



ELSEVIER

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Biodiversity, productivity, and the spatial insurance hypothesis revisited

David W. Shanafelt^{1,a,*}, Ulf Dieckmann^{2,b}, Matthias Jonas^{3,b}, Oskar Franklin^{4,b}, Michel Loreau^{5,c}, Charles Perrings^{1,a}^a Arizona State University, School of Life Sciences, PO Box 874601, Tempe, AZ 85287, USA^b Schlossplatz 1, Laxenburg A-2361, Austria^c Station d'Ecologie Expérimentale du CNRS, 09200 Moulis, France

HIGHLIGHTS

- Environmental risk and variable dispersal rates in a Loreau spatial insurance model.
- Spatial correlation of environmental risk decreases stabilizing effect of dispersal.
- Dispersal maintains productivity though biodiversity and stability decline.

ARTICLE INFO

Article history:

Received 30 September 2014

Received in revised form

9 June 2015

Accepted 10 June 2015

Available online 20 June 2015

Keywords:

Dispersal

Stability

Stochasticity

Risk

ABSTRACT

Accelerating rates of biodiversity loss have led ecologists to explore the effects of species richness on ecosystem functioning and the flow of ecosystem services. One explanation of the relationship between biodiversity and ecosystem functioning lies in the spatial insurance hypothesis, which centers on the idea that productivity and stability increase with biodiversity in a temporally varying, spatially heterogeneous environment. However, there has been little work on the impact of dispersal where environmental risks are more or less spatially correlated, or where dispersal rates are variable. In this paper, we extend the original Loreau model to consider stochastic temporal variation in resource availability, which we refer to as "environmental risk", and heterogeneity in species dispersal rates. We find that asynchronies across communities and species provide community-level stabilizing effects on productivity, despite varying levels of species richness. Although intermediate dispersal rates play a role in mitigating risk, they are less effective in insuring productivity against global (metacommunity-level) than local (individual community-level) risks. These results are particularly interesting given the emergence of global sources of risk such as climate change or the closer integration of world markets. Our results offer deeper insights into the Loreau model and new perspectives on the effectiveness of spatial insurance in the face of environmental risks.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Accelerating rates of biodiversity loss have led ecologists to explore the effect of changes in species richness on ecosystem

functioning, and the resulting flow of ecosystem services (Cardinale et al., 2012). While some studies have evaluated the effect of species richness on mean levels of ecosystem functioning, most have focused on the impact of biodiversity on the variability of ecosystem functioning.⁶ Several mechanisms have been proposed including overyielding (Lehman and Tilman, 2001; Tilman, 1999), statistical averaging or the "portfolio effect" (Cottingham et al., 2001; Doak et al., 1998; Isbell et al., 2009; Tilman et al., 1998), compensatory dynamics (Gonzalez and Loreau, 2009; Lehman and Tilman, 2001) and the spatial insurance hypothesis (Ives et al., 2000;

* Corresponding author.

E-mail addresses: dshanafefe@asu.edu (D.W. Shanafelt), dieckmann@iiasa.ac.at (U. Dieckmann), jonas@iiasa.ac.at (M. Jonas), franklin@iiasa.ac.at (O. Franklin), michel.loreau@ecoex-moulis.cnrs.fr (M. Loreau), Charles.Perrings@asu.edu (C. Perrings).

¹ School of Life Sciences, Arizona State University.² Ecology and Evolution, International Institute for Applied Systems Analysis.³ Advanced Systems Analysis, International Institute for Applied Systems Analysis.⁴ Ecosystem Services and Management, International Institute for Applied Systems Analysis.⁵ Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du CNRS à Moulis.⁶ These mechanisms are typically broken down into selection and functional complementarity classes (Loreau and Hector, 2001; Loreau, 2010; Loreau et al., 2012). Selection mechanisms involve the Darwinian selection of species that generate biodiversity such as niche specialization or differentiation. Mechanisms of functional complementarity focus on the interactions between species, which are in effect the consequences of selection mechanisms.

McNaughton, 1977; Yachi and Loreau, 1999).⁷ The last of these centers on the idea that the functional complementarity of species across space and time insures the system against environmental risk (Loreau et al., 2003). Specifically, the greater the number and spatial distribution of species, and the greater the functional redundancy of species at particular locations, the more the system is protected against spatio-temporal environmental variability, including spatially distributed anthropogenic shocks. As the productivity of one species falls, others can fill its functional niche and maintain productivity. At the global scale, dispersal between communities provides source populations in which migrants may both replace extirpated local populations and maintain functional groups of species.

Empirical evidence on the role of spatial insurance in the relationship between biodiversity and the stability of productivity has been mixed. In microbial microcosms, community biomass and density have been shown to be more stable in systems with greater functional biodiversity (Naeem and Li, 1997). Regional zooplankton biodiversity coupled with immigration has, for example, been shown to dampen the effects of temperature warming on net primary productivity (Thompson and Shurin, 2012). In a broad scale statistical analysis, Valone and Barber (2008) tested for evidence of spatial insurance across multiple taxa. They found the greatest support for the hypothesis in plant taxa, but little or no support in rodent, avian, and ant systems. Other empirical studies have found that spatial insurance is less critical to system stability than other mechanisms such as statistical averaging or overyielding (Aragon et al., 2011; Tilman et al., 1998). From a theoretical perspective, several papers have identified conditions in which spatial insurance might be expected to stabilize productivity (Gonzalez et al., 2009; Ives et al., 2000; Loreau et al., 2003; Mouquet and Loreau, 2003). Mouquet and Loreau (2003) used a metacommunity approach to show that intermediate dispersal rates between communities experiencing asynchronous environmental fluctuations enhanced global and local biodiversity, productivity, and system stability. Species dispersal, as a mechanism for maintaining biodiversity, insures the metacommunity by stabilizing productivity.

Several theoretical papers have extended the spatial insurance hypothesis to consider the effects of competition structure (Filotas et al., 2010; Loreau and de Mazancourt, 2013), species adaptation (Urban, 2006), and trophic structure (Ives et al., 2000). However, little has so far been done to investigate the effect of dispersal where environmental conditions and dispersal rates vary over space and time, as they do in most real ecosystems. In this paper, we re-evaluate the original model constructed by Loreau et al. (2003) and extend the model to consider stochastic temporal variation in resource availability, which we define as "environmental risk", and consider the effect of heterogeneity in species dispersal rates.

Spatial variation in resource availability reflects differences in, for example, climatic conditions in distinct habitat patches or communities, while temporal variation reflects effects such as random fluctuations in temperature or precipitation. Climate change is projected to affect both temporal and spatial variation in conditions—increasing both the frequency of extreme climate events, and the spatial correlation between events (Intergovernmental Panel on Climate Change, 2013). One consequence is a change in the temporal consistency of resource availability. Availability of water (through droughts or flooding) and nutrients such as nitrogen or phosphorus (via erosion and/or deposition) may directly alter populations of

primary producers or consumers, the effects of which cascade to organisms of other trophic levels. Another is that events occurring in one part of the world have an effect at spatial locations much further away. This is reflected in, for example, the growing intensity and global effects of El Niño and La Niña (Intergovernmental Panel on Climate Change, 2013). While research has been conducted to test the effect of stochastic variation in resource availability across space and time, less attention has been paid to their effects jointly.

Heterogeneity of species dispersal rates reflects two sets of processes that have been demonstrated to play roles in regulating biodiversity in real world systems. First, heterogeneity in dispersal rates between locations reflects the fact that some areas are naturally more strongly connected than others, and that the connections between areas are frequently directional. Air and water flows, for example, affect the direction of natural dispersal. This means that some locations will act as sink populations for dispersers, and others will act as sources. Source-sink dynamics have, for example, been shown to play a role in maintaining diversity in fisheries in economics (Sanchirico and Wilen, 1999), and in conserving spatially distinct populations of wild species such as the checkerspot butterfly, (Harrison et al., 1988) snowshoe hare, (Griffin and Mills, 2009) and predatory reef fish, (Russ and Alcala, 2011). Second, not all species disperse equally, naturally or by people. Anthropogenic dispersal through international trade and travel preferentially selects for species that are either the direct objects of trade, or incidentally incorporated in packaging, or as hitch hikers on the ships, planes, trains or trucks used to transport goods and people from place to place. Trade and travel is frequently cited as a major facilitator of the worldwide spread of invasive species (Costello et al., 2007; Lenzen et al., 2012) and pathogens (Kilpatrick, 2011; Smith et al., 2007; Tatem et al., 2006a). The pattern of international trade and travel also determines where species are moved from and to, and in what quantities.

Introduced species have the potential to cause shifts in species composition, environmental processes, and the evolution of species populations (Chisholm, 2012). We test the effect of species dispersal on productivity under local risk factors (affecting a single community) and global risk factors (affecting the whole metacommunity) that may alter both biodiversity and ecosystem functioning. We find that asynchronies across communities and species provide metacommunity-level stabilizing effects on productivity, despite variability in species richness. Our work provides new testable hypotheses about the effectiveness of spatial insurance when community level risks are more or less spatially correlated.

2. The spatial insurance hypothesis: the Loreau model

2.1. Loreau model—construction

We assume the same dynamics as Loreau et al. (2003) and Gonzalez et al. (2009). Consider a meta community with M communities and S species. Within each community, species compete for a single limiting resource of which the quantity consumed varies by species, environmental conditions (influencing how species consume the limiting resource), and time. Communities are coupled together by the natural dispersal of species. When dispersal is low, each community functions as a separate closed system; with high dispersal the entire metacommunity functions as a single patch.

Formally, the change in species biomass N and resource biomass R in the j th community is governed by the set of equations:

$$\frac{dN_{ij}}{dt} = N_{ij}(t)(ec_{ij}(t)R_j(t) - m) - aN_{ij}(t) + \frac{a}{M-1} \sum_{k \neq j}^M N_{ik}(t) \quad (1)$$

⁷ Many of these mechanisms are interlinked, implicitly derived from the same underlying concept (Loreau, 2010). For instance, within a community of species, total community biomass will exhibit a variance that is a function of the variances of each individual species (statistical averaging) as well as the covariances between them (broadly termed the "covariance effect") (Lehman and Tilman, 2001). For a detailed review of the mechanisms contributing to biodiversity and stability, see (Tilman, 1999; McCann, 2000; Lehman and Tilman, 2001; Loreau, 2010; Loreau and de Mazancourt, 2013).

$$\frac{dR_j}{dt} = I - IR_j(t) - R_j(t) \sum_{i=1}^S c_{ij}(t) N_{ij}(t) \quad (2)$$

for species $i = 1, 2, \dots, S$ and communities $j = 1, 2, \dots, M$ at time t . Species are assumed to consume resources at the normalized rate $c_{ij}(t)$, convert resources to new biomass with efficiency e , and die at rate m . The limiting resource is assumed to increase in all communities by a fixed amount I and to be lost at a constant rate l . Initially, species are assumed to disperse between communities at a constant rate a . Species consumption of natural resources is a non-linear function of species-specific traits and environmental variation, fluctuating over time for each species in each community according to:

$$c_{ij}(t) = \frac{1.5 - |H_i - E_j(t)|}{10} \quad (3)$$

$$E_j(t) = \frac{1}{2} \left[\sin \left(x_j + \frac{2\pi t}{T} \right) + 1 \right] \quad (4)$$

where H_i is a dimensionless, species and community-dependent competition parameter such that $H_1 = 1$ and $H_i = H_{i-1} - \frac{1}{M}$ for $i = 2, \dots, S$. It is assumed that environmental conditions, E_j , vary temporally, fluctuating over time as a sinusoidal function. The phase parameter, x_j , is a random variable drawn from a uniform distribution $[-2\pi, 2\pi]$, which shifts the environmental variation along its horizontal axis (Fig. 1). T determines the period of the environmental variation, and the subsequent periodicity of species consumption rates. We chose $T = 40,000$. In the absence of dispersal ($a = 0$), a single set of species quickly drives all other species to extinction (see below). It is known that in such cases local species coexistence is impossible (Armstrong and McGehee, 1980).

By construction, a single species will competitively exclude all others in a given community in the absence of dispersal. This will be the species that possesses the highest initial consumption rate, as measured by the interaction between the species competition parameter H and initial level of environmental variation. If there is dispersal such that the metacommunity begins to behave as a single community, the advantage lies with the most "generalist" species – defined as the species whose consumption rates are closest to the average over the course of the simulation period. This reflects the fact that "generalist" species are able to occupy a broad range of environments (Futuyma and Moreno, 1988; Schluter, 2000). In a tightly coupled, high dispersal system the most "generalist" species will exclude all others across the metacommunity.

Productivity is measured as the average increment in species biomass per unit of time given by the first term on the right side of Eq. (1):

$$\varphi(t) = \frac{\sum_{i=1}^S \sum_{j=1}^M e c_{ij}(t) N_{ij}(t) R_j(t)}{M} \quad (5)$$

System stability is then measured by the inverse of the coefficient of variation over time in productivity, a commonly used metric in ecology (Tilman et al., 1998)⁸

The original Loreau model made a number of assumptions. First, it assumed that communities initially contained the same set of species and differed only in their environmental variation over time as defined by the phase parameter x_j . Species differed only in consumption rates that varied by community and time as a function of H_i , x_j , and t .

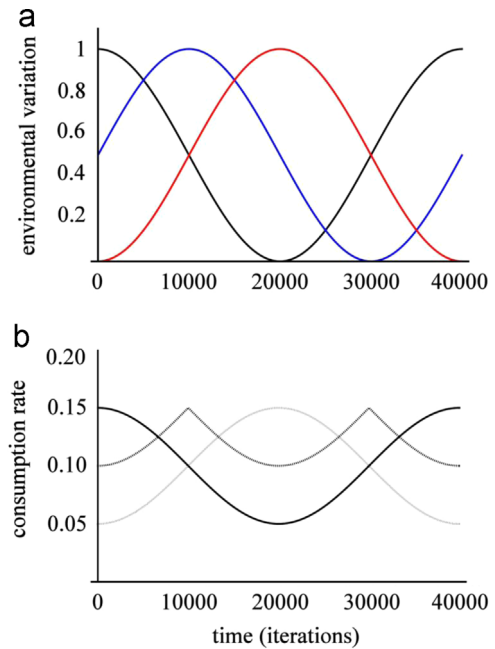


Fig. 1. Community environmental variation (a) and species consumption (b) over time. (a) color denotes community number: black (community 1, $x_1 = \pi/2$), blue (community 2, $x_2 = 0$), red (community 3, $x_3 = -\pi/2$). The phase parameter, x_j , shifts the environmental variation along the x -axis. (b) species consumption rates for community 1 indicated by color: black ($H_1 = 1$), charcoal ($H_2 = 1/2$), and light gray ($H_3 = 0$). Consumption rate is determined by the interaction between the species competition parameter times environmental variation. Values of x_j and H_i were chosen to illustrate the full spectrum of potential environmental variation and consumption rate curves.

Second, species were assumed to compete for a single limiting resource whose natural influx and loss rates were constant across time and communities. This could be thought of as water in a desert ecosystem or nitrogen in a forest ecosystem. Third, species competition arose solely from resource consumption; there was no direct interaction between different species within and across patches. Finally, species dispersed between communities at a constant rate. These assumptions simplified the analysis while providing a structure for species competition when environmental conditions varied. In the numerical experiments reported in this paper we relax certain of these assumptions in order to explore the effectiveness of dispersal in stabilizing productivity where environmental risk factors, e.g. stochastic variation in resource availability, are more or less spatially correlated.⁹

Maintaining the approach of the original papers, the differential equation system in (1) and (2) was numerically simulated using an Euler approximation with a step size (Δt) equal to 0.08. The Euler approximation saves computation time compared to higher order estimators, particularly when the system of equations is unstable. (When $M = 20$ and $S = 20$, simulating (1) and (2) simultaneously solves a system of 400 equations.) Simulations were run for 800,000 iterations. Mean local and global biodiversity, as well as productivity, were measured every 4000 iterations. Biodiversity was measured both

⁸ In our study, stability is measured by the temporal variability in productivity. A high coefficient of variation implies an unstable system; a low coefficient of variation a stable one. A suite of stability measures could have been used including the persistence time of a species, resistance to disturbance (e.g. a change in species diversity or abundance after the introduction of an invader), the time for the system to return to a steady state after a disturbance event, or the size of the perturbation needed to dislodge the system from its current functional state ("resilience") (Orians, 1975; Loeuille, 2012; Scheffer, 2012). Stability in one of these senses does not necessarily imply stability in another sense. We focus on a measure of stability that centers on productivity in a particular functional state.

⁹ We retain the assumptions that species dispersal is density-independent, and that all environmental variation involves the same period and amplitude. There is, however, good reason to believe that these may be too restrictive. Tradeoffs between a species' ability to disperse and colonize have been shown to be stabilizing mechanisms of diversity (Kareiva and Wennergren, 1995). Similarly, an explicit spatial structure including more complex networks and degrees of connectivity would likely alter biodiversity and the system's ability to withstand external shocks (Gardner and Ashby, 1970; Boitani et al., 2007). Finally, empirical systems often possess dynamics that operate on different spatial and temporal scales, between both state variables and patches, that may create a "panarchy" of potential systems (Gunderson and Holling, 2002). These are left for future work.

by species richness and by Shannon–Wiener indices.¹⁰ Average biodiversity, productivity, and stability values were generated from data in the last 200,000 iterations. To evaluate the insurance effect of dispersal where environmental risks are more or less spatially correlated we relaxed the assumption that resource influx is constant over time and across communities (see below). In order to test the effect of heterogeneity in species dispersal, dispersal rates were allowed to statically vary within the interval [0,1]. For each dispersal rate tested, a set of 50 simulations was run to generate new stochastic parameters. Species biomass was initially set at 10; resource biomass was set to the final (equilibrium) value of the previous simulation.¹¹ Species were assumed to be extinct if biomass fell below 0.10 units. This is meant to reflect a critical population threshold in which species are not able to recover due to demographic stochasticity, Allee effects and the like. For a list of model parameters, see Table 1.

2.2. Loreau model–results

At low dispersal rates ($0 \leq a < 0.001$), each community functions as a separate closed system. Within each community, a single set of species with the highest initial consumption rate out-competes all others for available resources leading to their extirpation. This leads to a high global (gamma) biodiversity but low local (alpha) biodiversity (Fig. 2). As the dispersal rate increases (within the range $0.001 \leq a < 0.2$), dispersal between communities allows local biodiversity to increase while global biodiversity is maintained. However, at high dispersal rates ($0.2 \leq a \leq 1$) the system becomes too closely coupled to maintain biodiversity locally or globally. The metacommunity functions as a single community and the set of species whose consumption rates are highest on average exclude all other species in the system. This produces the lowest global and local biodiversity.

A relationship exists between biodiversity, mean productivity, and the stability of productivity across the metacommunity, where system stability is measured by the inverse of the coefficient of variation of productivity over time. At low dispersal rates, the metacommunity generates the lowest mean productivity and highest coefficient of variation in productivity (lowest system stability). The stability of productivity increases with dispersal up to a point, at which the system becomes too coupled and both mean productivity and the stability of productivity decline. At low and high dispersal rates, productivity and the stability of productivity depend solely on the competitive dominant species whose biomass fluctuates over time. At intermediate dispersal rates, the greater local biodiversity stabilizes productivity.

It is worth noting, however, that maximum productivity does not correspond to the maximum biodiversity (Fig. 2a–d) – an observation not discussed in previous studies. Since productivity is maintained while biodiversity falls, the relative abundance of species must be changing. In fact, a trade-off exists between the degree of local biodiversity and aggregate species growth. With higher local biodiversity, more species exhibit growth but each grows at a lower rate than if fewer species were present. Maximum mean productivity is achieved when local biodiversity is relatively low, a significant proportion of biomass being accounted for by the most productive species. The latter condition

is reflected in the Shannon diversity values on the left and right side of the productivity "hump" (Fig. 2b and d). However, productivity differentials between species matter. A particular level of biodiversity does not guarantee a particular level of productivity. For example, the Loreau model experiences a species richness of 6 species at two dispersal rates, only one of which corresponds to maximum productivity (Fig. 2c; see also species richness of 2 and 10 in Fig. 2a and d).

As the dispersal rate increases from 0 to 1 we observe a shift in the dominant species from the initial best competitor in each community to the "generalist" species that does the best in average conditions. When dispersal rates are either very low or very high, the meta community is also characterized by low local biodiversity. But despite low biodiversity, productivity is higher at high than low dispersal rates. The average consumption rate of the "generalist" species is greater than that of the initially best competitor (Fig. 1). A dispersal rate increasing into the intermediate range allows the persistence of more species and a gradual extinction of the initial best competitor. When local and global biodiversity converge, the system exhibits the same species composition on the community and metacommunity scales (Fig. 2a). In all cases, mean productivity peaks immediately after this convergence. At that point the system contains both the initially best competitors of several patches and the species that do best in average conditions.

3. Robustness and the spatial correlation of risk: extensions of the Loreau model

The results reported by Loreau et al. (2003), summarized above, provide a simple illustration of the spatial insurance hypothesis. They demonstrated how dispersal, as a mechanism to increase biodiversity, insures the system against asynchronous environmental fluctuations. In what follows we extend the model to consider factors that affect the spatial correlation of environmental risk, and the capacity of dispersal to stabilize productivity both at the level of individual communities and across the metacommunity.

3.1. Stochastic resource availability–assumptions

Natural resources are rarely constant over time or space. To capture this variation we allow the natural resource influx, I , to vary stochastically over time, affecting the quantity of resources available for species consumption. This we define as "environmental risk".¹² (Note that "environmental risk" affects the equation of motion for the resource and not variation in species consumption rates). Several modeling options are available. Fluctuations of rainfall are often modeled as Poisson processes (Rodriguez-Iturbe et al., 1987). Many biological processes, on the other hand, including the growth of organisms and populations, are characterized by either normal or lognormal distributions (Mitzenmacher, 2004). Soil nutrients, for example, have been found to be both lognormally (Vieira et al., 2011) and normally distributed (Cusack et al., 2009). We chose I in (2) to be normally distributed with a mean equal to the value used by Gonzalez et al. (2009). We tested the sensitivity of productivity to variation in the standard deviation of the distribution. Initially, we considered two polar cases: (1) all communities experience the same realization of I , which we call global environmental risk; and (2) each community possesses its own natural resource influx rate, which we call

¹⁰ Biodiversity metrics were selected in order to capture changes in both the types of species (local and global species richness) and species abundance (Shannon index). A number of metrics exist to measure biodiversity, many of which are highly correlated (Bandeira et al., 2013). See Humphries et al. (1995) for a review of diversity metrics and their application for conservation.

¹¹ Altering the initial resource biomass causes a loss of the species coexistence result of Loreau et al. (2003) and Gonzalez et al. (2009). However, the productivity and stability results are maintained. A discussion of the relationship between species richness, productivity, and dispersal rate is discussed in the proceeding section. See Haegeman and Loreau (2014) for a detailed analysis of the conditions under which the biodiversity–productivity result arises.

¹² Other types of "environmental risk" could be stochastic disturbances that directly affect species biomass, such as extinction events or the removal of patches from the system (Nee and May, 1992). However, these are beyond the scope of the current manuscript.

Table 1
Parameter values for the Loreau et al. (2003) and Gonzalez et al. (2009) simulations.

Variable	Value	Interpretation	Units
S	20	Total number of species	–
M	20	Total number of communities	–
$c_{ij}(t)$	Variable [0, 0.15]	Species consumption rate of resource biomass	$\frac{1}{\text{species biomass} * \text{time}}$
e	0.2	Resource to species biomass conversion efficiency	$\frac{\text{species biomass}}{\text{resource biomass}}$
m	0.2	Natural mortality rate	time^{-1}
I	165	Patch resource influx	$\frac{\text{resource biomass}}{\text{time}}$
l	10	Rate of resource loss	time^{-1}
a	Variable [0, 1]	Dispersal rate	time^{-1}
T	40,000	Environmental periodicity	time
$N_{ij}(0)$	10	Initial species biomass	species biomass
$R_j(0)$	Equilibrium	Initial resource biomass	resource biomass
$\varphi(t)$	Variable	Productivity	$\frac{\text{species biomass}}{\text{time}}$

Note that a value of "–" indicates a dimensionless parameter.

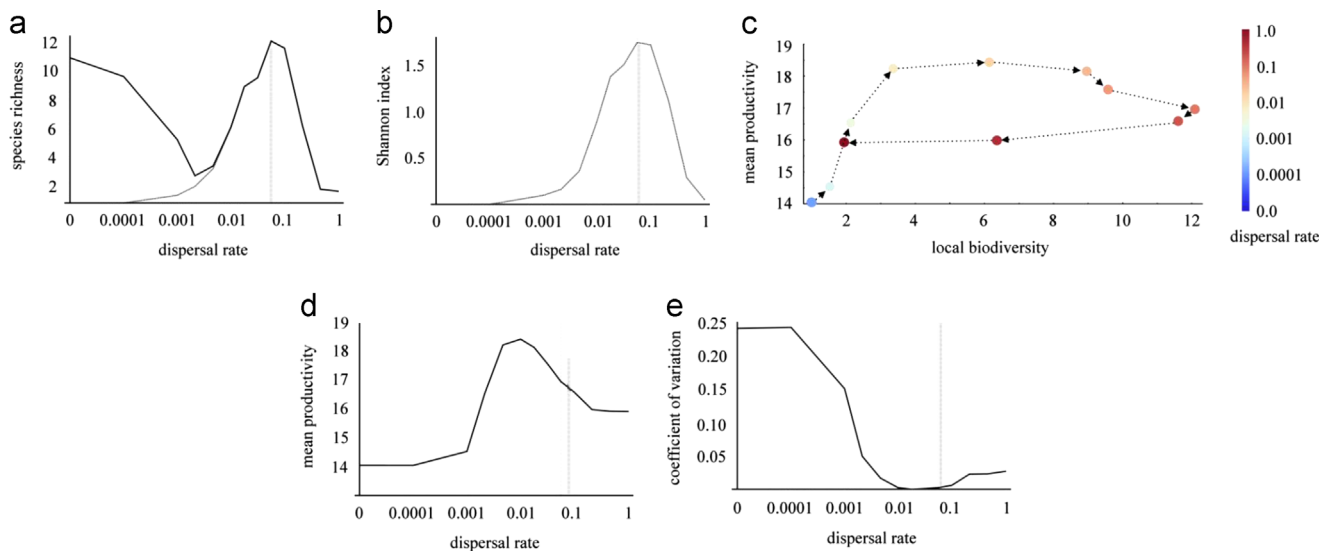


Fig. 2. Reproduction of biodiversity, mean net primary productivity, and stability results from the original Loreau model without spatial correlation and stochastic resource availability (Gonzalez et al., 2009). (a) Mean regional (black) and local (gray) biodiversity; (b) average local Shannon biodiversity index; (c) mean productivity against local biodiversity; (d) mean productivity; and (e) mean temporal coefficient of variation of productivity. In (c), dotted lines and arrows indicate the trend in dispersal rate. Reported values are the average of 50 simulations. The dotted vertical line indicates the dispersal rate at which biodiversity reaches its maximum value. Model parameter values are found in Table 1.

local environmental risk. This approach captures the degree of connectivity between communities (a risk event in a loosely/tightly connected system will affect few/many communities).

Formally, the "risk" of an outcome is the value of the outcome multiplied by the probability that it will occur. We take the value of outcomes to be the associated level of productivity, and tested the effect of different correlation coefficients of the probability distribution of the underlying environmental variables on productivity. Specifically, we consider two extreme cases of the spatial correlation of risks—local and global risk. Global risk implies that resource availability in each community is determined by the same set of environmental conditions, i.e. risks are perfectly correlated spatially. Local risk implies that communities are either far enough apart or sufficiently different in other respects that resource availability depends only on local environmental conditions, i.e. risks are uncorrelated spatially. We then tested intermediate levels of the spatial correlation of environmental risk by

allowing rates of resource influx in individual patches to be more or less spatially correlated. Influx values for the patches were drawn from a multivariate normal distribution with the same mean and standard deviation as the global and local risk scenarios, but with varying values for the correlation coefficients. Parameters used to generate resource influx rates are presented in Table 2.

3.2. Stochastic resource availability—results

Our primary result is summarized in Fig. 3. As in the original papers, we found that intermediate dispersal rates tend to stabilize productivity across the system. However, we also found that the stabilizing effect of dispersal depends strongly on the degree to which environmental risks are correlated across communities. Specifically, we found the stabilizing effect of dispersal to be weakest when resource availability is spatially perfectly correlated ($\rho_1 = 1$) across communities (Fig. 3). In these circumstances all

Table 2
Parameter values of model extensions.

Variable	Value	Interpretation	Units
μ_l	165	Average resource influx rate	Resource biomass
σ_l	Variable 1,5,10,25	Standard deviation of resource influx	–
ρ_l	Variable 0,0.1,0.2,0.4,0.7	Correlation coefficient of resource influx	–
μ_a	Variable [0,1]	Average dispersal rate	time ⁻¹
COV_a	Variable 0.1,0.2,0.4,0.7,1	Coefficient of variation of dispersal rate	Resource biomass ⁻¹

Note that a value of "–" indicates a dimensionless parameter. In our first extension, resource influx rates, I , are drawn from a normal distribution with a mean μ_l and covariance matrix composed of the standard deviation σ_l (diagonals) and spatial correlation coefficient ρ_l (off-diagonals). In our second extension, dispersal rates are drawn from a beta distribution where scale parameters are calculated using the average (μ_a) and coefficient of variation (COV_a) of the dispersal rate.

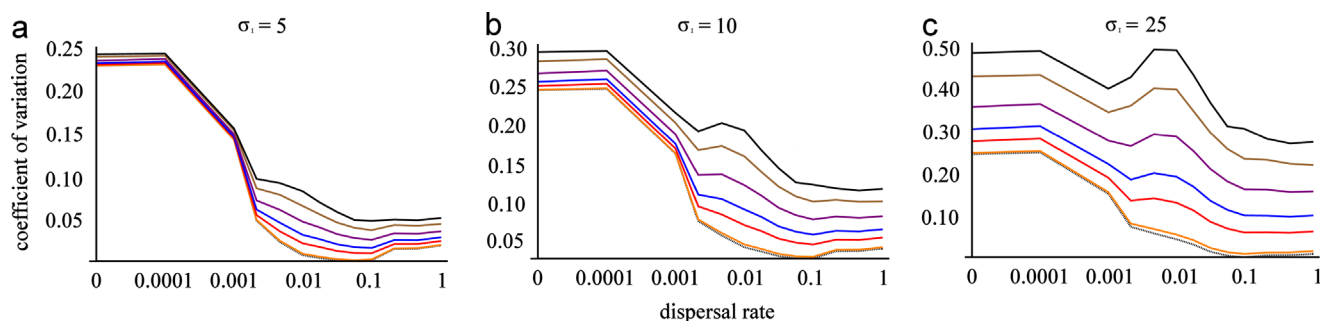


Fig. 3. Effect of spatial correlation (ρ_l) of stochastic resource availability on the mean coefficient of variation of productivity. Reported values are the average of 50 simulations. Colors indicate the degree of spatial correlation: black, solid (global risk; perfect spatial correlation, $\rho_l = 1$), brown ($\rho_l = 0.7$), purple ($\rho_l = 0.4$), blue ($\rho_l = 0.2$), red ($\rho_l = 0.1$), orange ($\rho_l = 0.01$), and black, dashed (local risk; no spatial correlation, $\rho_l = 0$). The standard deviation of the resource availability (σ_l) is given above each plot.

communities experience the same costs (benefits) of low (high) resource availability, and any compensation occurs temporally and at the level of the whole system. Periods of poor resource availability are compensated by periods of resource abundance. When environmental risks are not spatially correlated—implying that resource availability varies across communities—we found dispersal within the metacommunity to be more strongly stabilizing. A fall in productivity in one community where resource availability is low is compensated by an increase in productivity in other communities where resource availability is high. At intermediate levels of the spatial correlation of environmental risk, we found intermediate stabilizing effects of dispersal (Fig. 3).

We found little or no change from the original Gonzalez et al. (2009) results on species richness or productivity. Despite stochasticity in resources, dispersal is able to maintain mean biodiversity and productivity but the latter experiences greater variation around its mean. By definition, stochasticity of resource flows increases the chance that resources will be above or below the mean—this should affect species abundances. In our model, species growth is linearly related to resource abundance (see Eqs. (1) and (5)). Changes in R_j will linearly scale the abundances of all species within the subcommunity, other things being equal.¹³ Higher resource influxes

relieve competitive pressure on species (due to the greater resource availability), increasing both the abundance and diversity of species. Lower resource influxes reduce the abundance of the least competitive species, which increases the probability that those species will fall below the critical population threshold, leading to their extirpation. In addition, declines in resource influx intensify competitive pressure within communities. Under a global risk scenario, all communities share the same competitive pressure due to resource availability. As the spatial correlation between communities decreases (local risk scenario), asynchrony in resource abundance causes populations to grow in some communities and to crash in others. But in both global and local risk scenarios the "insuring" effect of dispersal maintains biodiversity and productivity.

3.3. Stochastic dispersal—assumptions

The next effect we considered was the impact of variation in dispersal rates on global productivity and the stability of global productivity. To do this we assumed that some species disperse at higher rates than others (e.g. invasive species, trans-migratory species). Similarly we assumed that some locations are easier to reach than others (e.g. island communities, barrier zones). Both factors may have a significant effect on species coexistence. We therefore allowed species dispersal rates to vary (1) across species (each species possesses its own dispersal rate regardless of community) and

¹³ Certainly this result is not always the case in real-world systems. For example, increases in nitrogen and phosphorous in freshwater systems can lead to spikes in algae populations (consistent with our model) but, through resulting effects such as the reduction of oxygen, also cause system crashes at higher trophic levels. It is important to note that our model only considers a single trophic level and a single resource. Processes such as eutrophication operate on multiple spatial and temporal scales and across multiple trophic levels. In addition, while an

(footnote continued)

increase in one resource, such as nutrients (eutrophication) reduces limitation and competition for that resource, it enhances limitation and competition for light, which may reduce diversity. Further investigation is warranted.

(2) between communities (all species within a community have a single dispersal rate). The latter increases the capacity for communities to be a source (high dispersal) or sink (low dispersal) community for dispersing species, though the mean capacity remains the same as the original model. Dispersal rates in (1) were generated from a beta distribution with a mean value taken from [Gonzalez et al. \(2009\)](#) and a user-defined coefficient of variation. The beta distribution, bounded between [0, 1], is often used in modeling dispersal rates ([Wiley et al., 1989](#)) and proportions ([Haskett et al., 1995](#)). We tested several coefficients of variation ranging between [0, 1]. Values greater than one lead to negative scale parameter values. See [Table 2](#) for a list of parameters used to generate dispersal rates.

3.4. Stochastic dispersal—results

Overall, heterogeneity in dispersal rates decreases system stability of the meta community. Relaxing the homogeneity conditions on dispersal imposed in [Loreau et al. \(2003\)](#) and [Gonzalez et al. \(2009\)](#) removes the guaranteed balance between in- and out-migration, leading to potential extinctions of all species in some patches.

We found that mean productivity and the stability of productivity were both more robust to species heterogeneity than to community heterogeneity in dispersal rates, particularly at high dispersal rates ([Fig. 4](#)). At low to intermediate dispersal rates, variation in dispersal rates by species had a greater effect than when dispersal rates varied by community, although the qualitative pattern conforms to the original [Gonzalez et al. \(2009\)](#) result. At intermediate to high dispersal rates the metacommunity underwent significantly greater declines in productivity and stability when dispersal rates varied by community than by when they varied by species. When dispersal rates varied by community, communities with high species dispersal rates ("sources") experienced greater rates of out-migration, which resulted in lower species abundances but also a release of competitive pressure within the community. However, if in-migration and new growth cannot compensate for out-migration, source communities will experience an exponential decline and eventual collapse of all species.

Low dispersal communities ("sinks") experience more in-migration, but potentially lower productivity due to greater interspecific resource competition. Most growth of biomass therefore arises from the migration of species into the community. At the metacommunity level, biomass growth in low-productivity sink communities is balanced by biomass growth in high-productivity source communities. But as dispersal rates become more variable, the difference between the two types of communities becomes more pronounced and productivity and stability both decline ([Fig. 4b](#) and [c](#)).¹⁴ We found that local biodiversity remained lower than global biodiversity at higher dispersal rates.

Heterogeneity in dispersal rates decreases both the maximum attainable level of biodiversity, and the stability of productivity ([Fig. 4c](#) and [g](#)). When dispersal is assumed to be constant across species and communities, communities experience synchrony in the exchange of species biomass. However, as dispersal rates vary between communities, some communities become sources while others become sinks. The direct effect on biodiversity is twofold. First, species that are able to persist in highly connected communities have a competitive advantage over other species on a system-level scale. Second, sink communities face internal competitive pressure on species biodiversity as in-migration places additional pressure on available resources.

Variation in dispersal rates between species generates lower biodiversity values than variation in dispersal by community. Species that disperse rapidly are at a competitive advantage over slow dispersers at the metacommunity level. We found a negative shift in the dispersal rate corresponding to the maximum biodiversity value. Even at low coefficients of variation, biodiversity peaked at lower dispersal rates than the homogeneous dispersal case. This implies that the competitive advantage of rapid dispersers is large enough to exclude slow or average dispersers across the metacommunity. Only a few rapid dispersers are required to alter community-level species dynamics significantly.

4. Discussion

[Loreau et al. \(2003\)](#) showed that dispersal can act to insure metacommunities against asynchronous temporal variation in environmental conditions. By increasing local and global species coexistence, dispersal increases mean productivity and the stability of productivity.

Asynchronies in species per capita growth rates within and between communities maintain productivity despite temporal fluctuations in species consumption.

We extended these findings to show how the system performs in the face of environmental risk that may be more or less spatially correlated. That is, we showed how dispersal effectively insures the system against local and global risks in environmental resource availability. We also showed how the insurance effect of dispersal is affected by variation in rates of species dispersal. We found that dispersal promotes stability of productivity under local and global environmental resource stochasticity, but that its effectiveness differs substantially depending on the degree of the spatial correlation of risk. We found that the insurance effect on productivity is greatest when environmental risks across communities are not correlated. In other words, the insurance function of dispersal is greatest where risks are local. Low productivity communities are compensated by high productivity ones. Where the environmental risks experienced by each community are highly spatially correlated, the insurance effects of dispersal still exist but are significantly weaker. This result is consistent with the asynchrony literature ([Loreau and de Mazancourt, 2013](#)). For instance, [Loreau and de Mazancourt \(2013\)](#) demonstrated analytically that asynchronies in species responses to environmental stochasticity stabilize community-level variation in species biomass. In source-sink and sink meta- populations, asynchronies in environmental fluctuations have been shown to have a stabilizing effect, increasing species persistence time in both theoretical and empirical applications ([Gonzalez and Holt, 2002](#); [Matthews and Gonzalez, 2007](#); [Roy et al., 2005](#)). In periods of high resource abundance, sink populations experience an "inflationary effect" characterized by high per capita growth rates and outbreak dynamics.

We also found that variability in the rate at which species disperse between communities has quite different effects on the stability of productivity when rates differ by community than where they differ by species. When rates fluctuate across communities, intermediate dispersal is more strongly stabilizing than where rates fluctuate across species. Symmetrically high dispersal rates are more strongly destabilizing. Few studies have tested the consequences of biodiversity loss due to dispersal on productivity, although several have considered the effects of stochasticity in dispersal rates on biodiversity. [Matias et al. \(2013\)](#) observed similar decreases in local species richness when species dispersal rates are stochastic, as well as a shift in the peak diversity to high dispersal rates. Altering dispersal rates between communities has been shown to affect diversity. [Altermatt et al. \(2011\)](#), in a Lotka–Volterra competition model testing the effects of dispersal and disturbance, found that adding directionality to dispersal significantly lowered biodiversity compared to a global dispersal case. Their results were supported by an empirical analysis of

¹⁴ Due to high degrees of biomass influx caused by migration, sink populations force resource biomass to zero. In sources, species biomasses decay exponentially due to high rates of out-migration.

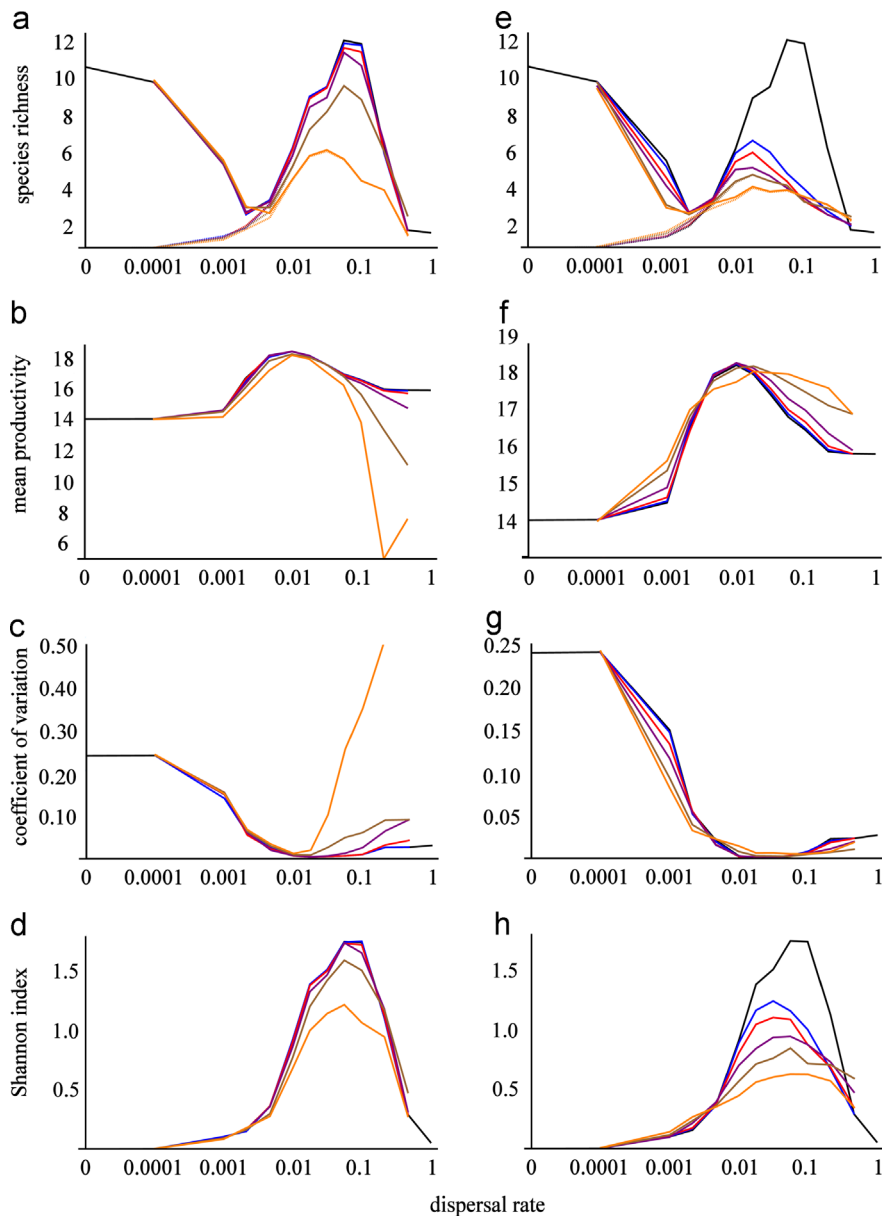


Fig. 4. Effect of heterogeneous species dispersal varying by community (a)–(d) and species (e)–(h). (a) and (e) Mean regional (solid) and local (dashed) species richness; (b) and (f) mean productivity; (c) and (g) mean temporal coefficient of variation of productivity; and (d) and (h) mean local Shannon diversity index. Reported values are the average of 50 simulations. Color indicates the coefficient of variation in dispersal rates: black (original Gonzalez et al. (2009) result), blue ($CoV_a = 0.1$), red ($CoV_a = 0.2$), purple ($CoV_a = 0.4$), brown ($CoV_a = 0.7$), and orange ($CoV_a = 1$).

protist-rotifer microcosms. In a metacommunity model incorporating evolution and food web dynamics, Allhoff et al. (2015) found that both increasing and directing dispersal rates resulted in declines in regional diversity.

While the original Loreau model and this extension are highly abstract, they do have implications for the conditions in which dispersal would enhance ecosystem stability. This is particularly important because empirical experiments are difficult if not impossible to carry out at the scale of the Loreau model (though see Thompson and Shurin (2012) and Howeth and Leibold (2010) for examples in plankton metacommunities). From the Loreau model, an interconnected metacommunity in which sub-communities possess different "optimal" sets of species can maintain productivity and the stability of productivity through intermediate dispersal. We considered the effect of dispersal when environmental conditions are stochastic, fluctuating across communities or uniformly over the whole system. We also considered the effect of mean dispersal when dispersal rates

are themselves stochastic, fluctuating either across communities or across species. While variability in environmental conditions leads to declines in system-wide biodiversity, we found little overall change in productivity. In other words, intermediate rates of species dispersal allow maintenance of mean productivity in highly variable environmental conditions, while simultaneously containing variation in that productivity. Moreover, they do so even at lower overall levels of biodiversity. Although there is a general consensus about the value of biodiversity in maintaining ecosystem functioning and the flow of ecosystem services, the level of biodiversity required to do this in particular cases is still unknown (Cardinale et al., 2012; Hooper et al., 2005; Isbell et al., 2011; Loreau et al., 2001).

Our central finding is that the stabilizing effect of dispersal is more robust to local risk factors than to global risk factors. We found that variability in global resource availability significantly reduced the stability of productivity. Although intermediate dispersal has a role to play in mitigating this impact, it is less effective

in protecting productivity against global risks than against local risks. This conclusion is interesting from a policy or management perspective because: (i) communities and ecosystems have become both more connected worldwide and more exposed to global risk events, (ii) global risk factors are on the rise, e.g. due to climate change, and (iii) dispersal rates are strongly affected by human activities.

The former is especially the case in production systems that are linked through international markets for inputs and outputs. In agriculture, for example, dispersal of cultivated crops is a result both of the development of global markets for foods, fuels and fibers, and of technological developments in plant breeding and more direct genetic engineering. For example, a major effect of the 20th century Green Revolution, was the displacement of many of the 7000 plants previously cultivated worldwide by a handful of widely adapted high-yielding varieties distributed by a small number of seed companies (Evenson and Gollin, 2003; Tisdell, 2003). The resulting homogenization of the global food supply (Khoury et al., 2014) has significantly increased mean global yields, but has also increased temporal variability in yields as cultivated crops exhibit similar responses to changes in temperature, precipitation, disease, pests and other environmental disturbances.

It is also the case for natural systems. Anthropogenic dispersal of species through trade and travel has led to the homogenization of many ecosystems, which increases the spatial correlation of environmental risks and dispersal rates. Dispersal rates are significantly higher than they were, and local exposure to global risk factors has become more frequent. Human behavior has increased the connectivity of the world's ecosystems, causing declines in both the number and functional diversity of species (Clavel et al., 2011; McKinney and Lockwood, 1999; Smart et al., 2006). Examples of invasive species being distributed globally and displacing native species are becoming more frequent in ecology (Hulme, 2009). Global risk factors may include the use of nitrogen-rich agricultural fertilizers and the burning of fossil fuels which has led to rates of terrestrial nitrogen fixation almost double the natural rate, stressing many terrestrial and aquatic systems, and exacerbating climate change (Canfield et al., 2010; Galloway et al., 2008; Moffat, 1998). Climate change in turn adds to the stress on local ecosystems by altering mean precipitation and temperature, water levels along coastal areas, and weather events (Karl and Trenberth, 2003).

At the same time, the increasing connectivity of ecosystems as a result of globalization has affected the spatial distribution of environmental risk. Indeed, the dispersal of species is frequently the mechanism by which risks are transmitted from one location to another (Perrings et al. 2010). This is obvious in the case of infectious diseases of plants, animals or humans transmitted through trade or travel (Tatem, 2009; Tatem et al., 2006a, 2006b), but it may also occur through the effect of anthropogenic climate change on the range size of species (Thomas and Ohlemüller, 2010). This mechanism, linking increased dispersal with risk globalization, may further aggravate the destabilizing effects of these two factors implied by our model. The potentially irreversible and severe consequences of these effects on both natural and human systems should warrant further evaluation of the spatial insurance hypothesis and the effect of global integration on the stability of ecological functioning.

Acknowledgments

David Shanafelt and Charles Perrings acknowledge funding from the National Science Foundation grant 0639252, and the National Institute of General Medical Sciences (NIGMS) (Grant #: 1R01GM100471-01) at the National Institutes of Health grant 1R01GM100471-01. Michel Loreau was supported by the TULIP

Laboratory of Excellence (ANR-10-LABX-41). The paper's contents are solely the responsibility of the authors and do not necessarily represent the official views of NIGMS.

References

- Allhoff, K.T., Weiel, E.M., Rogge, T., Drossel, B., 2015. On the interplay of speciation and dispersal: an evolutionary food web model in space. *J. Theor. Biol.* 366, 46–56.
- Altermatt, F., Schreiber, S., Holyoak, M., 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. *Ecology* 92, 859–870.
- Aragon, R., Oesterheld, M., Irisarri, G., Texeira, M., 2011. Stability of ecosystem functioning and diversity of grasslands at the landscape scale. *Landsc. Ecol.* 26, 1011–1022.
- Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. *Am. Nat.* 115, 151–170.
- Bandeira, B., Jamet, J.L., Jamet, D., Ginoux, J.M., 2013. Mathematical converges of biodiversity indices. *Ecol. Indic.* 29, 522–528.
- Boitani, L., Falcucci, A., Maiorano, L., Rondinini, C., 2007. Ecological networks as conceptual frameworks or operational tools in conservation. *Conserv. Biol.* 21, 1414–1422.
- Canfield, D.E., Glazer, A.N., Falkowski, P.G., 2010. The evolution and future of Earth's nitrogen cycle. *Science* 330, 192–196.
- Cardinale, B.J., Duffy, E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Chisholm, R., 2012. The ecology, economics, and management of alien invasive species. In: Levin, S. (Ed.), *Princeton Guide to Ecology*. Princeton University Press, Princeton, New Jersey.
- Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* 9, 222–228.
- Costello, C., Springborn, M., McAusland, C., Solow, A., 2007. Unintended biological invasions: does risk vary by trading partner? *J. Environ. Econ. Manag.* 54, 262–276.
- Cottingham, K.L., Brown, B.L., Lennon, J.T., 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.* 4, 72–85.
- Cusack, D., Silver, W., McDowell, W., 2009. Biological nitrogen fixation in two tropical forests: ecosystem-level patterns and effects of nitrogen fertilization. *Ecosystems* 12, 1299–1315.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* 151, 264–276.
- Evenson, R.E., Gollin, D., 2003. Assessing the impact of the Green Revolution, 1960–2000. *Science* 300, 758–762.
- Filotas, E., Grant, M., Parrott, L., Rikvold, P.A., 2010. The effect of positive interactions on community structure in a multi-species metacommunity model along an environmental gradient. *Ecol. Model.* 221, 885–894.
- Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. *Ann. Rev. Ecol. Evol. Syst.* 19, 207–233.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320, 889–892.
- Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature* 228, 784.
- Gonzalez, A., Holt, R.D., 2002. The inflationary effects of environmental fluctuations in source-sink systems. *Proc. Natl. Acad. Sci.* 99, 14872–14877.
- Gonzalez, A., Loreau, M., 2009. The causes and consequences of compensatory dynamics in ecological communities. *Ann. Rev. Ecol. Evol. Syst.* 40, 393–414.
- Gonzalez, A., Mouquet, N., Loreau, M., 2009. Biodiversity as spatial insurance: The effects of habitat fragmentation and dispersal on ecosystem functioning. In: Naeem, S., et al. (Eds.), *Biodiversity, Ecosystem Functioning, and Human Wellbeing*. Oxford University Press, Oxford.
- Griffin, P.C., Mills, L.S., 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. *Oikos* 118, 1487–1498.
- Gunderson, L.H., Holling, C.S., 2002. *Panarchy: Understanding transformations in human and natural systems*. Island Press, Washington, D.C.
- Haegeman, B., Loreau, M., 2014. General relationships between consumer dispersal, resource dispersal and metacommunity diversity. *Ecol. Lett.* 17, 175–184.
- Harrison, S., Murphy, D., Ehrlich, P.R., 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *Am. Nat.* 132, 360–382.
- Haskett, J.D., Pachepsky, Y.A., Acock, B., 1995. Use of the beta distribution for parameterizing variability of soil properties at the regional level for crop yield simulation. *Agric. Syst.* 48, 73–86.
- Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.
- Howeth, J.G., Leibold, M.A., 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. *Ecology* 91, 2727–2741.

- Hulme, P.E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* 46, 10–18.
- Humphries, C.J., Williams, P.H., Vane-Wright, R.I., 1995. Measuring biodiversity value for conservation. *Ann. Rev. Ecol. Evol. System.* 26, 93–111.
- Intergovernmental Panel on Climate Change, Fifth assessment report: Climate change 2013, 2013.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477, 199–203.
- Isbell, F.I., Polley, H.W., Wilsey, B.J., 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett.* 12, 443–451.
- Ives, A.R., Klug, J.L., Gross, K., 2000. Stability and species richness in complex communities. *Ecol. Lett.* 3, 399–411.
- Kareiva, P., Wennergren, U., 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373, 299–302.
- Karl, T.R., Trenberth, K.E., 2003. Modern global climate change. *Science* 302, 1719–1723.
- Khouri, C.K., Bjorkman, A.D., Dempewolf, H., Ramirez-Villegas, J., Guarino, L., Jarvis, A., Rieseberg, L.H., Struik, P.C., 2014. Increasing homogeneity in global food supplies and the implications for food security. *Proc. Natl. Acad. Sci.* 111, 4001–4006.
- Kilpatrick, A.M., 2011. Globalization, land use, and the invasion of West Nile virus. *Science* 334, 323–327.
- Lehman, C.L., Tilman, D., 2001. Biodiversity, stability, and productivity in competitive communities. *Am. Nat.* 156, 534–552.
- Lenzen, M., Moran, D., Kanemoto, K., Foran, B., Lobefaro, L., Geschke, A., 2012. International trade drives biodiversity threats in developing nations. *Nature* 486, 109–112.
- Loeuille, N., 2012. Evolution of communities and ecosystems. In: Levin, S. (Ed.), *The Princeton Guide to Ecology*. Princeton University Press, Princeton, NJ.
- Loreau, M., 2010. From populations to ecosystems: Theoretical foundations for a new ecological synthesis. Princeton University Press, Princeton, New Jersey.
- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76.
- Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* 16, 106–115.
- Loreau, M., Mouquet, N., Gonzalez, A., 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci.* 100, 12765–12770.
- Loreau, M., Sapijanskas, J., Isbell, F., Hector, A., 2012. Niche and fitness differences relate the maintenance of diversity to ecosystem function: comment. *Ecology* 93, 1482–1487.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804–808.
- Matias, M.G., Mouquet, N., Chase, J., 2013. Dispersal stochasticity mediates species richness in source-sink metacommunities. *Oikos* 122, 395–402.
- Matthews, D.P., Gonzalez, A., 2007. The inflationary effects of environmental fluctuations ensure the persistence of sink metapopulations. *Ecology* 88, 2848–2856.
- McCann, K.S., 2000. The diversity–stability debate. *Nature* 405, 228–233.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453.
- McNaughton, S.J., 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat.* 111, 515–525.
- Mitzenmacher, M., 2004. A brief history of generative models for power law and lognormal distributions. *Internet Math.* 1, 226–251.
- Moffat, A.S., 1998. Global nitrogen overload problem goes critical. *Science* 279, 988–989.
- Mouquet, N., Loreau, M., 2003. Community patterns in source-sink metacommunities. *Am. Nat.* 162, 544–557.
- Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. *Nature* 390, 507–509.
- Nee, S., May, R.M., 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Anim. Ecol.* 61, 37–40.
- Orians, G.H., 1975. Diversity, stability and maturity in natural ecosystems. In: van Dobben, W.H., Lowe-McConnell, R.H. (Eds.), *Unifying Concepts in Ecology: Report of the plenary sessions of the First International Congress of Ecology*. Dr W. Junk B.V. Publishers, The Hague, The Netherlands.
- Perrings, C., Fenichel, E.P., Kinzig, A.P., 2010. Globalization and invasive alien species: trade, pests, and pathogens. In: Perrings, C., et al. (Eds.), *Bioinvasions and Globalization: Ecology, Economics, Management, and Policy*. Oxford University Press, Oxford.
- Rodriguez-Iturbe, I., Cox, D.R., Isham, V., 1987. Some models for rainfall based on stochastic point processes. *Proc. R. Soc. London A Math. Phys.* 410, 269–288.
- Roy, M., Holt, R.D., Barfield, M., 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. *Am. Nat.* 166, 246–261.
- Russ, G.R., Alcala, A.C., 2011. Enhanced biodiversity beyond marine reserve boundaries: the cup spillith over. *Ecol. Appl.* 21, 241–250.
- Sanchirico, J.N., Wilen, J., 1999. Bioeconomics of spatial exploitation in a patchy environment. *J. Environ. Econ. Manag.* 37, 129–150.
- Scheffer, M., 2012. Alternative stable states and regime shifts in ecosystems. In: Levin, S. (Ed.), *The Princeton Guide to Ecology*. Princeton University Press, Princeton, NJ.
- Schluter, D., 2000. *The ecology of adaptive radiation*. Oxford University Press, New York.
- Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C., Firbank, L.G., 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proc. R. Soc. London B Biol. Sci.* 273, 2659–2665.
- Smith, K.F., Sax, D.F., Gaines, S.D., Guernier, V., Guegan, J., 2007. Globalization of human infectious disease. *Ecology* 88, 1903–1910.
- Tatem, A.J., 2009. The worldwide airline network and the dispersal of exotic species: 2007–2010. *Ecography* 34, 94–102.
- Tatem, A.J., Hay, S.S., Rogers, D.J., 2006a. Global traffic and disease vector dispersal. *Proc. Natl. Acad. Sci.* 103, 6242–6247.
- Tatem, A.J., Rogers, D.J., Hay, S.I., 2006b. Global transport networks and infectious disease spread. *Adv. Parasitol.* 62, 293–343.
- Thomas, C., Ohlemüller, R., 2010. Climate change and species distributions: an alien future?. In: Perrings, C., et al. (Eds.), *Bioinvasions and Globalization: Ecology, Economics, Management, and Policy*. Oxford University Press, Oxford, pp. 19–29.
- Thompson, P.L., Shurin, J.B., 2012. Regional zooplankton biodiversity provides limited buffering of pond ecosystems against climate change. *J. Anim. Ecol.* 81, 251–259.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455–1474.
- Tilman, D., Lehman, C.L., Bristow, C.E., 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* 151, 277–282.
- Tisdell, C., 2003. Socioeconomic causes of loss of animal genetic diversity: analysis and assessment. *Ecol. Econ.* 45, 365–376.
- Urban, M.C., 2006. Maladaptation and mass effects in a metacommunity: consequences for species coexistence. *Am. Nat.* 168, 28–40.
- Valone, T.J., Barber, N.A., 2008. An empirical evaluation of the insurance hypothesis in diversity–stability models. *Ecology* 89, 522–531.
- Vieira, S.A., Alves, L.F., Duarte-Neto, P.J., Martins, S.C., Veiga, L.G., Scaranello, M.A., Picollo, M.C., Camargo, P.B., do Carmo, J.B., Neto, E.S., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2011. Stocks of carbon and nitrogen and partitioning between above- and belowground pools in the Brazilian coastal Atlantic Forest elevation range. *Ecol. Evol.* 1, 421–434.
- Wiley, J.A., Herschkorn, S.J., Padian, N.S., 1989. Heterogeneity in the probability of HIV transmission per sexual contact: the case of male-to-female transmission in penile–vaginal intercourse. *Stat. Med.* 8, 93–102.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.* 96, 1463–1468.