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Biodiversity, productivity, and the spatial insurance hypothesis revisited

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HIGHLIGHTS

- We reevaluate the original Loreau spatial insurance model.
- We extend the Loreau model to consider stochastic temporal resource availability ("environmental risk") and static, heterogeneous species dispersal.
- The stabilizing effect of dispersal is less effective when environmental risk is spatially correlated.
- Despite declines in biodiversity and stability, dispersal is able to maintain productivity despite heterogeneity in species dispersal rates.

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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.

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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

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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.

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Tilman, 2001) and the spatial insurance hypothesis (Ives et al., 2000; 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

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; Lehman and Tilman, 2001; Loreau, 2010; Loreau and de Mazancourt, 2013).

(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 Alcalá, 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 (Levin et al., 2009). 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

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