatly advanced our understanding on the stability of ecosystem functioning in

local ecological systems. Given that management decisions are often made at the landscape scale, however, it is critical to extend the current knowledge on ecosystem stability to larger spatial scales. This is particularly urgent considering the current high rates of habitat alteration (Vitousek 1994; Foley *et al.* 2005).

At large spatial scales, the stability of ecosystem functioning may be regulated by other mechanisms. First, in the same way as local diversity enhances the stability of local ecosystems, spatial compositional differences ( $\beta$  diversity) may reduce the variability of ecosystem functioning at regional scales (Aragón *et al.* 2011; Pasari *et al.* 2013). One recent study found that higher  $\beta$  diversity could also decrease the temporal turnover in community structure (Mellin *et al.* 2014). This suggests that  $\beta$  diversity may provide a spatial version of the insurance effect (Loreau *et al.* 2003a; Pasari *et al.* 2013). Furthermore, within a spatial context, dispersal can have strong influences on the dynamics and functioning of ecosystems (Loreau *et al.* 2003a,b). Dispersal can stabilise ecosystem properties directly through a spatial averaging effect or indirectly by maintaining higher species diversity (Loreau *et al.* 2003a). Consequently, habitat destruction and fragmentation, which are major drivers of species extinctions, might increase the variability of ecosystems and reduce their resilience to disturbances (Fahrig 2003; Foley *et al.* 2005). Despite these theoretical insights, a general framework has yet to be developed to understand the mechanisms of ecosystem stability at large scales.

During the past decade, theoretical efforts have extended research to metacommunities and metaecosystems, which

designate sets of communities and ecosystems, respectively, that are spatially distinct but connected by dispersal or movement of abiotic entities (Loreau *et al.* 2003b; Leibold *et al.* 2004). Many issues that were studied previously at local scales – such as the coexistence of species, the assembly and functioning of food webs and ecosystem functioning – are being reexamined within the context of metacommunity and metaecosystem theories (Loreau *et al.* 2003a,b; Leibold *et al.* 2004; Holyoak *et al.* 2005; Loreau 2010; Logue *et al.* 2011). The metacommunity and metaecosystem approaches provide an ideal framework to study ecosystem stability at multiple spatial scales and to investigate the effects of biodiversity and habitat changes.

Within a metacommunity or metaecosystem, ecosystem properties vary both temporally and spatially. Stability can thus be defined in various dimensions: temporal stability of local communities, temporal stability of metacommunities and spatial stability among local communities. These different dimensions of stability are likely to be mutually related. First, spatial variability in population dynamics can generate an insurance effect that enhances the temporal stability of metapopulations (Schindler *et al.* 2010; Anderson *et al.* 2013; Thorson *et al.* 2014). For instance, the spatial population diversity of Bristol Bay salmon reduces the temporal variability of annual yields to only half that in a single homogeneous population (Schindler *et al.* 2010). Second, ecological processes regulating one dimension of stability can affect another

dimension simultaneously. Biodiversity not only stabilises temporal dynamics of local communities and metacommunities, it also affects the spatial stability of ecosystem properties (Fukami *et al.* 2001; France & Duffy 2006; Weigelt *et al.* 2008). Dispersal can enhance both the temporal stability of ecosystems within local communities (Mellin *et al.* 2010; Abbott 2011; Steiner *et al.* 2011) and the spatial stability among communities (Liebhold *et al.* 2004; France & Duffy 2006). Finally, environmental correlation synchronises population dynamics in space through the Moran effect (Hudson & Cattadori 1999; Liebhold *et al.* 2004), which consequently increases the spatial stability but reduces the temporal stability of metacommunities (Steiner *et al.* 2011, 2013).

In this study, we develop a general framework to explore the multiscale stability of aggregate ecosystem properties in metacommunities. We regard local communities and metacommunities as representing local and regional scales respectively. Stability is measured specifically by a lower variability, which is defined as the squared coefficient of variation (the ratio of the variance to the squared mean) of biomass (Pimm 1984). We propose the concepts of alpha, beta and gamma variability that establish an explicit link between the various dimensions of ecosystem stability. We also propose the variability–area relationship to illustrate the scale dependence of stability. We then present a simple statistical model of metacommunities to explore how different ecological factors affect ecosystem stability at different scales. We end up with a

**Table 1** Notations summary

Symbol	Description
$m$	Number of local patches in the metacommunity
$N_i(t)$	Community biomass in patch $i$ at time $t$
$\mu_i$	Temporal mean of community biomass in patch $i$
$w_{ij}$	Temporal covariance of community biomass between patches $i$ and $j$
$\mu_M = \sum_i \mu_i$	Temporal mean of metacommunity biomass
$\bar{\mu} = \sum_i \mu_i / m$	Regional average of temporal means of local community biomass
$\sqrt{w} = \sum_i \sqrt{w_{ii}} / m$	Regional average of temporal standard derivations of local community biomass
$CV_i = \frac{\sqrt{w_{ii}}}{\mu_i}$	Coefficient of temporal variation of community biomass in patch $i$
$CV_L = \frac{\sum_i \mu_i \sqrt{w_{ii}}}{\mu_M}$	Weighted average of coefficients of temporal variation across local patches
$CV_M = \frac{\sqrt{\sum_{ij} w_{ij}}}{\mu_M}$	Coefficient of temporal variation of metacommunity biomass
$CV_S^2 = CV_{S,uneven}^2 + CV_{S,asyn}^2$	Spatial variability: squared coefficient of spatial variation
$CV_{S,uneven}^2 = \frac{\sum_i [(\mu_i - \bar{\mu})^2 + (\sqrt{w_{ii}} - \sqrt{w})^2]}{m\bar{\mu}^2}$	Spatial variability solely due to spatial biomass unevenness
$CV_{S,asyn}^2 = \frac{\sqrt{w}^2 - \sum_{ij} w_{ij} / m^2}{\bar{\mu}^2}$	Spatial variability that is related to spatial asynchrony (but also affected by spatial unevenness)
$\phi = \frac{\sum_{ij} w_{ij}}{(\sum_i \sqrt{w_{ii}})^2}$	Spatial synchrony among local patches
$CV_{Species}^2$	Species-level variability within local patches: squared coefficient of temporal variation of species biomass
$\phi_{species}$	Species synchrony within local patches
$\alpha_{CV} = CV_L^2$	Alpha variability: temporal variability at local scale
$\beta_1 = 1/\phi$	Multiplicative beta variability: spatial asynchrony or the reciprocal of spatial synchrony
$\beta_2 = CV_{S,asyn}^2$	Additive beta variability: asynchrony-related spatial variability
$\gamma_{CV} = CV_M^2$	Gamma variability: temporal variability at the metacommunity scale

discussion about the implications of our framework for understanding ecosystem stability across scales and for predicting the consequences of global changes.

## A GENERAL FRAMEWORK FOR ECOSYSTEM STABILITY IN SPACE

We consider a metacommunity composed of  $m$  local communities (or patches), the dynamics of which have reached a stationary state. The temporal dynamics of the metacommunity can be described by a stationary random vector:  $\mathbf{N}(t) = (N_1(t), N_2(t), \dots, N_m(t))$ , where  $N_i(t)$  denotes community biomass, i.e. the total biomass of all individuals, in patch  $i$  at time  $t$ . The variability of the metacommunity at multiple scales can then be defined by the mean  $\boldsymbol{\mu} = (\mu_1, \mu_2, \dots, \mu_m)$  and covariance matrix  $\mathbf{W} = (w_{ij})$  of  $\mathbf{N}(t)$  (Table 1).

### Definition of temporal and spatial variability

For the  $i$ -th local community, temporal variability is calculated as the coefficient of temporal variation of its biomass, i.e.  $CV_i = \sqrt{w_{ii}}/\mu_i$ . We then define local-scale temporal variability by the weighted average of this coefficient across local patches:

$$CV_L = \sum_i \frac{\mu_i}{\mu_M} \cdot CV_i = \frac{\sum_i \sqrt{w_{ii}}}{\mu_M} \quad (1)$$

where  $\mu_M = \sum_i \mu_i$  is the temporal mean of the total metacommunity biomass. At the metacommunity scale, temporal variability is similarly defined as the coefficient of temporal variation of metacommunity biomass:

$$CV_M = \frac{\sqrt{\sum_{i,j} w_{ij}}}{\mu_M} \quad (2)$$

where  $\sum_{i,j} w_{ij}$  gives the temporal variance of the total metacommunity biomass. In the following, for convenience, we use the squared coefficients of temporal variations at local ( $CV_L^2$ ) and metacommunity ( $CV_M^2$ ) scales to represent local and regional (or metacommunity) variability respectively.

At a fixed time  $t$ , we can also calculate the spatial variance among local patches:  $V_S(t) = \sum_i (N_i(t) - \bar{N}(t))^2 / m$ , where  $\bar{N}(t) = \sum_i N_i(t) / m$  is the average biomass of local communities at time  $t$ . We derive its temporal expectation:  $v_S = E(V_S(t))$ , based on which we define spatial variability as follows (see Appendix S1 for derivation):

$$CV_S^2 = \frac{v_S}{\bar{\mu}^2} = \frac{\overline{w}^2 - \frac{1}{m^2} \sum_{i,j} w_{ij} + \frac{1}{m} \sum_i [(\mu_i - \bar{\mu})^2 + (\sqrt{w_{ii}} - \overline{\sqrt{w}})^2]}{\bar{\mu}^2} \quad (3)$$

where  $\bar{\mu} = \sum_i \mu_i / m$  and  $\overline{\sqrt{w}} = \sum_i \sqrt{w_{ii}} / m$  represent the spatial averages of the temporal mean and standard deviation, respectively, of local community biomass.

Spatial variability arises from two factors: biomass unevenness among patches and asynchronous dynamics among patches. By biomass unevenness, we mean any spatial or

interspecific variation in the mean and/or variance of biomass. Spatial biomass unevenness can result from spatial heterogeneities in patch properties (e.g. patch size, soil fertility, intensity of environmental fluctuations, etc.). When the dynamics of all patches are perfectly correlated (the correlation coefficient between any two patches equals one, i.e.  $w_{ij} = \sqrt{w_{ii}w_{jj}}$ ), spatial variability is (see Appendix S1):

$$CV_{S,uneven}^2 = \frac{\sum_i [(\mu_i - \bar{\mu})^2 + (\sqrt{w_{ii}} - \overline{\sqrt{w}})^2]}{m\bar{\mu}^2} \quad (4)$$

which is solely caused by spatial unevenness. When the dynamics are at least partially asynchronous, this asynchrony can further increase the spatial variability through the additional term:

$$CV_{S,asyn}^2 = CV_S^2 - CV_{S,uneven}^2 = \frac{\overline{w}^2 - \sum_{i,j} w_{ij} / m^2}{\bar{\mu}^2} \quad (5)$$

We call this term as the asynchrony-related spatial variability ( $CV_{S,asyn}^2$ ). In homogeneous metacommunities where all patches have identical mean and variance of biomass,  $CV_{S,asyn}^2$  results solely from spatially asynchronous dynamics; otherwise, it is also influenced by spatial biomass unevenness. We analyse the effects of spatial unevenness in detail in Appendix S2.

### Linking variability across multiple scales

Following Loreau & de Mazancourt's (2008) definition of species synchrony, we define an equivalent index of spatial synchrony:  $\phi = \frac{\sum_{i,j} w_{ij}}{(\sum_i \sqrt{w_{ii}})^2}$ , which takes values between 0 and 1.

The local and metacommunity variability are then easily linked by:

$$CV_M^2 = CV_L^2 \cdot \phi \quad (6)$$

Interestingly, spatial synchrony serves as a scaling factor that scales temporal variability from local to regional scales. The more local communities fluctuate synchronously, the higher the variability of the metacommunity. Note that a similar formula was recently derived to describe the relationship between community variability and population variability (Thibaut & Connolly 2013).

Following eqns (3–5), spatial variability can also be linked to local variability through spatial synchrony (see Appendix S1):

$$CV_S^2 = CV_L^2 \cdot (1 - \phi) + CV_{S,uneven}^2 \quad (7)$$

or

$$CV_{S,asyn}^2 = CV_L^2 \cdot (1 - \phi) \quad (8)$$

Combining eqns (6) and (8), we obtain:

$$CV_M^2 + CV_{S,asyn}^2 = CV_L^2 \quad (9)$$

In particular, when local communities have identical mean and variance of biomass ( $CV_{S,uneven}^2 = 0$  and  $CV_S^2 = CV_{S,asyn}^2$ ), we have  $CV_M^2 + CV_S^2 = CV_L^2$ .

Equation (9) establishes an additive relationship between regional and local variability, the difference of which corresponds to the asynchrony-related spatial variability ( $CV_{S,asyn}^2$ ). For simplicity, unless otherwise stated, spatial variability will henceforth refer to  $CV_{S,asyn}^2$ . In other words, the temporal variability of local communities ( $CV_L^2$ ) can be partitioned into two additive components corresponding to the temporal ( $CV_M^2$ ) and spatial ( $CV_{S,asyn}^2$ ) variability of the metacommunity, the relative weights of which are determined by spatial synchrony ( $\phi$  and  $1 - \phi$ , respectively; see eqns 6 and 8). Note again that an analogous additive partitioning can be obtained for local competitive communities. In local competitive communities, species-level variability can be partitioned additively into two components corresponding to community-level variability and asynchrony-related between-species variability, the relative weights of which are determined by species synchrony.

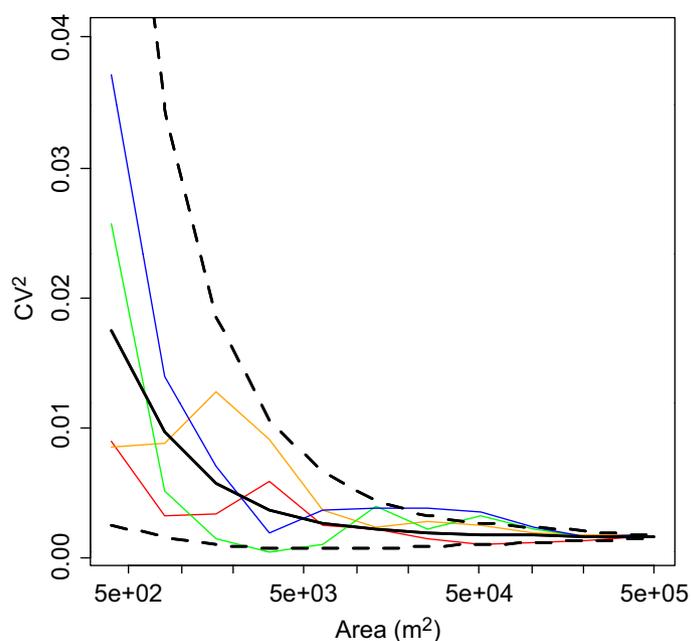
In biodiversity studies, ecologists have developed the concepts of alpha, beta and gamma diversity to study species diversity in space (Whittaker 1972). The regional (or gamma) diversity can be partitioned into local (or alpha) diversity and beta diversity components, either multiplicatively or additively (Whittaker 1972; Lande 1996; Loreau 2000; Chao *et al.* 2012). If we define the squared coefficients of variation at regional and local scales as gamma ( $\gamma_{cv} = CV_M^2$ ) and alpha ( $\alpha_{cv} = CV_L^2$ ) variability, respectively, we can similarly develop multiplicative and additive partitioning frameworks for variability by rewriting eqns (6) and (9) as:

$$\gamma_{cv} = \alpha_{cv} / \beta_1 \quad (10)$$

$$\gamma_{cv} = \alpha_{cv} - \beta_2 \quad (11)$$

Here  $\beta_1 = 1/\phi$  and  $\beta_2 = CV_{S,asyn}^2$ , which represent spatial asynchrony and asynchrony-related spatial variability respectively. We call both of them beta variability. Equations (10) and (11) thus provide multiplicative and additive partitions, respectively, of gamma variability into alpha variability and beta variability. Equation (8) shows that additive beta variability depends on alpha variability and multiplicative beta variability:  $\beta_2 = \alpha_{cv} \cdot (1 - 1/\beta_1)$ . In contrast to diversity, which increases with spatial scale such that gamma diversity is always larger than alpha diversity, variability decreases with spatial scale such that gamma variability is always smaller than alpha variability. Therefore, the two indices of beta variability above measure how much variability is reduced from local to regional scales.

The negative scale dependence of ecosystem variability creates a declining variability-area relationship, i.e. an increasing stability-area relationship. Note that the decrease in variability, or the increase in stability, from local to regional scales is a trend that holds on average, recalling that alpha variability is calculated from the weighted average across local patches (eqn 1). But this relationship can fluctuate for specific plots of increasing size. As an illustration, we examine the variability-area relationship within a 50-hectare plot ( $1000 \times 500 \text{ m}^2$ ) in the tropical moist forest of Barro Colorado Island, Panama. This plot was surveyed seven times during the past 30 years (nearly every 5 years), and has been widely employed to investigate community patterns and dynamics (Hubbell *et al.* 1999; Condit *et al.* 2012). In the absence of biomass data, we use the



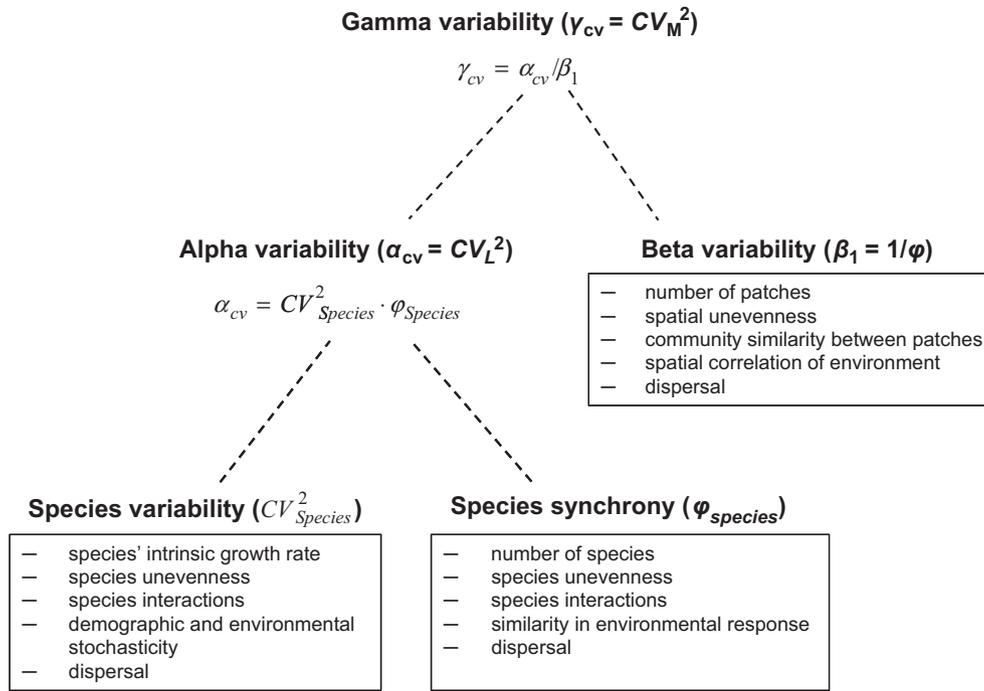
**Figure 1** Variability-area relationship in the 50-hectare plot of tropical forest in Barro Colorado Island, Panama. Variability is calculated as the squared coefficient of temporal variation of community abundance during the seven surveys, where we only consider tree individuals with diameter at breast height larger than 10 cm. The black solid and dashed lines represent the average (weighted by community abundance) and 2.5% and 97.5% quantiles of the 10 000 random samples respectively. The four coloured lines show variability-area relationships for nested subplots starting from the four corners of the 50-hectare plot.

number of individuals as a surrogate for biomass. We find that when subplots are sampled randomly within the large plot, the average variability of community abundance declines monotonically with increasing sampling area (Fig. 1). However, for the four series of nested subplots each starting from one corner to the whole plot, none exhibits a consistently declining variability-area relationship; instead, larger subplots can exhibit higher variability than their nested subplots (Fig. 1).

### A hierarchical perspective on metacommunity variability

In the previous section, we showed that metacommunity variability can be partitioned into two components: local alpha variability and spatial beta variability. As mentioned above, the local alpha variability can be further partitioned into species-level variability and between-species variability (see also Thibaut & Connolly 2013, which derived a multiplicative partition). The temporal variability of metacommunities can thus be partitioned hierarchically into within-patch species-level variability and between-species variability, and between-patch variability (i.e. beta variability). Again, this partitioning can be either additive or multiplicative. Since the additive beta variability depends on the multiplicative beta variability ( $\beta_2 = \alpha_{cv} \cdot (1 - 1/\beta_1)$ ), here we adopt the multiplicative partitioning to present our hierarchical framework.

In this framework, the variability of a metacommunity is determined by species-level variability and species synchrony within local patches, and spatial synchrony among patches



**Figure 2** A hierarchical framework of ecosystem variability in homogeneous metacommunities, where all local communities have identical species richness and identical mean and covariance of species biomass. Each box summarises several ecological factors (including species and spatial unevenness) that influence the variability or synchrony at that hierarchical level. See Fig. S1 for a more complex framework in the case of heterogeneous metacommunities, which shows the effects of biomass unevenness among species and among local communities.

(Fig. 2 and Fig. S1). This suggests that the mechanisms responsible for regional ecosystem stability can be understood by investigating the influence of ecological factors on these three components. In Fig. 2, we summarise some of the main factors that influence each component based on previous studies. In particular, species unevenness is known to affect the weighted averages of species-level variability and species synchrony (Thibaut & Connolly 2013); similarly, spatial unevenness can affect the weighted averages of local-scale variability and spatial synchrony (as demonstrated by a single-species metapopulation model in Appendix S2) (Fig. S1). In the special case where all local communities have identical species richness and identical mean and covariance of species biomass, alpha variability is equivalent to the variability of any specific community, i.e.  $\alpha_{CV} = CV_{Species}^2 \cdot \varphi_{Species}$ , where  $CV_{Species}^2$  and  $\varphi_{Species}$  denote species-level variability and species synchrony within local communities respectively (Table 1) (Thibaut & Connolly 2013). The metacommunity variability can thus be expressed as:  $\gamma_{CV} = \alpha_{CV} / \beta_1 = CV_{Species}^2 \cdot \varphi_{species} \cdot \varphi$ . This equation shows how species asynchrony and spatial asynchrony contribute to stabilising aggregate metacommunity properties from local population dynamics. In the next section, we use a simple statistical model to explore how ecological factors may affect the variability of a metacommunity with perfect evenness.

**METACOMMUNITY VARIABILITY IN A STATISTICAL MODEL**

We consider a metacommunity of  $m$  local communities, which have identical community biomass ( $N_0$ ) and species

richness ( $S$ ). We make three assumptions to derive the three components in Fig. 2. First, in each local community, all species have identical mean biomass ( $\mu = N_0/S$ ), and the variance of species biomass ( $\sigma^2$ ) scales with the mean according to the power function:  $\sigma^2 = c\mu^z$  (Taylor 1961). This scaling relationship is affected by species' intrinsic growth rates, interspecific interactions and stochastic factors (Ives *et al.* 1999; Linnerud *et al.* 2013; Loreau & de Mazancourt 2013). Empirical data indicate that the scaling coefficient  $z$  generally lies between 1 and 2 (Taylor 1961; Tilman 1999). Theoretically, the two extremes can occur when population fluctuations are dominated by demographic ( $z = 1$ ) and environmental stochasticity ( $z = 2$ ) respectively (Loreau 2010; Linnerud *et al.* 2013). The species-level variability within local patches is derived as  $CV_{Species}^2 = \frac{\sigma^2}{\mu^2} = c \cdot \left(\frac{N_0}{S}\right)^{z-2}$ . Second, in local communities, the temporal correlation coefficient between the biomasses of any two species is  $\rho_s$ . This correlation is determined by a number of local biotic and abiotic factors. Whereas interspecific similarity in environmental responses tends to produce positive correlations (Ripa & Ives 2003), interspecific competition tends to cause negative correlations between species' population dynamics (Ives *et al.* 1999; Loreau & de Mazancourt 2008). Species synchrony within local patches is easily obtained as  $\varphi_{Species} = \frac{1+(S-1)\rho_s}{S}$  (Loreau 2010). Third, for any two communities, the temporal correlation coefficient between their biomasses is  $\rho_p$ . This correlation can be enhanced by spatial correlations in environmental fluctuations and dispersal (Kendall *et al.* 2000; Liebhold *et al.* 2004; Gouhier *et al.* 2010; Abbott 2011), and

compositional similarity (i.e. low beta diversity; Fukami *et al.* 2001). Spatial synchrony among patches is obtained as  $\varphi = \frac{1+(m-1)\rho_P}{m}$ . The variability at the various scales can then be expressed as follows:

$$\alpha_{CV} = CV_{Species}^2 \cdot \varphi_{Species} = c \cdot \left(\frac{N_0}{S}\right)^{z-2} \cdot \frac{1+(S-1)\rho_S}{S} \quad (12)$$

$$\beta_1 = \frac{1}{\varphi} = \frac{m}{1+(m-1)\rho_P} \quad (13)$$

$$\beta_2 = CV_{Species}^2 \cdot \varphi_{Species} \cdot (1-\varphi) = c \cdot \left(\frac{N_0}{S}\right)^{z-2} \cdot \frac{1+(S-1)\rho_S}{S} \cdot \frac{(m-1)(1-\rho_P)}{m} \quad (14)$$

$$\gamma_{CV} = CV_{Species}^2 \cdot \varphi_{Species} \cdot \varphi = c \cdot \left(\frac{N_0}{S}\right)^{z-2} \cdot \frac{1+(S-1)\rho_S}{S} \cdot \left[\rho_P + \frac{1-\rho_P}{m}\right] \quad (15)$$

Our statistical metacommunity model is a simple extension of previous statistical models of local communities. In particular, eqn (12) was derived previously to illustrate the insurance effect of local species diversity (Loreau 2010). Local species diversity represents diversity in both species identity (species richness) and dynamics (species independence). Here, with eqns (12–15), we are particularly interested in comparing the effects of local diversity *versus* spatial factors on alpha, beta and gamma variability. More specifically, we compare the effects of local species richness ( $S$ ) *versus* the number of patches ( $m$ ), and species correlation ( $\rho_S$ ) *versus* spatial correlation ( $\rho_P$ ).

Because local and spatial processes operate independently in our statistical model, alpha variability and multiplicative beta variability are affected solely by local diversity and spatial factors respectively (Fig. 3a–d). In local communities, species correlations consistently increase species synchrony ( $\varphi_{Species}$ ) and thus alpha variability ( $\alpha_{CV}$ ) (Fig. 3b). A higher species richness decreases species synchrony, but it also increases population variability ( $CV_{Species}^2$ ) when  $z < 2$ . In the special case of independent species dynamics ( $\rho_S = 0$ ), the first effect is predominant and species richness stabilises  $\alpha_{CV}$  (Fig. 3a). Recent studies suggested that species richness can be a destabilising factor when the scaling coefficient ( $z$ ) is small and the species correlation coefficient ( $\rho_S$ ) is large (Loreau 2010; Thiabaut & Connolly 2013). But these two assumptions can be mutually incompatible (Loreau 2010). Therefore, we only consider the case of independent species dynamics when analysing the effects of species richness.

A higher number of patches decreases, and spatial correlations increase, spatial synchrony. Consequently, both the multiplicative ( $\beta_1$ ) and additive ( $\beta_2$ ) measures of beta variability increase as the number of patches increases and/or spatial correlations decrease (Fig. 3c–f). Note that the positive relationship between beta variability and the number of patches holds not only for independent spatial dynamics ( $\rho_P = 0$ ), but more generally for any  $\rho_P < 1$  (eqn 13). Although it has no effect on  $\beta_1$ , local diversity affects  $\beta_2$  through its effect on  $\alpha_{CV}$ . A higher local richness decreases (Fig. 3e), and higher species correlations increase,  $\beta_2$  (Fig. 3f). Thus, local species richness

and the number of patches have opposite effects on  $\beta_2$ , just as do local species correlations and spatial correlations.

Despite their inconsistent effects on alpha and beta variability, local diversity and spatial factors have similar effects on gamma variability. A larger number of patches and a larger local species richness both reduce gamma variability, and higher species correlations and spatial correlations both increase gamma variability (Fig. 3g,h). If we regard metacommunities with a higher number of patches and lower spatial correlations as having a higher diversity, local diversity and spatial diversity thus provide similar insurance effects on large-scale stability. When local patch size is fixed, the number of patches,  $m$ , represents the total area of the metacommunity. Equation (15) thus provides a quantitative prediction for the variability–area relationship. By defining  $C_1 = \alpha_{CV} \cdot \rho_P$  and  $C_2 = \alpha_{CV} \cdot (1 - \rho_P)$ , we can rewrite eqn (15) as follows:

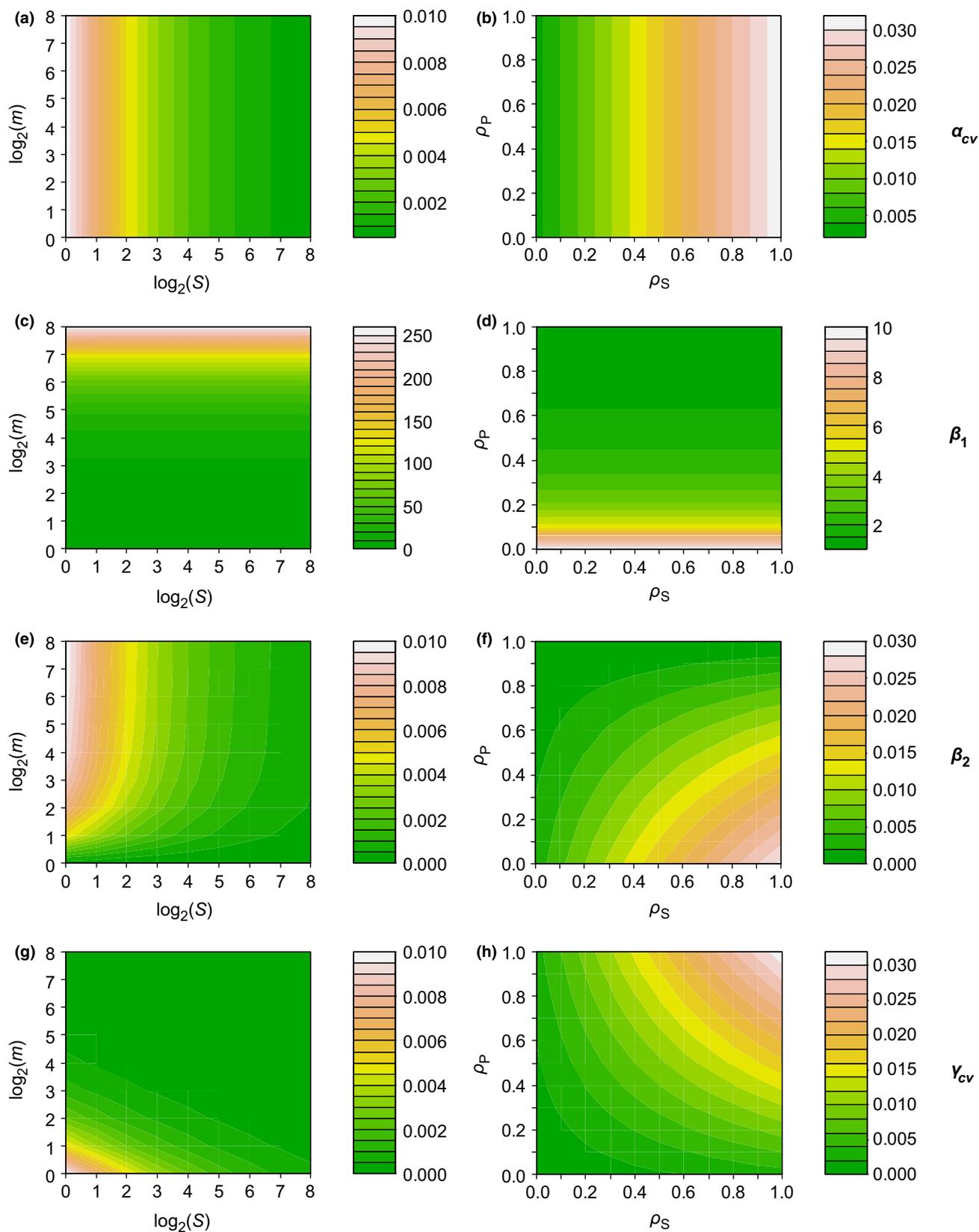
$$\gamma_{CV} = C_1 + \frac{C_2}{m} \quad (16)$$

Thus, gamma variability is inversely related to area. In particular, when communities fluctuate independently in space ( $\rho_P = 0$  and thus  $C_1 = 0$ ), gamma variability is inversely proportional to area:  $\gamma_{CV} = \frac{\alpha_{CV}}{m}$ .

## DISCUSSION

### A hierarchical perspective on ecosystem stability

In this study, we have developed a general framework to understand the stability and variability of ecosystems at multiple scales. Ecosystem variability at the regional (metacommunity) scale, which we call gamma variability, can be partitioned into local alpha variability and spatial beta variability. This partitioning framework for variability is analogous to that underlying the concepts of alpha, beta and gamma diversity (Whittaker 1972). In both frameworks, the alpha and gamma components represent properties at the local and regional scales respectively. While beta diversity represents the spatial variation in species composition, beta variability measures spatial variation in ecosystem dynamics. Just as in the partitioning of diversity (Lande 1996; Chao *et al.* 2012), the partitioning of gamma variability into its alpha and beta components can be either multiplicative or additive (eqns 8 and 9). Whereas the multiplicative beta term is dimensionless, the additive beta term is still a measure of variability (i.e. spatial variability) and is thus comparable to alpha and gamma variability. Also, just as with diversity (Chao *et al.* 2012), the additive beta variability ( $\beta_2$ ) depends on both alpha variability ( $\alpha_{CV}$ ) and multiplicative beta variability ( $\beta_1$ ). Specifically,  $\beta_2$  is a proportion of  $\alpha_{CV}$ , with the proportion given by  $1 - 1/\beta_1$ , i.e.  $\beta_2 = \alpha_{CV} \cdot (1 - 1/\beta_1)$ . But in contrast to beta diversity, which must be derived from alpha and gamma diversity, both measures of beta variability stand alone and can be calculated directly from empirical data. Furthermore, the partitioning of variability is scale dependent, just as is the partitioning of diversity (Loreau 2000). As the study system increases from local to regional scales, alpha variability converges on gamma variability and



**Figure 3** The effects of local diversity and spatial factors on alpha variability (a,b), multiplicative beta variability (c,d), additive beta variability (e,f) and gamma variability (g,h) in our statistical metacommunity model. (a, c, e, g) show the effects of local species richness ( $\log_2(S)$ ) versus number of patches ( $\log_2(m)$ ), and (b, d, f, h) show the effects of local species correlation ( $\rho_S$ ) versus spatial correlation ( $\rho_P$ ). Parameters are:  $N_0 = 10000$ ,  $c = 1$ ,  $z = 1.5$ ;  $\rho_S = \rho_P = 0$  for (a, c, e, g), and  $S = m = 10$  for (b, d, f, h).

beta variability converges on 1 ( $\beta_1$ ) or 0 ( $\beta_2$ ) (Fig. 1). One critical difference between the partitioning of diversity and that of variability, however, is that diversity increases with the spatial scale considered, whereas variability decreases from local to regional scales.

Our partitioning framework provides a hierarchical perspective on ecosystem stability. Just as variability can be partitioned in space, local alpha variability can be further partitioned into species-level variability and between-species variability (Fig. 2; see also Thibaut & Connolly 2013). From individual species to the local community and from local communities to the regional metacommunity, stability is enhanced by the diversity and asynchrony of lower level components (Fig. 2). In a recent study, Jørgensen & Nielsen (2013) summarised some of the implications of hierarchy theory for ecosystem stability. They concluded that stability should generally increase at higher hierarchical levels; they predicted more specifically that the ratio between variability at one hierarchical level and variability at the next higher level should be given by the square root of the number of lower level components (Jørgensen & Nielsen 2013). This result, however, relied on the assumption that within-level components have independent dynamics, which is a special case of our statistical metacommunity model (Fig. 3). When local communities fluctuate independently ( $\rho_p = 0$ ), our model predicts that the ratio between local variability and regional variability is equal to the number of local communities ( $\alpha_{CV}/\gamma_{CV} = m$ ), in agreement with Jørgensen & Nielsen (2013) (noting that variability in our study is defined as the square of the coefficient of variation). In general, however, the enhancement of stability as one moves from lower to higher hierarchical levels is determined not only by the number of lower level components but also by their correlations (eqns 12 and 15). The latter are particularly important to understand the consequences of large-scale disturbances. Large-scale disturbances occur less frequently than do small-scale disturbances (Jørgensen & Nielsen 2013) but when they do occur, they not only increase the variability of local ecosystems but also suddenly increase spatial synchrony, two factors that contribute to high variability at large scales. Thus, by including spatial (and species) synchrony explicitly, our hierarchical framework is more general and flexible than previous applications of hierarchy theory.

### Multiscale diversity–stability relationships

Our hierarchical framework suggests that the influence of local and spatial factors on regional ecosystem stability can be understood through their effects on alpha and beta variability, as demonstrated by our simple statistical model (Fig. 3). Such a perspective generalises previous findings from local ecosystem studies and single-species metapopulation studies, which explored how ecological factors affect local ecosystem stability and metapopulation dynamics respectively (as summarised in Fig. 2). More interestingly, the hierarchical framework implies multiscale diversity–stability relationships. Previous studies have highlighted the stabilising effects of diversity at the local scale (reviewed in Loreau & de Mazancourt 2013), and recent large-scale analyses have suggested that regional diversity can

similarly stabilise the dynamics of regional ecosystems (Aragón *et al.* 2011; Chalcraft 2013). Thus, previous studies have focused on the alpha and gamma components of the diversity–stability relationship. But for both diversity and stability, scale transition can be achieved by their beta component. It is therefore of great interest to understand how beta diversity affects beta variability. In general, a higher beta diversity means a lower community similarity and thus lower spatial correlations in ecosystem dynamics (Fukami *et al.* 2001; France & Duffy 2006), which consequently increases beta variability (Fig. 3). Such a positive relationship between beta diversity and beta variability suggests a negative beta diversity–stability relationship, contrasting to those at alpha and gamma scales. But, because beta variability measures how much temporal variability is reduced from local to regional scales (eqns 10 and 11), our framework implies that a higher beta diversity ultimately contributes to reducing gamma variability. Thus, similar to the insurance effect of alpha diversity, beta diversity provides a spatial insurance effect for regional ecosystem stability (Loreau *et al.* 2003a; Pasari *et al.* 2013). Therefore, biodiversity is important for ecosystem stability, not only through local diversity but also through spatial structure.

The spatial insurance hypothesis of biodiversity was proposed a decade ago (Loreau *et al.* 2003a). The concept of beta variability adds to this hypothesis by clarifying the link between beta diversity and gamma variability. In addition to beta diversity, other aspects of spatial diversity can also increase beta variability and thus provide insurance effects, such as landscape area and spatial environmental heterogeneity (Fig. 3). Therefore, the spatial insurance hypothesis can be generalised to include the effects of abiotic factors.

### Practical implications: predicting the consequences of biodiversity and habitat changes

Our hierarchical framework also has practical implications to predict the consequences of biodiversity loss and habitat alteration at the landscape scale. The destabilising effect of species loss has been widely documented at the local scale (Tilman *et al.* 2006; Hector *et al.* 2010; Cardinale *et al.* 2012). A recent meta-analysis, however, failed to reveal consistent net changes in local plant species diversity in nature, which the authors interpreted as negating the interest of biodiversity–ecosystem functioning relationships for biodiversity conservation (Vellend *et al.* 2013). Our multiscale diversity–stability framework shows that even if local diversity were not declining, the loss of biodiversity at larger spatial scales would weaken the stability of regional ecosystems due to reduced beta diversity. Therefore, the maintenance of ecosystem functioning at larger spatial scales might still be an important motivation for the conservation of global biodiversity.

Habitat loss is also expected to reduce the stability of ecosystem functioning. On average, ecosystem stability increases (or variability decreases) from local to regional scales, which generates a positive stability–area relationship (or a negative variability–area relationship) (Fig. 1). Our statistical metacommunity model provides a simple quantitative prediction for the variability–area relationship: under the assumption of

constant between-patch correlations, variability is inversely related to area (eqn 16). In reality, however, two processes can cause a steeper variability–area relationship, and hence a faster decline in stability following habitat loss. First, variations in the environment and in community composition generally increase with distance, exhibiting 1/f spectra (Halley 1996; Storch *et al.* 2002; Denny *et al.* 2004). Consequently, as area increases, the average spatial correlation ( $\rho_p$ ) should decrease. This generates stronger spatial asynchrony and insurance effects compared with those that result solely from increasing the number of patches, and consequently a faster decrease of variability as area increases (eqn 16). Second, habitat loss not only causes imminent extinction for species endemic to the destroyed habitats but also results in time-delayed species extinctions in remnant habitat fragments (Tilman *et al.* 1994; Gibson *et al.* 2013; Rybicki & Hanski 2013). Such an extinction debt can further destabilise large-scale ecosystems by increasing alpha variability and/or decreasing beta variability due to reduced species diversity.

## LIMITATIONS AND CONCLUSIONS

One important limitation of our simple statistical metacommunity model is the assumption that adding or eliminating one patch has no effect on others. In reality, landscapes are connected by the dispersal of organisms and movements of abiotic substances, such that spatial processes interact with local processes to regulate the diversity and functioning of ecosystems (Loreau *et al.* 2003a,b; France & Duffy 2006; Venail *et al.* 2008). Dispersal can simultaneously affect different levels of stability. On one hand, dispersal tends to synchronise spatial dynamics, and thus to reduce beta variability (Kendall *et al.* 2000; Liebhold *et al.* 2004; France & Duffy 2006; Abbott 2011). On the other hand, dispersal decreases the alpha variability of local communities by stabilising local population dynamics and reducing species synchrony (Loreau *et al.* 2003a; Abbott 2011; Steiner *et al.* 2011, 2013). Thus, the net effect of dispersal on gamma variability depends on its relative influences on alpha and beta variability, which can have contrasting outcomes (Loreau *et al.* 2003a; France & Duffy 2006; Howeth & Leibold 2010; Abbott 2011; Bouvier *et al.* 2012). Besides, although a higher beta diversity is expected to reduce the spatial correlations of community dynamics, an explicit link between these properties has yet to be established. Therefore, dynamical models are now required to better understand how local and spatial processes interact and affect metacommunity stability. By accounting for the delayed destabilising effects due to the extinction debt, dynamical models would also improve our ability to predict the consequences of habitat loss.

Current global environmental changes call for a synthetic understanding of the stability of ecosystem functioning (Loreau 2010). Our study proposes a general framework to study ecosystem stability at multiple scales. The concepts of alpha, beta and gamma variability extend existing knowledge on the diversity–stability relationships to a broader spatial context. The new hierarchical framework that we propose should contribute to advancing our understanding of macro-systems ecology (Heffernan *et al.* 2014). We hope that this

framework will stimulate a reanalysis of experimental data to evaluate diversity–stability relationships at alpha, beta and gamma scales, which in turn will improve our understanding of the ecological consequences of biodiversity loss. Future research should also develop dynamical models to understand how spatial and local processes interact to regulate ecosystem stability and to predict the ecological consequences of habitat loss and fragmentation. Such models are likely to have great practical implications for landscape management.

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## AUTHOR CONTRIBUTIONS

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

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