Biodiversity, Dispersal, and Risk:

Species Spread in Ecological and Social-Ecological Systems

by

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ABSTRACT

The closer integration of the world economy has yielded many positive benefits including the worldwide diffusion of innovative technologies and efficiency gains following the widening of international markets. However, closer integration also has negative consequences. Specifically, I focus on the ecology and economics of the spread of species and pathogens. I approach the problem using theoretical and applied models in ecology and economics. First, I use a multi-species theoretical network model to evaluate the ability of dispersal to maintain system-level biodiversity and productivity. I then extend this analysis to consider the effects of dispersal in a coupled social-ecological system where people derive benefits from species. Finally, I estimate an empirical model of the foot and mouth disease risks of trade. By combining outbreak and trade data I estimate the disease risks associated with the international trade in live animals while controlling for the biosecurity measures in place in importing countries and the presence of wild reservoirs. I find that the risks associated with the spread and dispersal of species may be positive or negative, but that this relationship depends on the ecological and economic components of the system and the interactions between them.

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1 INTRODUCTION

The closer integration of the world economy has yielded many positive benefits including the worldwide diffusion of innovative technologies, and the efficiency gains following the widening of international markets. However, there are also notable negative consequences. While these include unintended environmental impacts of land-use reallocation, pressure on natural resources, and changes in biogeochemistry (Millennium Ecosystem Assessment, 2005), my focus is on the spread of pests and pathogens. Indeed, trade and travel is cited as a major facilitator in the global spread of invasive species (Costello et al., 2007; Lenzen et al., 2012) and infectious disease (Kilpatrick, 2011; Smith et al., 2007; Tatem et al., 2006a).

Research on the general problem of introduced species has revealed two positive trends: the development of new trade routes and the rates of introduction of novel species and the growth in trade and the probability that that an introduced species will establish and spread (Cassey et al., 2004; Dalmazzone, 2000; Dehnen-Schmutz et al., 2010; Pavlin et al., 2009; Semmens et al., 2004; Smith et al., 2009a; Tatem, 2009; Tatem et al., 2006b; Tatem et al., 2006c; Vila and Pujadas, 2001). Many emerging infectious diseases in humans have their origins in the trade of livestock and wildlife products such as SARS, monkeypox, and H5N1 avian influenza (Karesh et al., 2012; Kilpatrick et al., 2006; Li et al., 2005; Smith et al., 2009b; Xu et al., 2004). Several emerging and re-emerging epizootic diseases are spread through trade including H9N2 avian influenza, foot and mouth disease, bovine spongiform encephalopathy, and swine fever (Drew, 2011; Fevre et al., 2006; Karesh et al., 2005; Rweyemamu and Astudillo, 2002). The list of pests spread through trade and travel is every growing (see Hulme (2009) for examples).

The impact of globalization on the spread of species will likely continue to grow in the future - the proportion of output traded internationally is rising rapidly. Since 1950, world exports have increased at rates more than three times that of GDP growth (World Trade Organization, 2013b). The structure of trade is also changing. Growth is more rapid in emerging and developing economies than developed ones. Since the 2007-2009 recession, exports in developing economies are growing 50 percent faster than developed ones (International Monetary Fund, 2013).

The consequences of the spread of organisms for biodiversity, ecosystem functioning, and resilience in ecological and social ecological systems vary depending on the scale of analysis and the system in question. Traditional ecological theory has yielded mixed findings on the effects of dispersal on biodiversity. On the one hand, dispersal may stabilize biodiversity. In microcosm experiments, increased connectivity between communities has been shown to increase persistence time and diversity of species (Holyoak, 2000; Warren, 1996), and dampen detrimental effects of habitat fragmentation (Gilbert et al., 1998; Gonzalez and Chaneton, 2002; Gonzalez et al., 1998). Mass effects (Shmida and Wilson, 1985) and rescue effects (Brown and Kodric-Brown, 1977) are known to prevent extinction of at-risk species. Source-sink dynamics are accepted as viable ways to maintain spatially distinct populations of species (Holt, 1985; Pulliam, 1988) such as the bay checkerspot butterfly in Southern California (Harrison et al., 1988), Montana snowshoe hare populations (Griffin and Mills, 2009), and several marine fish stocks in the central Philippines (Russ and Alcala, 2011).

On the other hand, dispersal and connectivity may reduce biodiversity. Classic species coexistence theory predicts that, due to competitive exclusion, it is impossible to maintain more than *n* types of species on *n* resources in isolated, closed, non-fluctuating environments (Hardin, 1960; Levin, 1970; MacArthur and Levins, 1964).[1] Indeed, increased connectivity has been shown to decrease species richness and increase similarity among species in systems such as zooplankton metacommunities (Forbes and Chase, 2002). As dispersal rates rise, spatially distinct habitats will increasingly function as a single closed system (Loreau et al., 2003; Mouquet and Loreau, 2002). Empirically, this phenomena is referred to a "biological homogenization" (McKinney and Lockwood, 1999; Olden et al., 2004). As trade and travel increase the linkages between ecosystems, the global distribution of species functions as a single set of "winner" species driving "loser" species to extinction. Although more recent research has found that species composition may remain constant or even increase with connectivity, the functional similarity of species between sites often declines (Fukami et al., 2005; Smart et al., 2006). As the functional similarity between sites converge, their responses to perturbations may synchronize, which may have profound effects on the stability of the system (Hooper et al., 2005; Ives and Carpenter, 2007; Loreau, 2010b).

Although the long-term effects of the introduction of species are uncertain (Mooney and Cleland, 2001; Strayer, 2012; Strayer et al., 2006; Vellend et al., 2011), many of the above conclusions are supported by examples in natural and managed systems. A now classic example of species extinction is the brown tree snake of Guam

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[1] This is a quite simplistic view. Due to temporal fluctuations in species populations and environmental conditions, niche gradients, and disturbance, the maintenance of multiple species is possible (Armstrong and McGehee, 1980; Hutchinson, 1961).

(*Bioga irregularis*) which, after its introduction, extirpated at least 9 of the island's 12 native bird species and 6 of 12 native lizard species (Rodda et al., 1997; Savidge, 1987). Similarly, the introduction of the Nile perch (*Lates niloticus*) into Lake Victoria led to the mass extinction of the lake's cichlid fish species (Worthington and Lowe-McConnell, 1999). By altering fire regimes and nutrient dynamics, introduced grasses may cause significant changes in species composition (D'Antonio and Vitousek, 1992). Hybridization of introduced and native species has been documented to lead to declines in species richness (Mooney and Cleland, 2001; Vellend et al., 2011).

Another suite of studies hypothesize a non-monotonic relationship between dispersal and biodiversity. That is, species richness is maximized at intermediate dispersal rates (Amarasekare and Nisbet, 2001; Kareiva et al., 1990; Loreau et al., 2003; Mouquet and Loreau, 2003). At "low" dispersal rates, spatially distinct habitat patches function as individual closed systems; at "high" dispersal rates, the system functions as a single environment. In each case, competitive exclusion leads to a single set of species driving the others to extinction. "Intermediate" dispersal rates provide individuals to replace locally extirpated species while maintaining diversity where it would otherwise prove impossible. Cadotte (2006) provides a broad review of the empirical evidence on the non-monotonic relationship between dispersal and biodiversity. Using a meta-analysis, he argues that the "hump" shaped relationship is more common in animal than plant systems.

Despite the body of literature evaluating the effects of dispersal on species diversity, few studies measure the effect of dispersal on ecosystem functioning. There are some exceptions. For example, in microcosm experiments, regional zooplankton diversity coupled with immigration were found to buffer the detrimental effects of temperature warming on net primary productivity (Thompson and Shurin, 2012). In pond metacommunities, low dispersal networks had higher species diversity and ecosystem stability compared to zero and high dispersal configurations (Howeth and Leibold, 2010). Finally, in a flow-through mesocosm experiment, dispersal nullified the stabilizing effect of diversity on net primary productivity (France and Duffy, 2006).

The conclusions from ecology are largely in a world without people. The composition and abundance of species in most ecosystems are, however, the result of the ecological relationships between species and human efforts to promote or suppress species. For example, species may be selected for or against based on the perceived services that they provide. Crops are promoted while crop competitors, predators, and pathogens are suppressed; charismatic megafauna are conserved while inconspicuous species are ignored. People also indirectly alter species composition. For instance, agricultural runoff often deposits large quantities of nutrients into aquatic ecosystems potentially leading to the depletion of oxygen in those systems - a process called eutrophication (Chapin et al., 2012). In this case, people indirectly select for algae growth and against organisms requiring greater quantities of oxygen. Behavior in the human domain (e.g. a society's demand for harvesting a particular species) has a direct effect on the ecological domain (harvest decreases the number of species in the wild) and vice versa. In a world where human beings have impacted virtually every world system (Crutzen and Stoermer, 2000; Lewis and Maslin, 2015; Monastersky, 2015; Steffen et al., 2007; Vitousek et al., 1997) consideration of both the ecological and socio-economic components is becoming more important to an understanding of general system dynamics.

In human systems, many of the negative effects associated with the spread of pests and pathogens are well documented. The Columbian Exchange of 1492 facilitated the global spread of small pox, measles, and typhus to the New World and syphilis to the Old World (Crosby, 2003). The 1918 flu pandemic led to over 40 million human deaths (World Health Organization, 2005). More recently, in 2013 approximately 35 million people were infected with HIV-AIDS with about 2.1 million new cases and 1.5 million HIV-AIDS related deaths per year (World Health Organization, 2014). This equates to between 1 and 3.5 percent of GDP in severely affected countries (Lule and Haacker, 2012). Since the mid 1990s, infectious livestock diseases have been estimated to cause over 80 billion dollars of damages worldwide (Karesh et al., 2005). For example, the 2001 United Kingdom foot and mouth disease epidemic resulted in the culling of over 2 million heads of livestock (Sobrino and Domingo, 2001) and income losses to farmers, agriculture, the food chain, and tourism totaling around £6 billion (Thompson et al., 2002). Though not significantly altering gross domestic product, invasive species may impose significant losses to local and regional economies (Pimentel et al., 2005). In agricultural systems, Pimentel et al. (2005) estimated that weeds and insects caused losses of 12% and 13% of total crop production in the United States respectively, each amounting to 33 billion dollars worth of damages. The Asian citrus psyllid (*Diaphorina citri*), an introduced insect carrying citrus greening disease, has caused an estimated 23% decline in orange production (16% decrease in revenue) in the state of Florida between 2006 and 2011 (Hodges and Spreen, 2012).

Models that account for ecological dynamics and human behaviour as coupled social-ecological systems largely lie in the fields of natural resource economics. Hotelling (1931), Dasgupta and Heal (1974), Solow (1974), and Hartwick (1977) provide classic examples of the optimal extraction of single exhaustible resources. Single species, renewable resources include the optimal rotation of timber stocks (Conrad, 1999) and numerous examples in the management of fisheries (Clark, 1973; Clark and Munro, 1976; Clark and Kirkwood, 1986; Gordon, 1954). These studies have been extended to include more complex systems and dynamics such as the harvest of multiple species and resource stocks (Brock and Xepapadeus, 2002; Crocker and Tschirhart, 1992; Hartwick, 1978; Hilborn, 1976; Mesterton-Gibbons, 1987), multi-trophic level systems (Mesterton-Gibbons, 1988; Wilen and Brown, 1986), and the management across multiple patches or environments (Brown and Roughgarden, 1997; Rich et al., 2005a; Sanchirico and Wilen, 1999). Recent advances have extended these concepts to include variation in environmental conditions and species growth rates (Clark, 1976; Costello et al., 1998; Kellner et al., 2011; Parma, 1990), benefits other than those associated with harvest (Brock and Xepapadeus, 2002; Hartman, 1976; Horan and Shortle, 1999), and the more explicit consideration of space (Bhat et al., 1996; Brock and Xepapadeus, 2008; Brock and Xepapadeus, 2010; Lenhart and Bhat, 1992; Wilen, 2007).

With increasing collaboration between ecologists and economists, recent research applies economic tools to the optimal management of invasive species and infectious disease spread.[2] Ecologically the spread of an organism occurs in three stages -

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[2] Though a more recent trend in mainstream economics, the agricultural economics literature has long been devoted to the study of pest management and control (Shoemaker, 1981; Shogren and Tshirhart, 2005).

introduction, establishment, and spread - and control or management can occur in any of these stages (Epanchin-Niell and Hastings, 2010).

Economists broadly classify management strategies as mitigation (often referred to as prevention) and adaptation (Perrings, 2005; Shogren, 2000; Shogren and Crocker, 1999). Mitigation includes actions designed to decrease the probability of an event, such as the probability of introduction or establishment (Perrings, 2005). Adaptation refers to actions that reduce the cost of an outcome without changing the probability of that outcome occurring, e.g. the damages of an invader (Perrings, 2005). Mitigation implies action before an event. Adaptation can occur before, during, or after an event. It includes, for example, control and eradication of an established species (Epanchin-Niell and Hastings, 2010).

The optimal strategy depends on the species and system in question. For example, Barbier (2001) presents a general bioeconomic model of a species invasion. Perrings et al. (2002) and Perrings (2005) discuss the optimal conditions to invest in mitigation or adaptation. Horan et al. (2002) specifically address investment in mitigation under ignorance and uncertainty. Leung et al. (2002) compare investment in prevention and control of an invader. Olson and Roy (2002) evaluate the eradication or control of an invader whose growth and spread are subject to environmental conditions. Perrings et al. (2000) and Epanchin-Niell and Hastings (2010) provide a broad overviews of the literature on managing introduced species.

Parallels exist between the management of invasive species and infectious disease. In fact, the application of the tools of economics to problems of infectious disease management is the basis for the emerging field of epidemiological economics

(Fenichel et al., 2011; Morin et al., 2013; Morin et al., 2014). Using wildlife disease as an example, Horan and Fenichel (2007) and Fenichel et al. (2010b) compare conventional R_0 threshold and bioeconomic approaches to management. They find that conventional methods rely on fixed ecological parameters and fail to account for economic and epidemiological tradeoffs in disease spread. See Horan and Wolf (2005), Fenichel et al. (2010c), and Horan et al. (2010) for other applications in wildlife disease management. In human systems bioeconomic approaches have been used to account for adaptive human behavior in response to infectious disease, e.g. changing the number of people a person comes in contact with (Fenichel et al., 2011; Morin et al., 2013; Morin et al., 2014).

Though many coupled social-ecological models assume a homogenous landscape, there exists a suite of literature that captures the effect of species spread and dispersal. The management of spatially distributed biological resources has long been a focus of resource economics (Brown and Roughgarden, 1995; Brown and Roughgarden, 1997; Sanchirico and Wilen, 1999), though only recently have economists begun to account for the spread of species across an explicit, continuous space (Brock and Xepapadeus, 2010; Costello and Polasky, 2008; Wilen, 2007). Previous modeling frameworks treat the spread of species as occurring across and between discrete patches, such as metapopulations (Brown and Roughgarden, 1997; Sanchirico and Wilen, 1999) or a lattice of discrete habitats (Rich et al., 2005a; Rich et al., 2005c).

More recent applications assume a continuous space which, though useful, are notoriously difficult to solve (Holmes et al., 1994). For example, Epanchin-Niell and Wilen (2012; 2014) evaluate the individual and coordinated management of an invasive species spreading across a two-dimensional lattice. Homans and Horie (2011) investigate the optimal level of effort dedicated to detecting an invading species expanding from its known population range. More generally, Lenhart and Bhat (1992) and Bhat et al. (1996) numerically solve for the optimal level of harvest of a species dispersing across a two-dimensional landscape. Brock and Xepapadeus (2008; 2010) analytically derive the optimal harvest of a species exhibiting diffusion-type dispersal and demonstrate the spatial distribution of the species under different harvest regimes.

Yet while these models consider the economic costs and benefits associated with the spread and management of species, they do little to account for the effect of species spread on the ecological properties of the system - biodiversity, ecosystem functioning, and resilience. A deeper understanding of the role of dispersal and its effect on both social and ecological properties of systems is largely lacking in the literature.

My research contributes to the literature by evaluating the ecological and economic risks associated with the spread and dispersal of species. I approach the problem using theoretical and empirical models in ecology and economics. Broadly speaking I find that the risks associated with the spread and dispersal of species may be positive or negative, but that this relationship depends on the ecological and economic components of the system and the interactions between them.

In chapter 2, I model species dispersal in a purely ecological system. Using a theoretical multi-species theoretical network model I extend a model of the spatial insurance hypothesis - one of the proposed mechanisms for the positive relationship between biodiversity and ecosystem stability (Ives et al., 2000; McNaughton, 1977; Yachi and Loreau, 1999). I evaluate the ability of dispersal to maintain system-level biodiversity and productivity in the face of fluctuating resource distribution and differences in species' dispersal ability. Despite declines in species richness, I find that dispersal is able to maintain biodiversity and stabilizes productivity. This work provides new insights into the spatial insurance hypothesis.

In chapter 3 I extend this analysis to test the spatial insurance hypothesis in a coupled social-ecological system where "people" harvest species. I assume that that people derive benefits from (a) the direct consumption (harvest) of species, (b) aggregate species biomass, and (c) the diversity of species (e.g. regulating ecosystem services). These include, for example, foods, fuels, and fibres (a), carbon sequestration (b), or the protection of ecological functions against environmental fluctuations. In a world where socially isolated human groups control the abundance of local species, I find that the background dispersal of species between locations can either increase or decrease biodiversity and productivity. The relationship between biodiversity and dispersal depends on both the ecological and economic components of the coupled model - the competitive interactions between species, the structure of preferences at each location, and the set of relative prices for species harvest. That is, I find that the results of the ecological spatial insurance hypothesis do not always hold in a coupled system.

Chapter 4 estimates an empirical model of foot and mouth disease risk. By combining outbreak and trade data I estimate the disease risks associated with the international trade in live animals while controlling for the biosecurity measures in place in importing countries and the presence of wild reservoirs. My primary contribution is to account explicitly for the bi-directional movement of animals - imports and exports - thereby considering the direct and indirect risks of trade. This chapter extends studies that have shown that current trade-related animal disease risk assessments understate risk when ignore indirect trade linkages (Barker et al., 2006; King et al., 2006; Mur et al., 2012) and overstate risk when they treat all commodities as equal (Bruckner, 2011; MacDiarmid, 2011). I find that biosecurity measures and bidirectional trade volume are two sources of risk for the international spread of foot and mouth disease. Perhaps counter intuitively, I also find that some biosecure regions are high risk due to the volume of trade undertaken (e.g. North America and Eastern Asia).

My final chapter synthesizes the conclusions from each of my substantive chapters and draws out the implications for science and management.

2 BIODIVERSITY, PRODUCTIVITY, AND THE SPATIAL INSURANCE HYPOTHESIS REVISTED

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 chapter, 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.[3]

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[3] This chapter was prepared as a collaborative manuscript and published in the Journal of Theoretical Biology: Shanafelt, D.W., Dieckmann, U., Jonas, M., Franklin, O., Perrings, C., Loreau, M. Biodiversity, productivity, and the spatial insurance hypothesis revisited. Journal of Theoretical Biology 380, 426-435.

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.[4] 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; McNaughton, 1977; Yachi and Loreau, 1999).[5] 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 spatiotemporal environmental variability, including spatially distributed anthropogenic shocks. As the productivity of one species falls, others can fill its functional niche and maintain

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[4] 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.

[5] 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.

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 chapter, 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., 2006b). 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.

THE SPATIAL INSURANCE HYPOTHESIS: THE LOREAU MODEL

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:

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

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

for species $i = 1,2,...,S$ and communities $j = 1,2,...,M$ 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:

[3] $$c_{ij}(t) = \frac{1.5 - \left|H_i - E_j(t)\right|}{10}$$

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

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 $i = 1,2,...,S$. 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 [-2π, 2π], which shifts the environmental variation along its horizontal axis (Figure 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]:

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

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).[6]

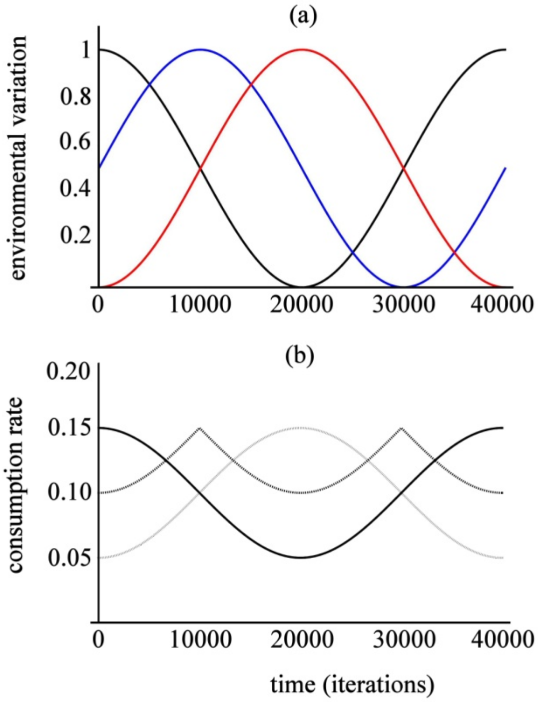

Figure 1. Community environmental variation (a) and species consumption (b) over time. (a) color denotes community number: black (community 1, $x_1 = \pi/2$), blue (community 2, $x_2 = 0$), red (community 3, $x_3 = -\pi/2$). The phase parameter, x_j, shifts the environmental variation along the x-axis. (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.

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[6] 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; 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.

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. 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 chapter 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.[7]

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

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[7] 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, 1972; 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.

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 4,000 iterations. Biodiversity was measured both by species richness and by Shannon-Wiener indices.[8] 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.[9] 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.

Loreau model - Results

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[8] 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.

[9] 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.

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 outcompetes all others for available resources leading to their extirpation. This leads to a high global (gamma) biodiversity but low local (alpha) biodiversity (Figure 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 (Figures 2a, b, c, 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" (Figures 2b, 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 (Figure 2c; see also species richness of 2 and 10 in Figures 2a, 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 (Figure 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 (Figure 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.

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	$\frac{1}{\text{species biomass * time}}$
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.

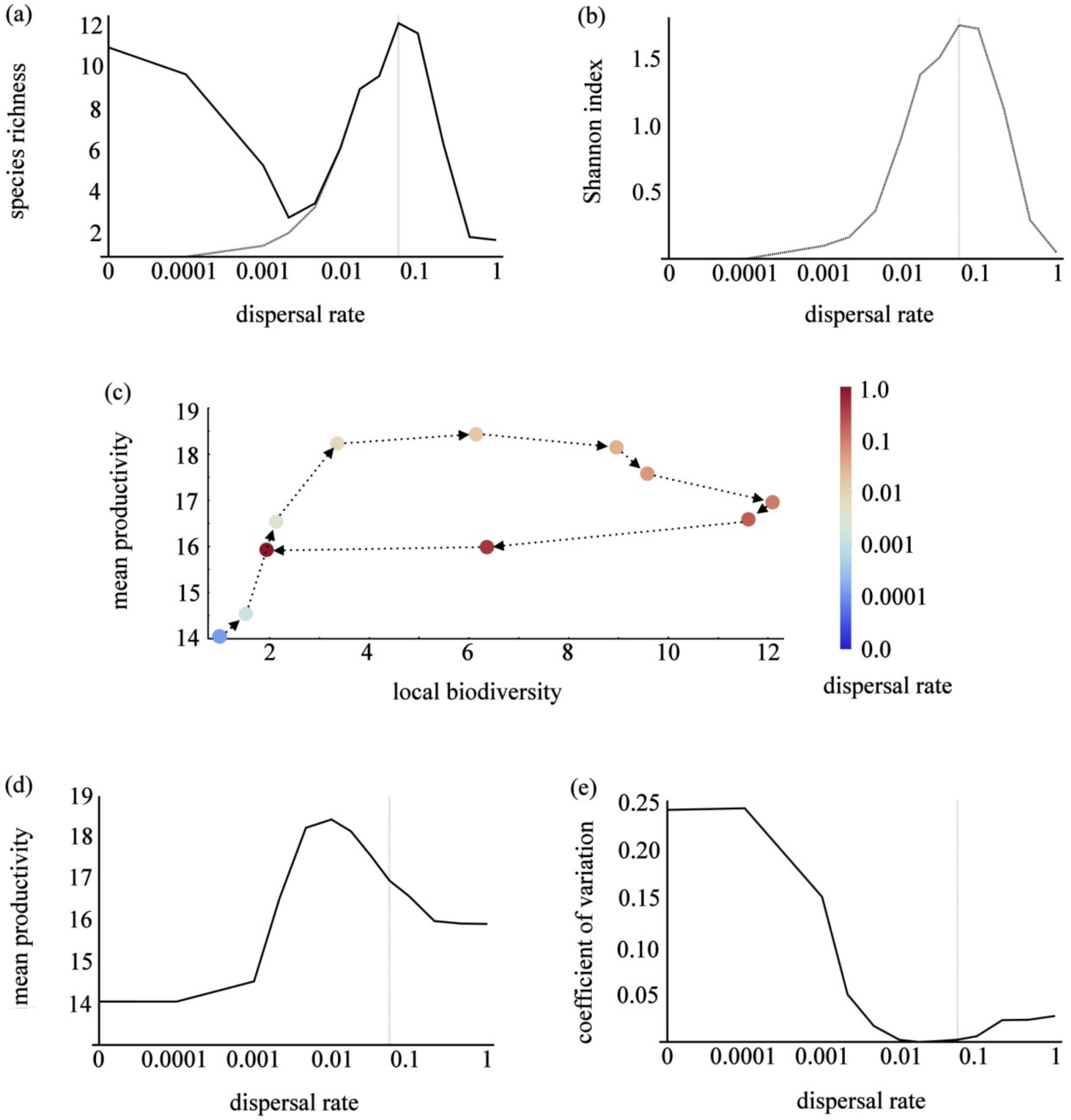

Figure 2. Reproduction of biodiversity, mean net primary productivity, and stability results from the original Loreau model without spatial correlation and stochastic resource availability (Gonzalez et al., 2009). (a) Mean regional (black) and local (gray) biodiversity; (b) average local Shannon biodiversity 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.

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.

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."[10] (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

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[10] 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.

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 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.

Table 2. Parameter values of Loreau model extensions.

Variable	Value	Interpretation	Units
μ_I	165	Average resource influx rate	resource biomass
σ_I	variable 1,5,10,25	Standard deviation of resource influx	-
ρ_I	variable 0.01,0.1,0.2,0.4,0.7	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_I and covariance matrix composed of the standard deviation σ_I (diagonals) and spatial correlation coefficient ρ_I (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.

Stochastic resource availability - Results

Our primary result is summarized in Figure 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 ($\rho_I = 1$) across communities (Figure 3). In these circumstances all 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 (Figure 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 equations [1] and [5]). Changes in R_j will linearly scale the abundances of all species within the sub-community, other things being equal.[11] Higher resource influxes relieve competitive

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[11] 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 increase in one resource, such as nutrients (eutrophication) reduces

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.

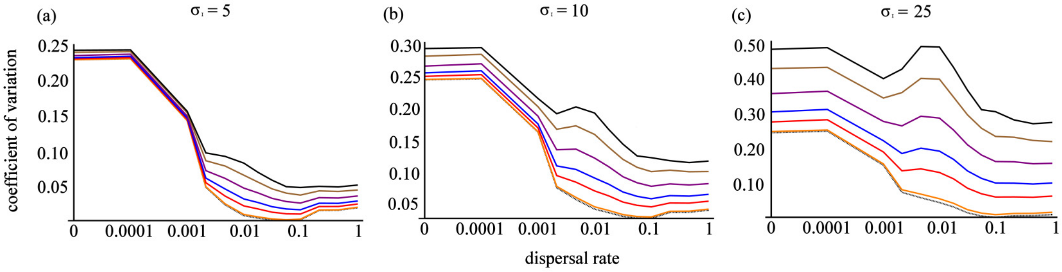

Figure 3. Effect of spatial correlation (ρ_I) of stochastic resource availability on the mean coefficient of variation of productivity. Reported values are the average of 50 simulations. Colors indicate the degree of spatial correlation: black, solid (global risk; perfect spatial correlation, $\rho_I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

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limitation and competition for that resource, it enhances limitation and competition for light, which may reduce diversity. Further investigation is warranted.

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 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.

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 (Figure 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

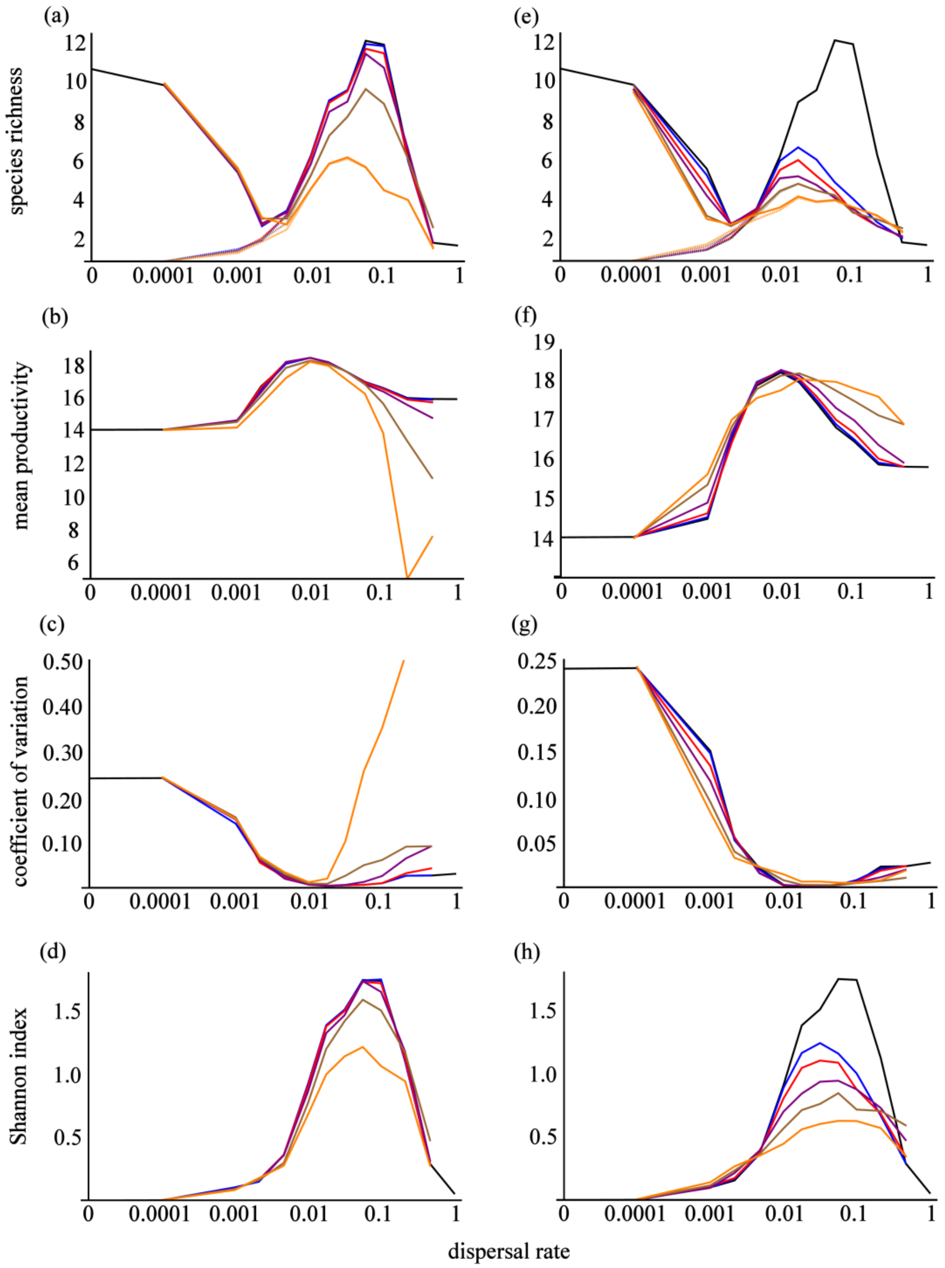

Figure 4. Effect of heterogeneous species dispersal varying by community (a-d) and species (e-h). (a, e) Mean regional (solid) and local (dashed) species richness; (b, f) mean productivity; (c, g) mean temporal coefficient of variation of productivity; and (d, h) mean local Shannon diversity index. Reported 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 ($CoV_a = 1$).

becomes more pronounced and productivity and stability both decline (Figure 4b, c).[12] 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 (Figure 4c, 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.

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[12] 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.

DISCUSSION

Loreau et al. (2003) showed that dispersal can act to insure meta-communities 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 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., 2006b; Tatem et al., 2006c), 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.

3 SPECIES DISPERSAL AND SPATIAL INSURANCE IN HUMAN-DOMINATED ECOSYSTEMS

ABSTRACT

The Anthropocene concept suggests that human impacts are ubiquitous and permeate ecological processes. Yet most ecological models abstract from the influence people have on ecosystems or treat human impacts on ecosystems as constant. This undermines the ability of ecological models to definitely predict the relationship between dispersal, biodiversity, and ecosystem functioning. We evaluate the stabilizing effect of dispersal in a social-ecological system in which human society derives benefits from species. Using a bioeconomic model we analyze the effects of human resource use decisions on biodiversity and productivity, where resource use reflects preferences for (a) the direct consumption (harvest) of species (food, fuels, fibers), (b) the non-consumptive benefits from species abundances (cultural and regulating services), and (c) the non-consumptive benefits generated from an even mix of species (regulating services). We find that the relationship between biodiversity and dispersal depends on the competitive interactions between species, the distribution of preferences between alternative localities, and the set of relative monetary values of species biomass.

INTRODUCTION

It is widely accepted that within an ecological community there is a positive relationship between biodiversity (species richness), ecosystem functioning, and the flow of ecosystem services (Millennium Ecosystem Assessment, 2005). Similarly, species richness is sensitive to species dispersal between ecological communities. One of the mechanisms proposed to explain the impact of dispersal on ecosystem functioning is the spatial insurance hypothesis (Loreau et al., 2003; Yachi and Loreau, 1999). The insurance mechanism works through the functional complementarity of species across space and time. The greater the number and redundancy of species at particular locations, the more the system is protected against spatiotemporal environmental variability. At the local scale, as the productivity of one species falls others may fill its functional niche and maintain overall productivity. When this phenomenon is examined at the global scale, dispersing individuals may replace locally extinct populations and maintain functional groups of species and the flow of ecosystem services. Thus, dispersal is the stabilizing mechanism that insures system stability and in so doing, maintains species diversity and community productivity.

Despite a number of studies that have tested the spatial insurance hypothesis (Filotas et al., 2010; Gonzalez et al., 2009; Ives et al., 2000; Loreau and de Mazancourt, 2013; Loreau et al., 2003; Mouquet and Loreau, 2003; Shanafelt et al., 2015; Urban, 2006), none have considered the stabilizing effect of dispersal when people are explicitly part of the system. In human-dominated ecosystems, human behavior alters relative species abundances by promoting or suppressing particular species. Species are directly selected for or against depending on the ecosystem services/disservices they provide. Crops are promoted while crop competitors, predators, and pathogens are suppressed. Charismatic mega-fauna are protected while inconspicuous plants or insects are ignored. People indirectly select for or against species as in, for example, the effects of nutrient deposition from agriculture into aquatic ecosystems or the accidental introduction of invasive species (Levin et al., 2009). The resulting mix of species reflects the joint effects of human control and natural ecological dynamics. Accounting for the role of humans in ecosystems is necessary if we are to better understand the processes that structure ecological communities.

We extended previous models of the spatial insurance hypothesis (Gonzalez et al., 2009; Loreau et al., 2003) to test the stabilizing effect of species dispersal in a social-ecological system in which people derive value from: consumptive benefits from species consumption (harvest) and non-consumptive benefits from species abundance and richness (biodiversity). We investigate the role of natural species dispersal on the biodiversity and productivity of a human-dominated metacommunity where people manage stocks of species to meet their own goals. We find that in each social-ecological community the structure of human preferences determines harvest policies and hence the relative abundance of species. However, harvest decisions change when relative abundance is modified by the effect of dispersal between communities. We also find that the stabilizing effect of dispersal is highly sensitive to the relative value (to humans) of species at different locations. Dispersal may be stabilizing or destabilizing depending on the relative stock and flow values of species, but in all cases dispersal lowers aggregate biomass and productivity.

THE MODEL

We adapted the model developed by Loreau et al. (2003) and Gonzalez et al. (2009) to identify the role of dispersal in the spatial insurance hypothesis. We assume a metacommunity comprising three communities, each initially having three species. Within each ecological community, each species competes for a single limiting resource. Species consume a deterministically variable quantity of resource depending on species, environmental conditions, and time. Communities are coupled together by dispersal. When dispersal rates are low, each community effectively functions as a separate closed subsystem; when dispersal rates are high, the metacommunity functions as a single integrated system.

The change in species biomass N and resource biomass R in the jth community are described by the equations:

[5]
$$\frac{dN_{ij}}{dt} = N_{ij}(t)(ec_{ij}(t)R_j(t) - m) - qE_{ij}(t)N_{ij}(t) - aN_{ij}(t) + \frac{a}{M-1}\sum_{k\neq j}^{M} N_{ik}(t)$$

[5]
$$\frac{dR_j}{dt} = I - lR_j(t) - R_j(t)\sum_{i=1}^{S} c_{ij}(t)N_{ij}(t)$$

for species $i = 1,2,3$ and communities $j = 1,2,3$ at time t. Species are assumed to consume resources at 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 be lost at a constant rate l. Species disperse among communities at a constant rate a.

Species consumption of the resource is a non-linear function of species-specific competitive ability and environmental variation fluctuating over time for each species in each community where $c_{ij}(t) = \left(1.5 - \left|H_i - F_j(t)\right|\right)/10$ and $F_j(t) = \frac{1}{2}\left[\sin\left(x_j + 2\pi t/T\right) + 1\right]$. Consumption rates are constrained to the range [0.05, 0.15]. H_i is a dimensionless, species-dependent competition parameter such that $H_1 = 1$, $H_2 = 1/2$, and $H_3 = 0$. It is assumed that environmental conditions, F_j, fluctuate over time as a sinusoidal function. A phase parameter ($x_1 = \pi/2$, $x_2 = 0$, and $x_3 = -\pi/2$) shifts the environmental variation along its horizontal axis. T is the period of environmental variation and hence consumption rates. See Appendix A for a detailed discussion of the assumptions of the ecological model.

Effort in harvesting species i, j is given by E_{ij} ($0 \le E_{ij} \le E_{\max}$) and q is the constant efficiency of effort. This is a Schaefer harvest function, common in economics and fisheries science (Schaefer, 1957). We arbitrarily set the maximum harvest effort such that it is possible to maintain species biomass at any chosen level.

We assume that people obtain benefits from the direct consumption of species (flows), from non-consumptive benefits arising from species abundance (stocks), and from biodiversity (the composition of those stocks). The flow benefits from consumption include the provisioning services of the ecosystem (e.g. the production of foods, fuels, fibers etc). The non-consumptive stock benefits of species abundance include, for example, cultural and regulating services such as the value of biomass for carbon sequestration, and the aesthetic, totemic or spiritual values of species. The non-consumptive stock benefits of species richness include the stabilizing effects of biodiversity on ecosystem functioning and the subsequent flow of ecosystem services (the regulating services). We assume all species to be positively valued for harvest and abundance, and so excluded cases where some species are a direct source of disutility (e.g. pests or pathogens).

We further assume that in each social-ecological community a social planner of some kind manages harvest of the species in that community in order to maximize an index of net social benefits, ignoring the actions of social planners in other communities where species disperse from or to. That is, managers act completely independently, and do not condition their decisions on the harvest decisions of others. Formally, we define the social welfare maximization problem as:

$$[5] \qquad V_j\left(\boldsymbol{N},\boldsymbol{R},t\right)=\max_{E_{ij}}\int_0^{\tau}\left[\begin{array}{c}\sum_{i=1}^{3}\left(p_{ij}qE_{ij}(t)\,\mathrm{N}_{ij}(t)-wqE_{ij}(t)+\alpha_{ij}N_{ij}(t)\right)\\ +\beta_j\left(1-\sum_{i=1}^{3}\left(\frac{N_{ij}(t)}{N(t)}\right)^2\right)\end{array}\right]e^{-\delta t}dt$$

subject to [5] and [5], and to the initial species and resource endowments, $N_{ij}(0)$, $R_j(0)$. In addition to these constraints, harvest is selected so that species biomass and the resource are always non-negative, $N_{ij}(t)\geq 0$, $R_j\left(t\right)\geq 0$, and that the terminal social value (the shadow value) of both species and the resource are equal to zero, $e^{-\delta\tau}\lambda_{ij}(\tau)=0$, and $e^{-\delta\tau}\mu_j(\tau)=0$. The unit price of each species harvested (a measure of the marginal benefit of consumption of the species) is p_{ij}. The cost of harvest effort is given by w.

α_{ij} is a measure of the marginal non-consumptive benefits of the abundance of species i in community j. β_j is a measure of the non-consumptive benefits of biodiversity in community j. For simplicity of analysis, it is taken to be a non-saturating, linear function. For simplicity β_j is a weighted Simpson's index of diversity (Simpson, 1949). δ is a discount rate, and τ is the time horizon over which harvest is determined.

Suppressing time arguments, solving the problem for the optimal level of harvest effort yields the following expression (see Appendix B for its derivation):

[5]
$$E_{ij}^{*} = \frac{N_{ij}}{wq}\left[\begin{array}{c} \dfrac{ec_{ij}R_j \sum\limits_{k=1}^{S}\left(p_{kj}N_{kj}c_{kj} - wc_{kj}\right)}{l + \sum\limits_{k=1}^{S}\left(c_{kj}N_{kj}\right) + \delta} + \left(p_{ij} - \dfrac{w}{N_{ij}}\right)\left(m + a - ec_{ij}R_j + \delta\right) \\ -\alpha_{ij} - \beta_j\left(\dfrac{2\left(\sum\limits_{k\neq i} N_{kj}^2 - N_{ij}\sum\limits_{k\neq i} N_{kj}\right)}{\left(\sum\limits_{k=1}^{S} N_{kj}\right)^3}\right) \end{array}\right]$$

It implies separate optimal harvest policies for each species and patch in each moment of time. The first term in the square brackets is the present value of marginal benefits from conserving the resource to be consumed by species in the future - the benefit comes from preventing species from over utilizing the resource (Melstrom and Horan, 2013). The second term represents the marginal user costs of harvest: the forgone future growth in the abundance of all species as a result of harvesting now. The final two terms are the marginal non-consumptive benefits of species abundance and biodiversity, respectively.

The full solution to the system [1], [2], [5] is set of feedback responses that approach the optimal harvest at the most rapid rate possible. When the marginal net benefit of harvest effort is positive for a species, then harvest effort should be set to its maximum level, $E_{\max}$. If the marginal net benefit of harvest effort for a species is negative, then harvest effort should be set to zero. When the marginal net benefit of harvest effort is zero, then harvest effort should equal the singular solution, the optimal level, E_{ij}^{*} . At the singular solution, E_{ij}^{*} , harvest balances the marginal benefits and costs of a change in stock size (Clark, 2010; Conrad and Clark, 1987).

It is worth re-emphasizing an important assumption of the model. The decision-maker in each social-ecological community focuses only on conditions in that social-ecological community. They do not take into account the harvest of species in other patches, nor is there trade of harvested resources among social-ecological systems. They also take the dispersal of species between communities as given and at a constant proportion. Thus the harvest regime in a particular community is optimal only with respect to conditions in that community. Any impacts that local decisions have on other communities are 'external effects' of those decisions.

We considered three preference structures: 1) people derive utility from the direct consumption of species only (provisioning services secured by harvest), 2) people derive utility from the direct consumption of species and from the non-consumptive use of aggregate biomass (provisioning services from harvest plus regulating services from standing biomass), and 3) people derive utility from the direct consumption of species and from the non-consumptive benefits of the composition of species (provisioning services from harvest plus cultural and/or regulating services from biodiversity).

Using numerical methods, we identified the optimal harvest in each case, and then varied the rate of dispersal among cases to study its effects on productivity and biodiversity. To identify the optimal level of harvest we adopted the forward-backward sweep method to solve optimal control problems (Lenhart and Workman, 2007). This method exploits the fact that the optimal control problem is constrained to respect a set of initial conditions for the state variables, $N_{ij}\left(0\right), R_j\left(0\right)$, and a set of terminal conditions for the co-state variables, $e^{-\delta\tau}\lambda_{ij}(\tau)=0$, and $e^{-\delta\tau}\mu_j(\tau)=0$. Given $N_{ij}\left(0\right), R_j\left(0\right)$ and an initial guess as to the harvest trajectory, the state variables are solved forward to the terminal time. Using the transversality conditions and the values of the state and control variables, the co-state variables are solved backwards to the origin. Harvest is updated, and the procedure repeated until the solution converges. Simulations were run for a time horizon of 100 time steps (years) with environmental variation cycling with a period of 25 time steps. For a full list of parameter values, see Appendix A, Table A1.

RESULTS

The main finding of Loreau et al. (2003) and Gonzalez and Loreau (2009) is that intermediate rates of species dispersal between communities maximize community-level (local) and metacommunity-level (global) biodiversity, productivity, and stability. At low dispersal rates, each community functions as a separate closed system and the species with the highest initial consumption rate competitively excludes all others (lowest local biodiversity; highest global biodiversity). At high dispersal rates, the system functions as a single community and the species with the highest average consumption rate dominates (low local and global biodiversity). At intermediate dispersal rates immigration maintains local biodiversity while preserving global biodiversity and maximizing ecological productivity and stability of productivity. For details and extensions of the ecological model, see Loreau et al. (2003), Urban (2006), Gonzalez et al. (2009), and Shanafelt et al. (2015).

In the social-ecological system we assume the same structure of three communities, each composed of three species. We are concerned with environmental conditions on a human timescale (as opposed to an evolutionary one) and therefore take the time horizon to be 100 periods and fluctuations in environmental conditions to occur on 25-year cycles. On this time scale, in the absence of human harvest, the species with the highest average consumption rate (the "generalist" species) dominates the system regardless of the natural dispersal rate. This is because populations of the generalist species are never driven down enough in adverse environmental conditions to prevent them from suppressing other species under favorable environmental conditions. We report results of three cases.

Case 1: Harvest of functionally identical for consumptive and non-consumptive benefits where there is no dispersal. This case offers a baseline for subsequent comparisons. All species within each patch are functionally identical. They have the same response to environmental conditions, and possess the same resource consumption rate curves. We present results for $H_i = 1/2$ for all *i*. For the outcome with other species competition parameters, see Appendix E. When benefits are obtained solely through species harvest (there are no non-consumptive benefits), managers initially drove the stock to its equilibrium value by allocating harvest effort at the maximum. Managers then

Table 3. Summary of key results in the social-ecological system.

species	benefits	dispersal	prices between patches	result
same $H_i = 1/2$	harvest	no	-	harvest of all species suppression of the least valuable
	harvest abundance	no	-	decreasing to zero harvest for all species
	harvest biodiversity	no	-	high but even harvest of all species
	harvest	yes	same	even harvest of all species diversity increasing with dispersal
	harvest	yes	different	even then divergent harvest of species diversity maximized at intermediate dispersal
different $H_i = 1, 1/2, 0$	harvest	yes	same	least valuable species dominates diversity maximized at intermediate dispersal
	harvest	yes	different	coexistence of less valuable species diversity increasing with dispersal

maintained the equilibrium stock via harvest effort at the singular solution, which fluctuated over time by species and patch. In our case the equilibrium is a stationary cycle that oscillates deterministically according to a sine function. As in other studies of stochastic (Clark, 1976; Parma, 1990; Reed, 1979) and fluctuating (Carson et al., 2009; Costello et al., 1998; Costello et al., 2001) growth rates, we found that species harvest rates fluctuated with species consumption rates, with more valuable species being extracted at higher rates than less valuable species (Figure 5a). In choosing the level of harvest, managers balanced current net benefits of harvest against the benefits of future harvests. Since species compete for resources within the ecological community, managers suppressed less valuable species in order to relieve competitive pressure on more valuable species. This effect involves a high initial pulse of harvest that drives down the biomass of all species, but particularly the biomass of the least valued species. The result is that abundance of the least valued species is reduced, and abundance of the more valued species is increased (Figure 5d). The lower the price of a species, the greater its initial suppression. See Appendix F for examples when the price is low or negative (a pest species).

Moreover, for this case, the shadow values for species and resource stocks behaved as expected (Appendix G, Figure A6). Since species differ only in their harvest price ($p_{ij} > 0$), we expected the marginal impact of an extra unit of species biomass on net benefits to be positive, to fluctuate with environmental conditions, and to be highest in the most valuable species. Note that this may not occur if species have different consumption rate curves. Indeed we would expect the shadow values to be negative if the species were a pest (negatively valued), or if the species were weakly positively valued

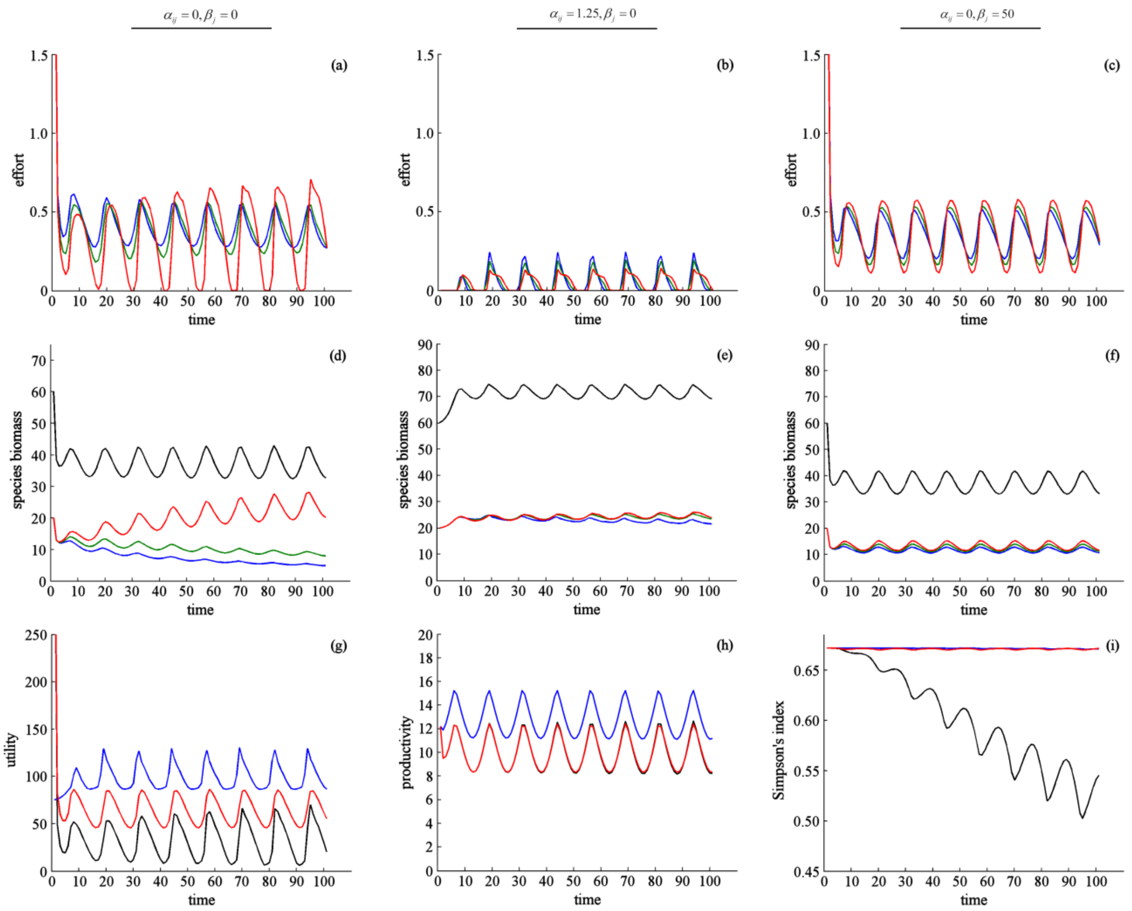

Figure 5. Effect of harvest price when benefits are obtained from harvest only (a, d), harvest and abundance (b, e), and harvest and the mix of species (c, f). Harvest effort (a-c), species biomass (d-f), utility (g), productivity (h), and biodiversity (i). In (a-f) color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates the types of benefits: harvest only (black), harvest and abundance (blue), harvest and the mix of species (red).

but strongly competed with a highly-valued species.

Productivity, as measured by new species biomass, converged on a stationary cycle. Declines in populations of the less valued species were compensated by growth in populations of the most profitable species (Figure 5d, h). Suppression of the less valued species then relieved competitive pressure for the limiting resource, increasing the growth rate of the most profitable species. However, this came at the expense of biodiversity as measured by the Simpson's index (Figure 5i), which declined and became more variable over time. As less profitable species are suppressed, fluctuations in the proportion of species biomasses reside increasingly in the single, most profitable species.

When people derived benefits from harvest and abundance ($p_{ij}, \alpha_{ij} > 0$, $\beta = 0$), managers harvested less and more evenly across species (Figure 5b, e; Appendix G, Figure A7). As stock benefits exceeded market prices species became more valuable if left in the "wild" than for consumption. When harvest price was held constant, increasing α_{ij} resulted in the aggregate benefit of all species approaching the same value. This was reflected in the convergence of species biomass shadow values (Appendix G, Figure A8). Managers maximize net benefits by choosing harvest to balance benefits from harvesting and abundance - the behavior of which depends on the ratio of p_{ij} to α_{ij}. A given species is harvested only if the harvest benefits exceed abundance benefits. If a desirable species is being excluded by a competing species, and the value of suppressing the competing species exceeds the benefits from its abundance, then the competing species will be suppressed.

As harvest declined, aggregate species biomass increased and consumed a greater quantity of the resource (Appendix G, Figure A8). The shadow value of the resource varied inversely with resource biomass (Appendix G, Figure A8). Species growth is linearly tied to resource biomass. The value of an extra unit of resource biomass is greatest when the resource is scarce. Utility and productivity increased with α_{ij} and reached a maximum at zero harvest (Figure 5g, h; Appendix G, Figure A7). When harvest rates are zero the community functions in effect as one species. Utility and productivity reside in fluctuations in species biomass, which is higher due to lower species extraction.

When people derive benefits from harvest and the mix of species, harvest effort resulted in an even distribution of species abundances (Figure 5c, f; Appendix G, Figure A9). The Simpson's biodiversity index increased with the benefits from biodiversity, β_j. Though the most desirable species stock was maintained at a higher level than other species, we did not observe suppression of less valuable species.

Productivity, resource biomass, and the shadow value associated with the resource stock changed little with a more evenly distributed harvest regime (Figure 5h; Appendix G, Figure A10). Earlier studies of the Loreau model found a positive relationship between biodiversity and productivity (Gonzalez et al., 2009; Loreau et al., 2003), though Shanafelt et al. (2015) found that productivity was maintained over a broad range of biodiversity values. In the present model growth rates are perfectly synchronized across species. If aggregate species biomass is maintained, then shifts in individual species abundances do not affect aggregate productivity.

Case 2: Harvest of functionally identical species for consumptive benefits where there is dispersal. Consider a system of three communities in each of which a single institution or manager maximizes social welfare by deriving benefits from species harvest. We first considered the case where preferences for species were the same among communities. The value of each species were identical among communities ($p_{i,1} = p_{i,2} = p_{i,3}$ for all i). This means that in the absence of dispersal, each community is harvested in the same fashion. Differing environmental conditions would affect fluctuations in species biomass but not the harvest decision. In the presence of dispersal, however, optimal harvest patterns change. As dispersal rates increase we observed a shift in harvest away from the suppression of less valuable species and towards identical harvest rates for all species (Figure 6a-c). As a consequence, species populations converged to the same level of biomass. This was reflected in the shadow value of species, which followed a similar pattern (Appendix G, Figure A13). As expected the Simpson's index also increased with dispersal (Figure 6i). Overall, harvest rates increased with the dispersal rate because the marginal benefit of conserving species fell due to the positive externality associated with the inflow of species. Since managers fail to internalize this externality harvest drives down the size of breeding stocks retained in each community while greater harvest pressure limited local productivity in each community (Figure 6h).

We next considered the case where species were valued differently in each community. That is, the set of relative prices for each unit of species harvested varied between communities. The most highly valued species in one community could be the least valued in another. Harvest regimes, and by extension the abundance of species, differed between communities. At low and intermediate dispersal rates, we found the same harvest strategies as when preferences for species were the same between patches. However, at high dispersal rates, we found a strong effect on harvest. The greater the rate of dispersal between communities, the stronger the source-sink effect —the rate at which depleted populations were replenished. This additional biomass was harvested depending on its relative value: the highest valued species being harvested the most, the lowest valued being harvested the least (Figure 7a-c). The Simpson's index was maximized at an

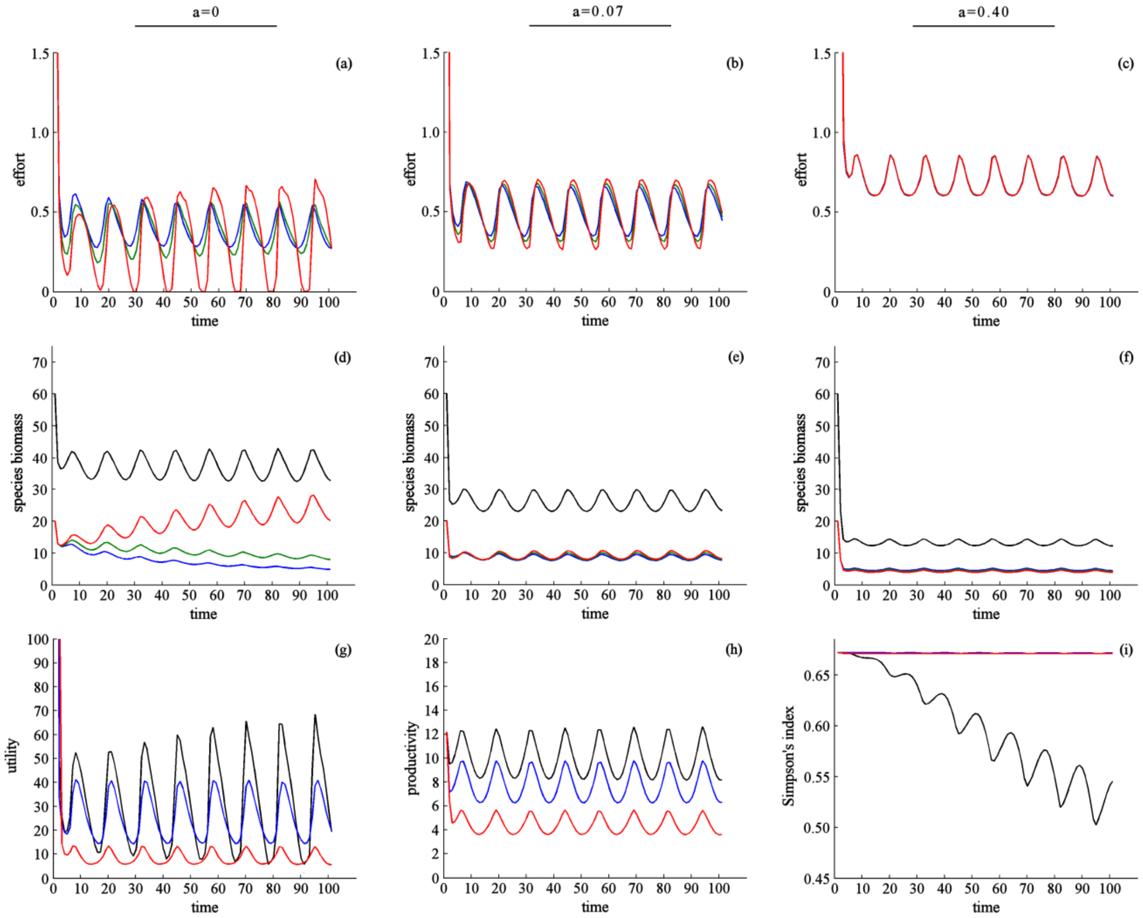

Figure 6. Effect of dispersal when species have *identical* ecological parameters, benefits are obtained through harvest only, and preferences for species are *identical* across patches. Environmental conditions *differ* between patches. Harvest effort (a-c), species biomass (d-f), utility (g), productivity (h), and biodiversity (i). In (a-f) dispersal rate is indicated by column: . $a = 0$.(a, d), $a = 0.07$ (b, e), and $a = 0.40$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates the dispersal rate: low (black, $a = 0$), intermediate (blue, $a = 0.07$), high (red, $a = 0.40$).

intermediate dispersal rate, although the difference in the index "over the hump" was found to be negligible (Figure 7i).

Case 3: Harvest of functionally different species for consumptive benefits where there is dispersal. In this case we assumed all species within each community to be

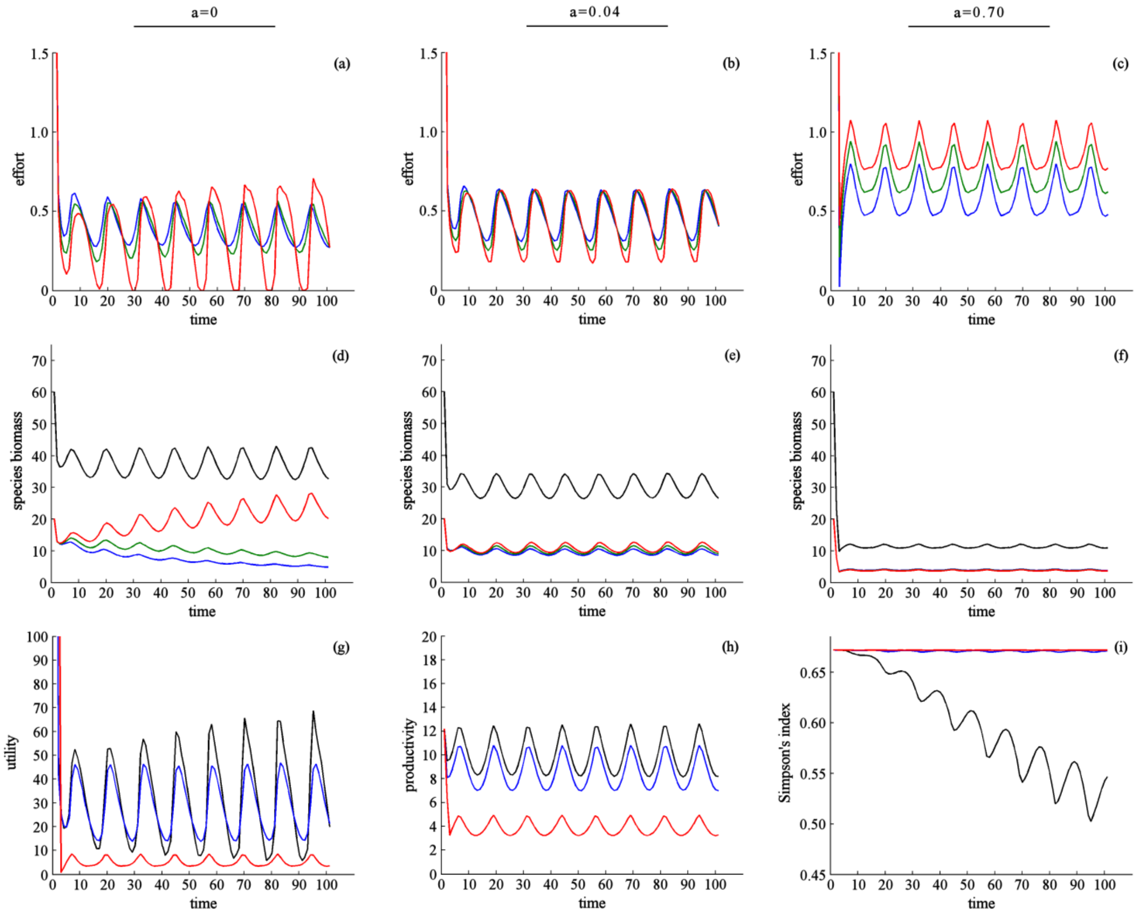

Figure 7. Effect of dispersal when species have *identical* ecological parameters, benefits are obtained through harvest only, and preferences for species *differ* across patches. Environmental conditions differ between patches. Harvest effort (a-c), species biomass (d-f), utility (g), productivity (h), and biodiversity (i). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.04$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates the dispersal rate: low (black, $a = 0$), intermediate (blue, $a = 0.04$), high (red, $a = 0.70$). Results are presented for patch 1. Other patches are symmetric with respect to the preferences for each species.

functionally different - they respond to environmental conditions differently

($H_1 = 1; H_2 = 1/2; H_3 = 0$). We further assumed all species to be positively valued for harvest ($p_{ij} > 0$) and preferences only for on the consumptive benefits of harvest. Our results are summarized in Figures 8 and 9. Recall that in the absence of harvest the

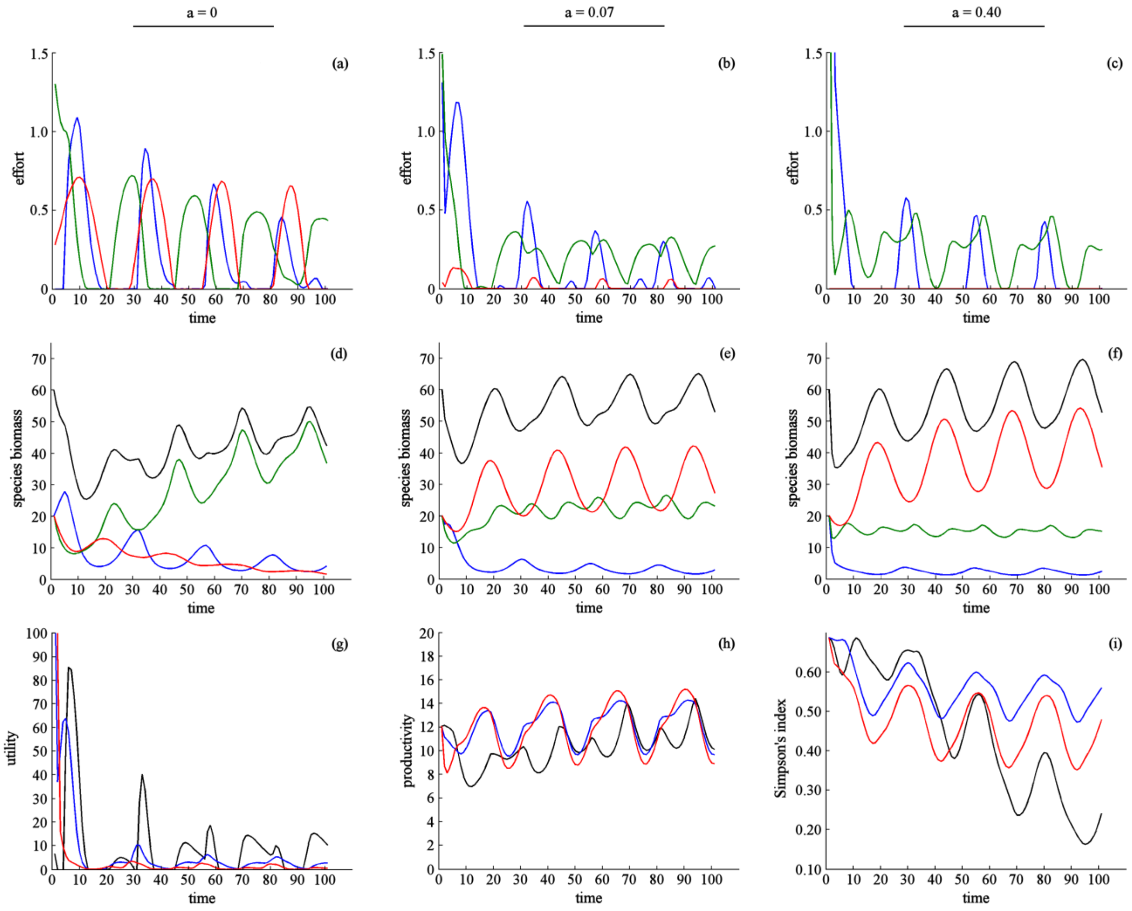

Figure 8. Effect of dispersal when species have *different* ecological parameters, benefits are obtained through harvest only, and preferences for species are *identical* between patches. Environmental conditions are the *same* across patches. Harvest effort (a-c), species biomass (d-f), utility (g), productivity (h), and biodiversity (i). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.04$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates the dispersal rate: low (black, $a = 0$), intermediate (blue, $a = 0.04$), high (red, $a = 0.70$).

generalist species, or the species with the highest average consumption rate, dominated the system. The effect of harvest is twofold. If the prices of other species are significantly greater than that of the generalist species, then the generalist species will be suppressed. Harvest also places additional pressure on species biomass. At low rates of dispersal, however, we found that the combination of harvest and competition allowed the

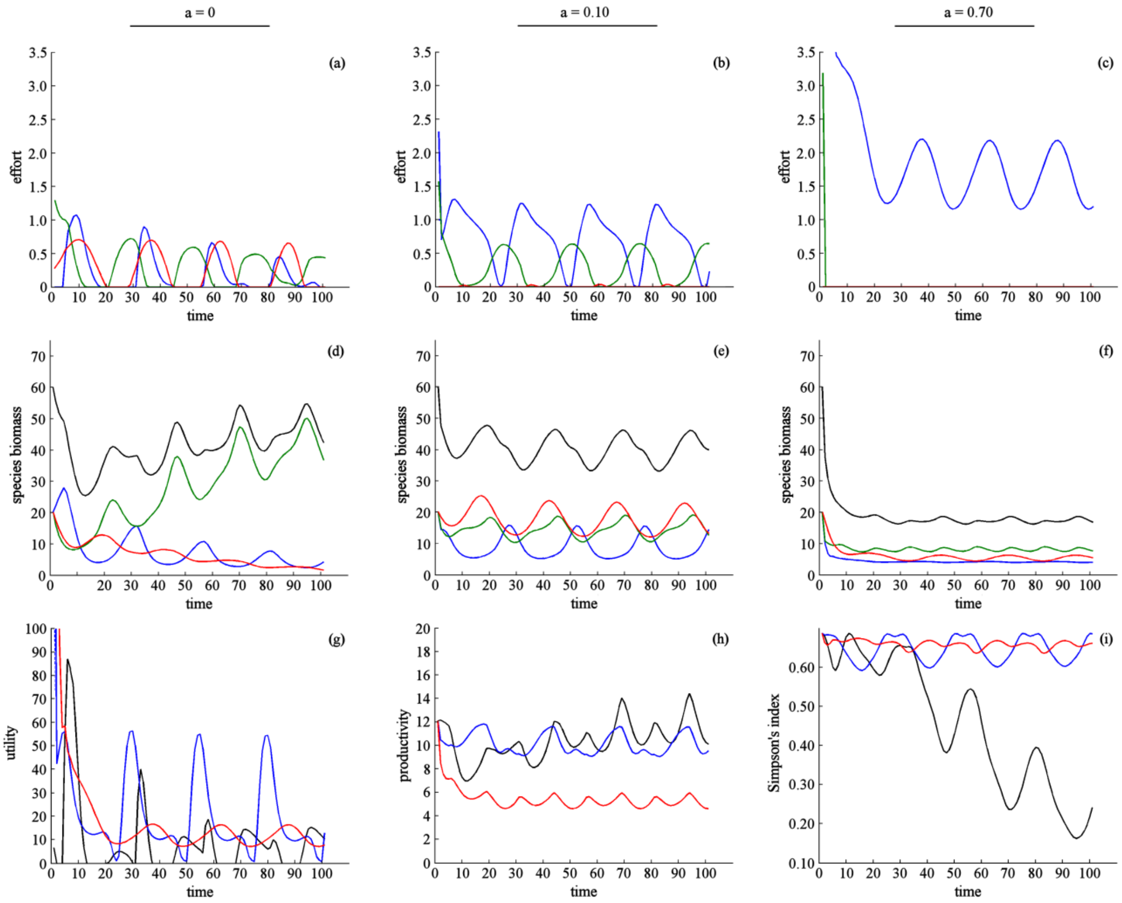

Figure 9. Effect of dispersal when species have *different* ecological parameters, benefits are obtained through harvest only, and preferences for species *differ* between patches. Environmental conditions *differ* across patches. Harvest effort (a-c), species biomass (d-f), utility (g), productivity (h), and biodiversity (i). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.04$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates the dispersal rate: low (black, $a = 0$), intermediate (blue, $a = 0.04$), high (red, $a = 0.70$). Results are presented for patch 1. Other patches are symmetric with respect to the preferences for each species.

generalist species to dominate the system, even if it was the least valued. As before, we first considered the case where preferences for species were the same across communities ($p_{i,1} = p_{i,2} = p_{i,3}$). In this case, increasing dispersal rates caused harvest to decline, particularly for the least valued species (Figure 8a-c). The most valued species were heavily harvested, while the generalist species were only partially suppressed. What is particularly interesting is that at intermediate dispersal rates harvest relieved competitive pressure on the least valued species, allowing for a more even distribution of species abundances. However, at high dispersal rates the least valuable species was able to dominate the system (Figure 8d-f). Indeed, biodiversity measured by a Simpson's index first rose and then fell (Figure 8i). We observed two shifts in the ratio of species abundances. At low dispersal rates generalist species dominated. At intermediate dispersal rates the least valuable species and the generalist species coexisted. At high dispersal rates the least valuable species dominated. Overall, productivity increased with dispersal, while the net social benefit to the community declined due to the fall in biomass of the most highly valued species.

We finally considered the case where preferences (prices) for species were different between patches. Specifically, species 1 was assumed to be the highest valued species in patch 1, species 2 the highest valued species in patch 2, and species 3 the highest valued species in patch 3. We found that as dispersal rates increased, harvest increased in the most valuable species. For the less valuable species, we observed two simultaneous shifts in harvest. Specifically, we observed declining rates of pulsed (on-off) harvest, and increasing rates of initial suppression. After the initial suppression, competition and dispersal maintained a more even ratio of species abundances (Figure 9a-f), implying that biodiversity, as measured by the Simpson's index, increased with dispersal (Figure 9i). However, aggregate species biomass and productivity both decreased as the metacommunity became more connected; utility was maximized at intermediate dispersal rates (Figures 9g-h).

DISCUSSION

The effect of dispersal on biodiversity in a social-ecological system depends only partly on the competitive interactions between species. More important is the structure of human preferences over species within and across locations. Since the structure of preferences over species determines the rate at which each species is harvested, it also determines relative abundances. Society creates the desired mix of species. If the managers value some species more than others, harvest strategies will promote the most valued species, and suppress the least valued species. However, background species dispersal in these circumstances plays a different role than it does in the spatial insurance hypothesis. Specifically, we find that biodiversity increases with dispersal when species possess the same (different) ecological competition parameters and preferences are identical (different) across patches. Biodiversity is maximized at intermediate dispersal rates when species possess the same (different) ecological competition parameters and preferences are different (identical) between patches.

This is unexpected given that the spatial insurance hypothesis predicts, in the absence of harvest, a strictly non-monotonic relationship between biodiversity and dispersal (Gonzalez et al., 2009; Loreau et al., 2003; Mouquet and Loreau, 2003; Shanafelt et al., 2015), though see Haegeman and Loreau (2014). This difference is due to the non-random pressure harvest places on particular species, which is based on the preferences for one species over another. The interaction between harvest, competition between species, and the dispersal of species between communities, determines the relative abundances of species in the system. The desirability of the resulting outcome and "ideal" level of connectivity may be positive or negative. If people’s preferences are for the consumption of a single highly-valued species, then dispersal is undesirable. Indeed, this is often the case in agriculture where people select for productive monocultures. If people’s preferences are for services supported by aggregate biomass, such as carbon sequestration, or for services supported by the diversity of species in the system (e.g. the regulation of soil erosion), then the desirable degree of connectivity is less clear.

Our model also presents an interesting spatial externality. Because managers of each community do not consider the effects of dispersal to other communities, the impacts of their local decisions on other communities are said to be 'external effects' of those decisions (Bird, 1987; Brock and Xepapadeus, 2010; Fenichel et al., 2014; Shogren and Crocker, 1991; Smith et al., 2009c). The effect of the externality may be positive or negative depending on people’s preferences. In ecology, species dispersal can provide a stabilizing mechanism for maintaining biodiversity. Mass and rescue effects (Brown and Kodric-Brown, 1977; Shmida and Wilson, 1985) are known to prevent extinction of at-risk species, and source-sink effects are accepted as a viable way to maintain spatially distinct populations of species (Holt, 1985; Pulliam, 1988). But dispersal may also be detrimental to ecological systems by causing distinct changes in species composition and/or ecosystem dynamics (Chisholm, 2012; Ehrenfeld, 2010; McKinney and

Lockwood, 1999; Rhymer and Simberloff, 1996). In economics, when properly accounted for, dispersal may provide additional individuals to replenish depleted stock populations (Brown and Roughgarden, 1997; Sanchirico and Wilen, 1999). This is particularly apparent in motivating the establishment of marine protected areas (Gell and Roberts, 2003; Lubchenco et al., 2003). On the other hand, dispersing species may constitute a form of "biological pollution" (Horan et al., 2002) with potentially harmful species dispersing from weakly (un)managed spatial environments into managed ones. The sign (positive or negative) of the externality depends on the nature of the species in question and on the values of people in the system.

Indeed, we find that the inclusion of different types of benefits matter in determining optimal harvest policies. In the absence of dispersal, when only benefits from the direct consumption of species are considered, we observe the suppression of less valuable species within a given patch. Initially the less (more) profitable species are heavily (lightly) harvested. They are then harvested at rates that maintain negative (positive) growth of those species. This removes competitive pressure on the most preferred species and allows its population to grow enough to support higher harvest rates. This effect is driven by preferences over species. In a multispecies model with constant species growth rates, Brock and Xepapadeus (2002) solved for the optimal harvest of species within a single patch and jointly across all patches in a system and also found specialization of harvest rates among species. This behavior was driven by the price per unit species harvest and the rate of resources consumed per species (Brock and Xepapadeus, 2002). Other joint-harvest models predict that the selection of species to harvest depends on the balance between their value and growth parameters (Hilborn, 1976; Mesterton-Gibbons, 1996). Driving the least profitable species to extinction may be optimal in certain cases (Clark, 1973; Mesterton-Gibbons, 1996).

It follows that the tradeoff between the consumptive and non-consumptive benefits of species is sensitive to the nature of these benefits. Our model captures the tradeoffs associated with each type of benefit - how a species is harvested depends on the weights associated with each type of value. In reality, species deliver a mix of benefits, depending on one or more of: species traits, biomass, functional redundancy, and taxonomic uniqueness. System management in such cases reflects the values delivered by both the conservation and the harvest of a given species. It also reflects the ecological interactions between species, which will also depend on species dispersal from surrounding spatial locations. In cases where the species might not naturally persist, management of the system can either accelerate or slow the loss of biodiversity, depending on the value attached to the various services that individual species provide.

Our model has limitations. First, managers in each community are assumed to take no account of species biomass in other patches, and the harvest decisions of other managers. This may be a reasonable assumption in some situations, but not in others. Other interesting cases would include strategic behavior among managers, and the aggregate social-planner problem, in which a manager possessing perfect information about the states of the world and the behavior of all individuals, selects harvests rates of species across all communities to maximize aggregate system-level social welfare. Second, we employed a specific form of interspecific species competition. It has been demonstrated that the type and strength of the interactions between species may alter the relationship between diversity and dispersal in ecological systems (Filotas et al., 2010;

Loreau and de Mazancourt, 2013) and optimal harvest in social-ecological ones (see, for example, optimal harvest in systems with predator-prey interactions (Mesterton-Gibbons, 1988), non-interacting species (Hilborn, 1976), or intra-guild predation (Horan et al., 2011)). Finally, we assumed a constant rate of dispersal, which for many species may be too restrictive. With the growth in world trade and travel, ecological systems are becoming increasingly connected and experiencing greater rates of the introduction of new species - hardly a random process. Trade and travel are cited as significant causes of the worldwide spread of invasive pests (Costello et al., 2007; Lenzen et al., 2012) and pathogens (Kilpatrick, 2011; Smith et al., 2007; Tatem et al., 2006a). These extensions are left for future work. We would not, however, expect that such modifications would change our basic finding: that the relationship between dispersal and biodiversity in a social-ecological system depends both on the competitive interactions between species, and the preference structures that drive human interventions in the system.

4 FOOT AND MOUTH DISEASE: INTERNATIONAL TRADE AND RISK

ABSTRACT

The growth in world trade has generated significant benefits to humankind, but it has also generated costs. Among these is an increase in the dispersal of pests and pathogens across the globe. Trade has been the source of several emerging zoonoses and re-occurring livestock diseases. In this chapter, we focus on the risk of foot and mouth disease (FMD) associated with the international trade in live animals. We estimate a model of foot and mouth disease risk that incorporates the effects of international trade of live animals, controls for biosecurity measures undertaken by importing and exporting countries, and accounts for the presence of wild FMD reservoirs. Our main finding is that the indirect risks associated with exports may be as great as the direct risks associated with imports, and that this does not necessarily correlate with the endemic status of the disease. For countries where livestock production occurs in disease free zones (with or without vaccination) the trade risks vary both with species and trading partner. These findings may assist the targeting of disease risk mitigation activities.[13]

INTRODUCTION

The growth in world trade has delivered significant benefits to consumers worldwide. At the same time it has dramatically increased the rate at which pests and pathogens are dispersed. Indeed, the increased spread of human, animal, and plant

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[13] This chapter was prepared as a collaborative paper with (in order of authorship): Shanafelt, D.W., Perrings, C.

diseases is argued to be among the most important side effects of the growth of international trade (Perrings, 2014). Research on the general problem of invasive species has revealed strong positive relationships between the development of new trade routes and the introduction of new species, and between the growth in trade volumes and the probability that introduced species will establish and spread (Cassey et al., 2004; Dalmazzone, 2000; Dehnen-Schmutz et al., 2010; Pavlin et al., 2009; Semmens et al., 2004; Smith et al., 2009a; Tatem, 2009; Tatem et al., 2006b; Tatem et al., 2006c; Vila and Pujadas, 2001). Among pathogens, many emerging zoonotic diseases of humans have their origins in the trade in livestock and wildlife products with developing countries. The list of emerging zoonoses spread this way includes SARS, monkeypox, and H5N1 avian influenza (Karesh et al., 2012; Kilpatrick et al., 2006; Li et al., 2005; Smith et al., 2009b; Xu et al., 2004). Epizootic diseases spread through trade include both emerging diseases such as H9N2 avian influenza and re-emerging livestock diseases such as foot and mouth disease, bovine spongiform encephalopathy, and swine fever (Drew, 2011; Fevre et al., 2006; Karesh et al., 2005; Rweyemamu and Astudillo, 2002).

In this chapter we focus on the epizootic disease risks of trade, and in particular on the foot and mouth disease (FMD) risks of the trade in live animals. We estimate an empirical model of foot and mouth disease risk that incorporates the direct (imports) and indirect (exports) risks of the international trade of livestock, and controls for biosecurity measures in place in importing and exporting countries and the presence of endemic wild reservoirs.

Previous research has shown that the probability that animal or plant pathogens will be transmitted from one location to another via the movement of goods depends on propagule pressure in the form of imports of risk materials (Dalmazzone, 2000; Vila and Pujadas, 2001), and on the biosecurity measures undertaken by those who produce and transport the goods (Brasier, 2008; Perrings et al., 2010a; Perrings et al., 2010b; Scott et al., 2006; Whittington and Chong, 2007). However, a number of studies have found that focusing only on imports and assuming the same biosecurity measures across all goods can be misleading.

There are concerns that current trade related animal disease risk assessments understate risk when they ignore indirect trade linkages (Barker et al., 2006; King et al., 2006; Mur et al., 2012) and overstate risk when they treat all commodities as equal (Bruckner, 2011; MacDiarmid, 2011). The direction of trade, and the risks associated with the biosecurity measures involved in the production and transport of specific trade commodities, both matter.

Contaminated materials indirectly imported into an exporting country in return cargo or transport vehicles may pose a potential source of risk that is often neglected in risk analyses. For example, African swine fever in the Russian Federation continues to pose a serious risk to the European Union swine industry even though trade in pigs and pig products from the Russian Federation has been banned since June 2007. This is because infection may occur via contaminated waste or infected vehicles used to trade goods not subject to the ban (Mur et al., 2012). In ecology, this is equivalent to invasive species being unintentionally imported into countries as "passengers" on cargo or transport vessels. See, for example, the large number of aquatic species transported via ballast water (Hulme, 2009)).

We estimate two sets of disease risk models that incorporate the effects of the two-way international trade in livestock. One set of models captures the disease risks associated with national imports and exports of all susceptible animals into all countries of a given disease status.[14] The other set of models captures the disease risks associated with national exports and imports of different animals into all countries in a given geographical region, using the Food and Agriculture Organization regions. This enables us to identify the relative significance and strength of the different risk factors identified including the impact of imports from/exports to groups of countries. We find that trade into and out of countries are disease-free everywhere (nowhere) is negatively (positively) correlated with disease risk and, when trade is aggregated regionally, risk varies by trading partner and species. While we identify other risk factors for FMD spread, our main finding is that the indirect effect of exports may be positively correlated with disease risk - and that these results are not always intuitive.

Our findings are important in light of current trends in international trade. Since 1950, world merchandize exports have increased at more than 3 times the rate of GDP growth (World Trade Organization, 2013a), and the regional structure of exports has changed. Export growth has been more rapid in emerging markets and developing economies than in developed economies—a trend that has accelerated since the recession (International Monetary Fund, 2013). In the first decade of this century the world trade in live animals susceptible to FMD increased by over 50%. While it is recognized that this has implications for the spread of foot and mouth disease (Di Nardo et al., 2011),

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[14] The World Organization of Animal Health (OIE) recognizes five states: disease free everywhere (with and without vaccination), disease free in specified zones (with and without vaccination), and not disease free anywhere (World Organisation of Animal Health (OIE), 2015). The disease-free categories used by the OIE are also trade categories since they determine which countries have access to which markets.

there are relatively few attempts to quantify the associated risks (Berentsen et al., 1992; Garner and Lack, 1995; Hartnett et al., 2007; Jori et al., 2009; Martinez-Lopez et al., 2008; Miller et al., 2012). We estimate the significant risk factors involved in the global spread of foot and mouth disease, and specifically the indirect risks associated with exports - a factor often ignored in current risk analyses.

BACKGROUND

The biology of the foot and mouth disease virus is well understood (see Alexandersen et al. (2003), Arzt et al. (2011a), Arzt et al. (2011b), and Sutmoller et al. (2003) for reviews of this literature). Transmission may occur through a number of pathways such as via airborne droplets, entry through cuts and abrasions in the skin, and consumption of contaminated fodder (Alexandersen et al., 2003). The virus is able to persist in a variety of materials. For example, the FMD virus has been found to survive in hay, soil, fodder, milk, hair, machinery, and clothing though the persistence time varies by environmental conditions and the type of contaminated material (Alexandersen et al., 2003; Callis, 1996; Cottral, 1969; Paton et al., 2010; Ryan et al., 2008; Sutmoller and Casas Olascoaga, 2003; Sutmoller et al., 2003). Persistence time ranges from several days to greater than six months (Callis, 1996; Cottral, 1969; Paton et al., 2010).

Virtually every cloven-hoofed animal is susceptible, but susceptibility and infectivity vary with the virus strain and host species (Alexandersen and Mowat, 2005; Alexandersen et al., 2003). In livestock, the disease causes the formation of lesions within and around the mouth and feet, lameness, fever, depression, loss of appetite, reduction in milk yields and reproductive potential, but causes mortality only in rare cases (Alexandersen et al., 2003; Knight-Jones and Rushton, 2013).

The primary cost of the disease lies more in the trade response it induces rather than its clinical effects. The primary response to a foot and mouth disease outbreak in disease-free zones is to ban the exports of risky goods until satisfactory sanitary conditions have been restored and to slaughter infected and potentially infected livestock (Grubman et al., 2008; World Organisation of Animal Health (OIE), 2015).

The economic damage caused by FMD outbreaks is frequently very large (Knight-Jones and Rushton, 2013; World Organisation of Animal Health (OIE) and Food and Agriculture Organization (FAO), 2012). For example, the 2001 United Kingdom outbreak resulted in the culling of over two million head of livestock (Sobrino and Domingo, 2001), and income losses to farmers, agriculture, the food chain, and tourist revenues of around £6.5 billion (Thompson et al., 2002). That is, the cost of the outbreak comprised both the loss of a substantial proportion of standing stock, and the loss of trade in both agriculture and related industries. Similarly, the 1997 Taiwan FMD outbreak caused $378 million in damages to the livestock industry, but also led to the loss of over 65,000 jobs spanning pharmaceutical, animal fodder, meat packaging, equipment manufacture and supply, and transportation industries (Yang et al., 1999). FMD outbreaks in disease free countries frequently induce additional impacts for disease monitoring, vaccinations, and the isolation of disease free areas as a conditions for restoring trade, while trade restrictions imposed in response to an outbreak as frequently affect sectors other than agriculture (Garner and Lack, 1995; Knight-Jones and Rushton, 2013; World Organisation of Animal Health (OIE) and Food and Agriculture Organization (FAO), 2012).

The international management of trade-related animal disease risks is governed by the Sanitary and Phytosanitary (SPS) Agreement, which regulates the trade interventions allowed to protect animal health under Article 20 of the General Agreement on Tariffs and Trade. The standards applied by the SPS Agreement are determined by the World Organization for Animal Health (OIE) and Codex Alimentarius, and include health standards for international trade in animals and animal products. The SPS Agreement permits trade interventions to protect animal health, but also requires those interventions to be informed by a scientific assessment of risk. The risk assessment methodology developed by the OIE aims to establish the likelihood of the introduction, establishment and spread of disease within the territory of an importing country, and to assess its biological and economic consequences (MacDiarmid, 2011).

Typically, risk assessments for both pests and pathogens transmitted through trade assume that risk is a function of propagule pressure (approximated by the volume of imports) and biosafety measures (the sanitary capabilities of exporting countries). For FMD, the OIE applies the principles specified in the Terrestrial Animal Health Code, which require the geographical separation of production zones from areas where FMD is endemic (World Organisation of Animal Health (OIE), 2015). Permitted policy responses include trade restrictions that either ban exports from areas where no separation has been established, or allow exports only from particular zones or compartments within a country that are recognized as applying acceptable biosecurity standards (Alexandersen et al., 2003; Grubman et al., 2008; Leforban, 1999; Ratananakorn and Wilson, 2011; Sugiura and Murray, 2011; Sutmoller et al., 2003).

DATA DESCRIPTION

Our dataset spans 216 countries over the period between 1996 and 2011. It reports the number of monthly outbreaks published by the World Organization of Animal Health or OIE (http://www.oie.int/). The OIE consists of 180 member countries with an additional 24 member countries since 2002. Beginning in 1996, participating countries filed both annual and monthly reports of the number of new outbreaks within their border.

Because trade data were, until recently, reported on an annual basis, we aggregated outbreak data to the annual level. In order to test two different aggregations of trade data, we constructed two sets of dependent variables: a count of the number of outbreaks reported in each country, and a binary outbreak(s)/no outbreak measure for each country. These are the primary dependent variables in our analysis.

To identify the value at risk during outbreaks we secured proxies for the economic consequences of outbreaks. We considered three measures of the potential economic losses due an FMD outbreak or "value at risk": agriculture value added, livestock production index, and the standing stock of livestock. The first is agriculture value added or agricultural GDP, as reported by the FAO. This is a measure of value added in the agricultural sector—the annual income the sector yields to farmers, farm workers, and associated industries. Since it is not possible to isolate the livestock sector within agriculture, this is an overestimate of the value at risk. The second is a measure of the growth trajectory of the livestock sector: the FAO's livestock production index (LPI) calculated as a country's aggregate volume of production compared to a base period (in this case, between 2004 and 2006). It includes meat and milk, dairy products, eggs, honey, raw silk, wool, and animal hides and skins, and is a proxy for the development of a country's livestock industry. The third is a measure of the assets that may be destroyed during efforts to control and outbreak—the standing stock of cattle, sheep and pigs in a country. We expect all three measures to be positively correlated with ex ante risk mitigation measures, and hence negatively correlated with the likelihood that the disease will be detected in the national herd.

We are interested in two sets of risk factors: those relating to the structure and volume of international trade in risk materials, and those relating to the biosecurity measures taken along trade routes. Our trade dataset includes the volume of imports and exports of all cloven-hoofed animals reported to the Food and Agriculture Organization between 1996 and 2011 (http://faostat3.fao.org/home/E). While the FAO makes available data on the trade of other risk materials (e.g. meats, milk, hides, skins, and genetic material) these are beyond the scope of our analysis.

We aggregated country imports and exports in two different ways. The first was by the disease-free categories recognized by the OIE (Figure 10). Using this aggregation we explored country risks in terms of the volume of imports from and exports to all countries in each designation.[15] The number of countries in each disease-free category

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[15] For countries that possess multiple disease-free designations, I group the country according to the designation with the highest risk.

and aggregate number of annual outbreaks per category are presented in Figure 11. Aggregate imports and exports by base category with all other categories are presented in Appendix H. While low risk disease-free designations trade more with similar low-risk countries, a large quantity of imports and exports come from countries with FMD. This suggests that while disease history plays a role in trade decisions, it is not the only driving factor.

The second was by geographically defined regions. More particularly, we aggregated imports from and exports to each of the twenty-two geographical regions of the Food and Agriculture Organization (FAO) (Figure 12). Due to low trade volumes, we lumped Melanesia, Polynesia, and Micronesia into a single "Pacific Islands" region. While we do lose resolution by aggregating the data into regions as opposed to individual countries, not aggregating causes significant collinearity in the trade data among members of particular regional groups.[16]

Certain countries and regional groups of countries are regarded as safer trading partners than others (Figures 10-13). For example, India, Iran, Thailand, Turkey, and Vietnam are known to be high-risk areas for FMD (mean number of annual outbreaks of 1555, 4850, 69, 436, and 822 respectively). Other countries, such as the United States and Australia and New Zealand, are known to be FMD disease-free.

We expect the volume of livestock imports to capture the direct impact of trade on disease risk - the probability of importing an infected animal. We expect the volume of livestock exports to capture the indirect impact of trade on disease risks - the probability

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[16] In order to check for collinearity between imports and exports (e.g. balanced trade) we plotted imports against exports (Appendix I, Figure A23). We find that while some countries balance their imports and exports of livestock, most do not.

that sending livestock transport vessels/vehicles into particular ports will lead to outbreaks in the exporting country. While we do not have data on the specific mechanisms involved, these may include mechanisms similar to those reported for African swine fever (Mur et al., 2012). That is, there is some probability that FMD contaminated material is "picked up" and transported back to the exporting country, as occurs with, for example, the global transport of invasive species in ballast water or transport containers (Hulme, 2009).

On biosecurity measures, foot and mouth disease spread is affected by how well a country manages disease within its borders (Berentsen et al., 1992; Garner and Lack, 1995; Schoenbaum and Disney, 2003). We do not have direct measures of the biosecurity measures applied in the livestock sector. We therefore focus on a number of indirect measures. One is the density of veterinarians registered for each country with the OIE. This measure includes veterinarians in both private and public sectors, but does not include associated personnel such as veterinary technicians.

A second set of biosecurity measures comprises binary data on the control measures reported to the OIE that a country undertakes prior to an FMD outbreak, including 1) inspection and interception at the border; 2) monitoring and surveillance of livestock; 3) the existence of measures for the control of wild reservoirs; and 4) the presence of measures, such as veterinary cordon fences, that isolate disease-free regions within the country (http://www.oie.int). The last three are also indirect proxies for the existence of wild reservoirs within countries. For example, zoning isolates the quarantined zone areas where FMD is present. We expect these measures to be positively related to the likelihood that an FMD outbreak will be reported as 'present' in the national herd. The presence of endemic, non-commercial livestock reservoirs may potentially affect commercial disease incidence rates by providing sources of disease that

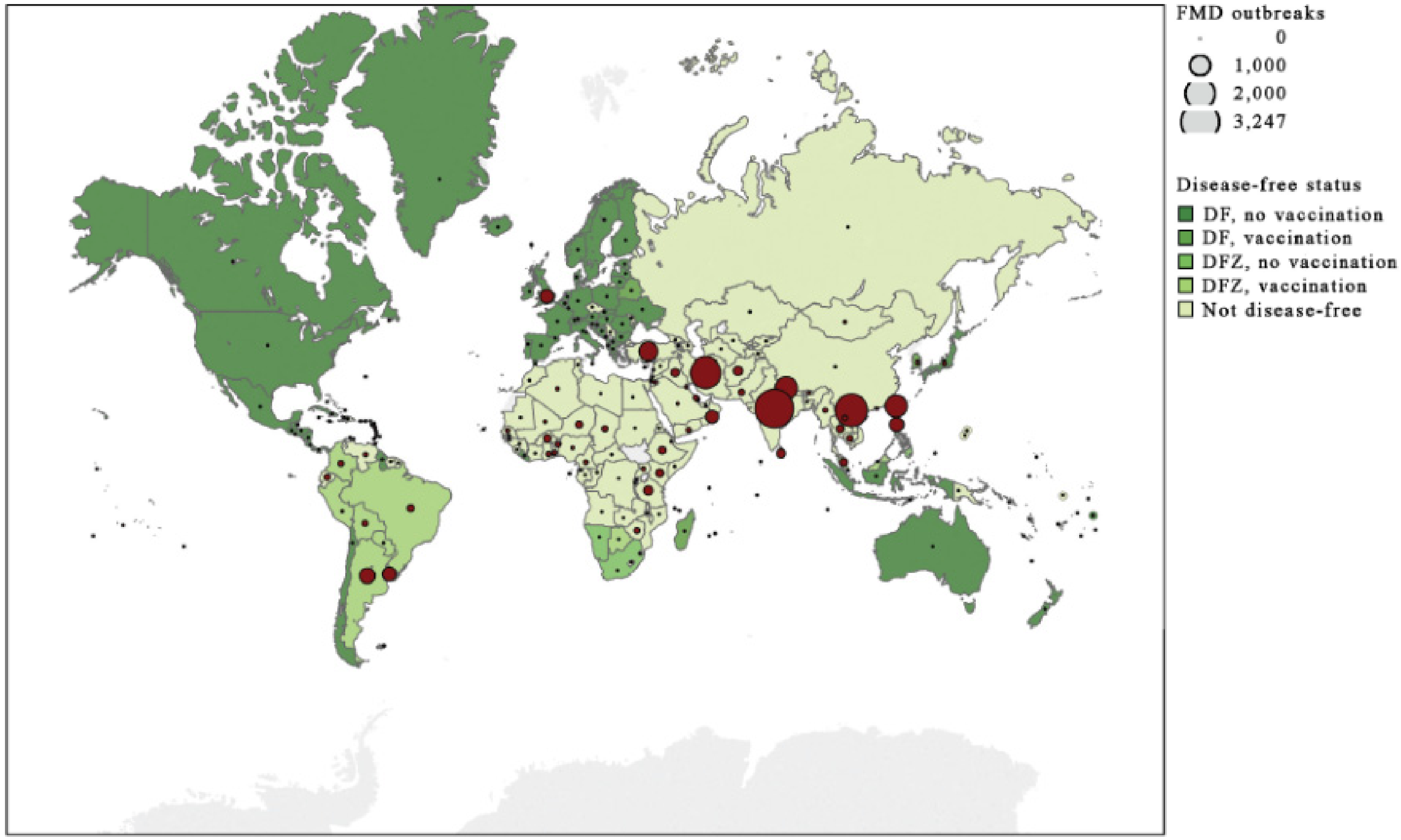

Figure 10. Global distribution of OIE disease-free designations as of 2011. Individual countries are colored according to their disease-free designation: disease free, no vaccination; disease free, with vaccination; disease-free zones, no vaccination; disease-free zones, with vaccination; and not disease-free. Circle size indicates the number of cumulative FMD outbreaks within a country during our study period. Data are from the World Organization of Animal Health (http://www.oie.int/).

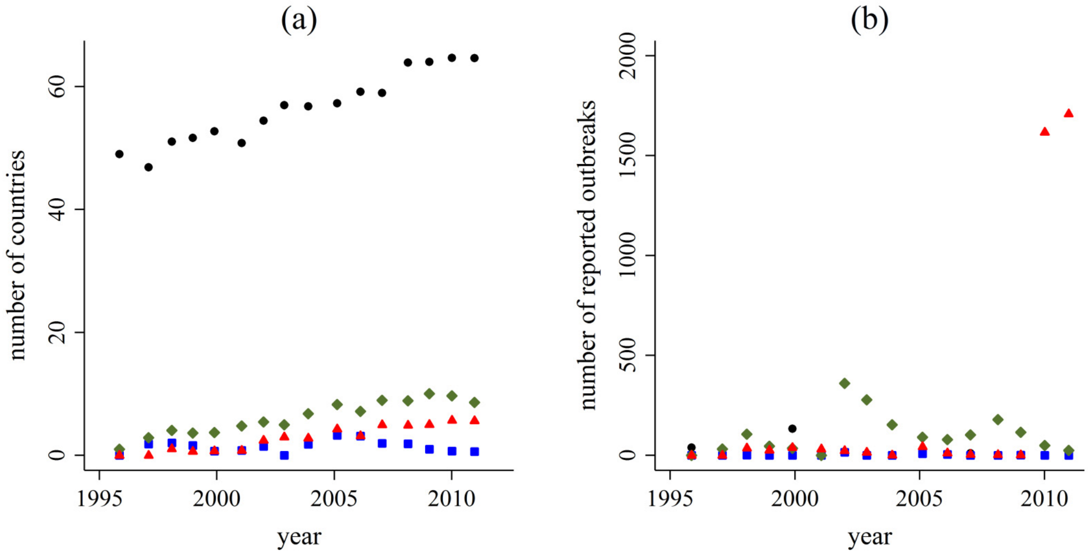

Figure 11. Annual aggregate number of countries (a) and number of reported outbreaks (b) by disease-free category. Symbol and color indicate the disease-free category: disease-free everywhere, no vaccination (black, circle); disease-free everywhere, vaccination (square, blue); disease-free zones, no vaccination (diamond, green); disease-free zones, vaccination (triangle, red). Total outbreaks by countries without a designation ("not disease-free") ranged between 2164 to 24321 outbreaks annually.

may spread to commercial livestock (Jori et al., 2009; Sutmoller et al., 2003; Thomson et al., 2003).

Finally, the trading status of a country as recognized by the OIE includes the separation of production zones, but also a commitment to certain management practices prior to and in response to an outbreak (World Organisation of Animal Health (OIE), 2015). Therefore, we include a second set of binary variables that reflect disease management practices within a country and contribute to its 'disease-free' designation given by the OIE, such as the practice or prohibition of vaccination (http://www.oie.int). In addition to indicating the existence of wild endemic reservoirs, these variables serve as proxies for the trading behavior of a country - a country that prohibits vaccination will be more cautious of who and what they trade than a country that vaccinates its entire

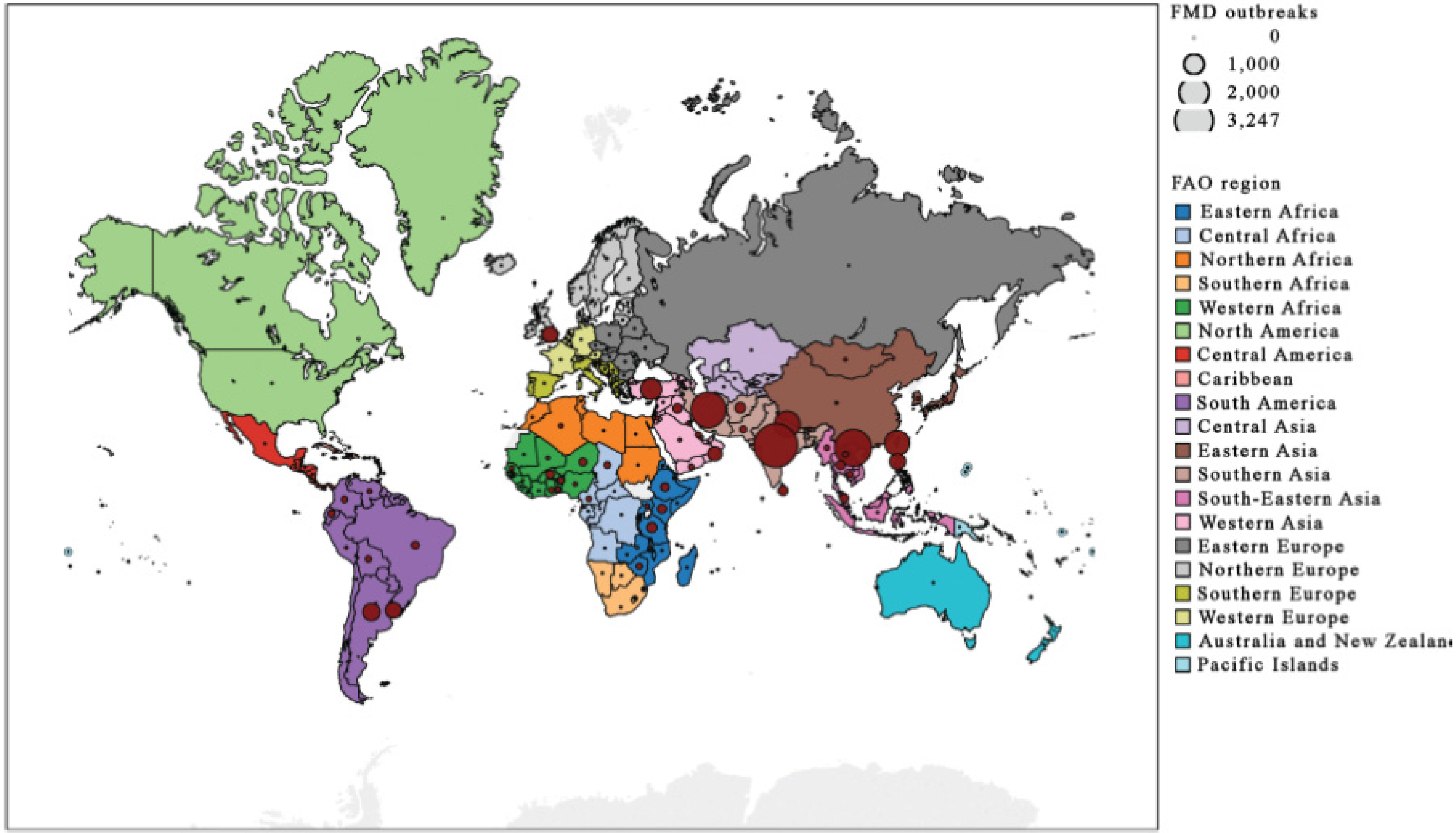

Figure 12. Global distribution of Food and Agriculture Organization (FAO) geographical regions as of 2011. Individual countries are colored according to their FAO geographic group. Melanesia, Polynesia, and Micronesia are lumped into a single "Pacific Islands" region. Circle size indicates the number of cumulative FMD outbreaks within a country during our study period. Information on the regional grouping of countries may be found at the FAO Trade Statistics Division (http://faostat3.fao.org/home/E). Outbreak data are from the World Organization of Animal Health (http://www.oie.int/).

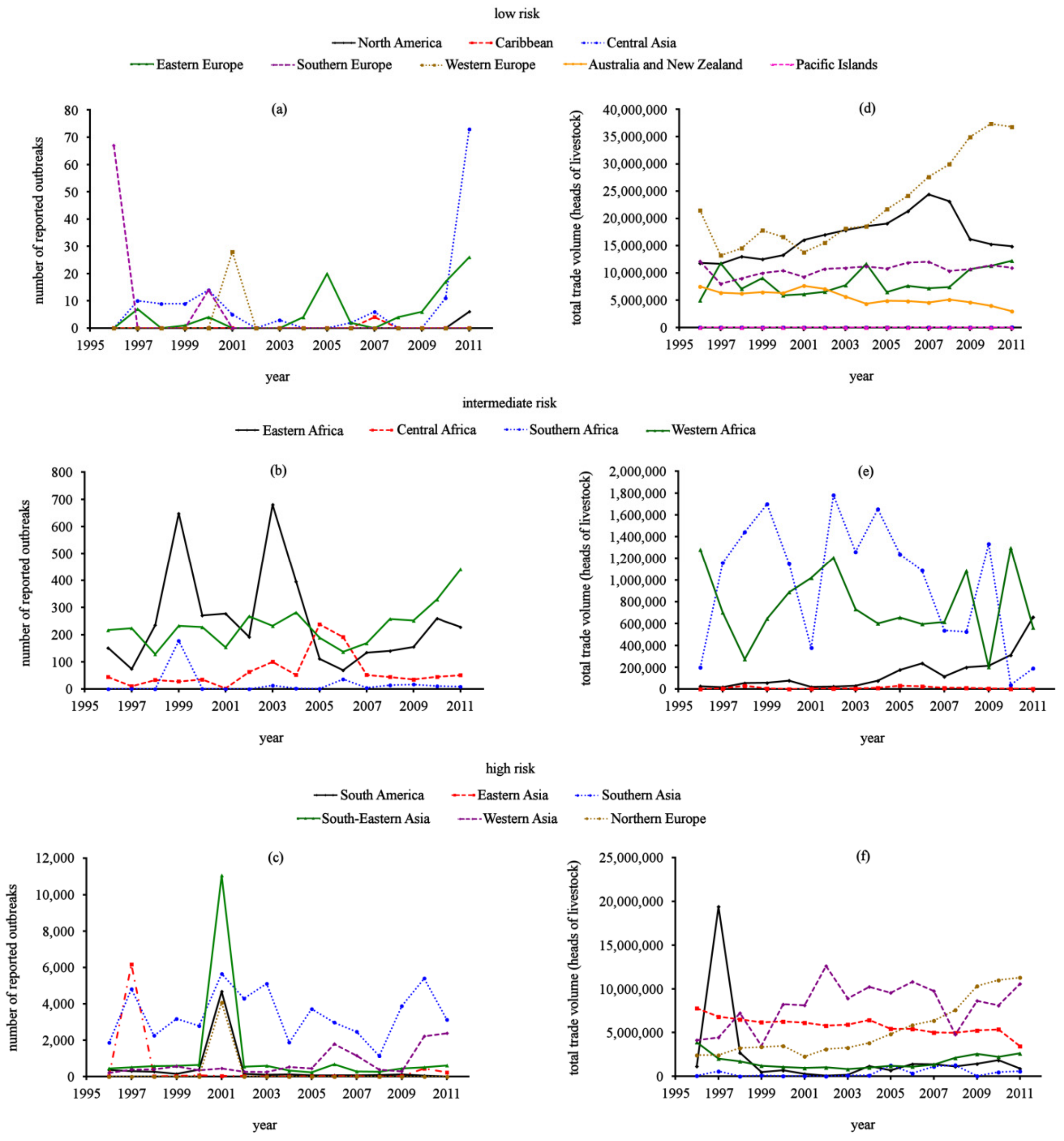

Figure 13. Regional number of reported outbreaks (a-c) and total trade volume (d-f) over time. Regions are sorted into three categories based on the maximum number of outbreaks in a single year: (a, d) low risk (< 100 outbreaks), (b, e) intermediate risk (< 1,000 outbreaks), and (c, f) high risk (> 1,000 outbreaks). The following regions reported no outbreaks in our study period: Central America, Australia and New Zealand, and the Pacific Islands. Total trade volume (d-f) is the regional sum of import and export quantity (heads) of cattle, sheep, and pigs.

national herd.[17] Similarly, countries that meet the requirements for a high disease-free designation will behave in ways that maintaining that designation.

Table 4 reports detailed summary statistics of the data included in our analysis. Table 5 presents correlation coefficients for all non-trade variables.

METHODS

In order to evaluate the effect of trade on relative disease risk, we first considered the impact of our various risk factors on the probability that an FMD outbreak was reported in the national herd in a given period. We report estimates of two models. The first is designed to give an overview of the relative risks associated with trade into and out of those countries in each of the five disease-free categories used by the OIE. The dependent variable is the number of new outbreaks reported in a country per year in our study period.

Traditionally various forms of the Poisson and negative binomial regressions are used to analyze count data (Cameron and Trivedi, 2005). While the Poisson is more robust to model misspecification than the negative binomial, our data are highly over-dispersed ($\mu = 40.15$, $\sigma = 316.20$) making the Poisson inappropriate. A zero-inflated Poisson with scaled variances also proved inadequate. Therefore we estimated a negative binomial, explicit panel model assuming fixed effects and standard errors. Our estimated negative binomial model is written as:

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[17] International market prices of meat are closely tied with a country's OIE disease-free designation with the lowest risk designation fetching the highest market price.

Table 4. Summary of outbreak data and independent variables.

Variable	Units	Mean	St. Dev.	Min	Max	Source
FMD outbreak	count	40.15	316.20	0	10625	OIE
FMD outbreak	binary	0.34	0.47	0	1	author
Agriculture value added	current US$	110.97E8	369.2E8	2802446	734.9E9	FAO
Livestock production index	-	99.07	17.04	36.15	236.08	FAO
Veterinarian density	#/km^2	0.29	2.12	8.58E-7	53.03	author
Existence of wild reservoirs	binary	0.06	0.23	0	1	OIE
Monitoring	binary	0.26	0.44	0	1	OIE
Precautions at the border	binary	0.60	0.49	0	1	OIE
Vaccinations practiced	binary	0.31	0.47	0	1	OIE
Vaccinations prohibited	binary	0.27	0.44	0	1	OIE
Zoning	binary	0.19	0.40	0	1	OIE
Stocks, cattle	# heads	8256939	2.49E7	5	2.13E8	FAO
Stocks, pigs	# heads	5673672	3.43E7	0	4.76E8	FAO
Stocks, sheep	# heads	6591824	1.70E7	420	1.78E8	FAO

The livestock production index is a unit less index of the aggregate volume of production of a country's livestock sector compared to a baseline (in this case, the production between 2004 to2006). Sources of data include the World Organization of Animal Health ("OIE"), Food and Agriculture Organization ("FAO") and author calculations ("author"). See text for details.

Table 5. Correlation coefficients for independent variables.

	FMD outbreak	Ag Val Ad	LPI	Vet density	Existence of wild	Monitoring	Border precautions	Vacc. practiced	Vacc. prohibited	Zoning	Stocks, cattle	Stocks, pigs	Stocks, sheep
FMD outbreak	1												
Ag Val Ad	0.12	1											
LPI	-0.05	0.08	1										
Vet density	-0.12	-0.06	0.09	1									
Existence of wild	0.15	0.18	0.11	-0.05	1								
Monitoring	0.26	0.08	0.27	-0.12	0.23	1							
Border precautions	0.02	0.09	0.24	-0.09	0.17	0.35	1						
Vacc. practiced	0.43	0.12	-0.01	-0.12	0.20	0.32	0.21	1					
Vacc. prohibited	-0.35	-0.02	0.15	-0.12	0.02	-0.03	0.40	-0.40	1				
Zoning	0.17	0.12	0.11	-0.10	0.39	0.33	0.37	0.35	0.06	1			
Stocks, cattle	0.17	0.64	-0.01	-0.07	0.06	0.06	0.10	0.22	-0.09	0.12	1		
Stocks, pigs	0.08	0.81	-0.00	-0.03	0.16	0.06	0.02	0.06	-0.02	0.10	0.44	1	
Stocks, sheep	0.11	0.72	0.02	-0.07	0.16	0.05	0.06	0.12	-0.10	0.06	0.53	0.73	1

[6] $$y_{it} \sim \text{Negative binomial}(\theta_{it}, \kappa)$$

[7] $$\theta_{it} = \exp\left[\alpha_i + \sum_{j=1}^{9} Z_{jit}^{'}\beta_j + \sum_{k=1}^{5} M_{ikt}^{'}\beta_{k+9} + \sum_{k=1}^{5} X_{ikt}^{'}\beta_{k+14} + \varepsilon_{it} \right]$$

for country *i* in year *t,* where the dependent variable is the probability that a number of FMD outbreaks were reported to the OIE by a country conditional on the linear predictors. The elements of *Z* include the following: values at risk, veterinarian density, and binaries for disease control measures and management factors contributing to a country's disease-free designation. Elements of *M* and *X* include the aggregate imports and exports of all cloven hoofed livestock between the country *i* and all other countries within each OIE disease-free designation category. The constant intercept and error terms are represented by α and ε respectively. The over-dispersion parameter, κ, is estimated automatically in the regression.

The data comprise an unbalanced panel. The model was estimated as a fixed effects negative binomial using the method of maximum likelihood with standard errors in Stata 14.0 (StataCorp, 2015). To correct for temporal autocorrelation and account for variation within individual countries, we treat the data explicitly as a panel and assume that country is a fixed effect.[18]

The second model is a more disaggregated model of trade by species in and out of the 20 FAO regions. This is meant to capture differences in risk between regions for the main species traded internationally. Due to nonlinearity in the model structure, estimation of the negative binomial by maximum likelihood methods can be difficult,

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[18] Nonlinearity in model structure prevented specification tests for fixed versus random effects. Independence between the fixed effect (country) and other covariates is a strong assumption. Relaxation of this assumption is left for future work.

particularly when dummy variables are used in the analysis (Allison and Waterman, 2002). Therefore we use a binary outbreak/no outbreak measure as our dependent variable (μ = 0.34, σ = 0.47).

Linear regression, logit/probit, and tobit models are frequently used for binary data (Cameron and Trivedi, 2005). Our data hardly fit the assumptions for ordinary least squares regression, nor is the data truncated. We therefore estimated a logit model of the form:

[8] $$\Pr(y_{it} = 1) = \left[1 + \exp\left(-\theta_{it}\right)\right]^{-1}$$

[9] $$\theta_{it} = \exp\left[\alpha_i + \sum_{j=1}^{12} Z'_{jit}\beta_j + \sum_{s=1}^{3}\sum_{k=1}^{20} M'_{ikt}\beta_{20s+k-8} + \sum_{s=1}^{3}\sum_{k=1}^{20} X'_{ikt}\beta_{20s+k+52} + \varepsilon_{it}\right]$$

for country *i* in year *t*, where the left-hand side of equation [1] is a binary indicator that an FMD outbreak was/was not reported to the OIE conditional on the linear predictors. Specifically $y_{it} = 1$ when a country reported an outbreak; $y_{it} = 0$ when no outbreaks were reported to the OIE. The elements of Z include the value at risk, veterinarian density, and a set binary biosecurity variables. Elements of *M* and *X* include aggregate imports and exports between the country *i* and all regions *k* of cattle, pigs, and sheep. Although trade data are available on other species that may transmit FMD, far fewer countries are involved and there is a high degree of collinearity between the data on other species. The constant intercept and error terms are represented by α and ε respectively. The logistic model was estimated using the method of maximum likelihood with robust standard errors in Stata 14.0 (StataCorp, 2015), explicitly treating country as a random effect.

We estimated the logistic model with and without a one-year lag in trade. Disease spread, particularly through trade, is not instantaneous. Like an invasive species, a virus must be physically transported to a new location and establish a large enough population to be detected. However, there is uncertainty about the mean length of the lag. The FMD virus may persist in animals, animal products, and the environment from days to months (Cottral, 1969; Paton et al., 2010). Once introduced, spread and detection will vary by species and biosecurity in the new location (Alexandersen et al., 2003).

We then used our estimates to calculate the relative economic risks associated with trade. We took the trade-related relative economic risk of FMD outbreak as the product of the relative probability of disease occurrence and the magnitude of potential damages of an FMD outbreak. The former was calculated directly from the odds ratio, the exponential of the betas generated from the logistic regression (Gelman and Hill, 2007). By subtracting one from the odds ratio we calculate the change in the odds for a unit change in the independent variable. Although it is generally understood that the odds ratio overestimates relative risk when greater than one and underestimates when less than one, the degree of deviation between the two is more severe at high odds ratios and when the event is very likely to occur (Cohen, 2000; Davies et al., 1998; Zhang and Yu, 1998). The magnitude of potential damages is taken as the value at risk. Using the United Kingdom in 2011 as an example, we present two potential values of the economic value at risk: the value of all exports of cattle, sheep, and pigs (direct economic losses of a time-lapse of trade) and the dollar value of the agriculture sector. These provide lower and upper bounds to risk.

RESULTS

Our results on the relative disease risks of trade, and the impacts of risk factors are summarized in Tables 6 through 10. The results of the disease-free designation trade aggregation model (negative binomial, explicit panel, fixed effects and standard errors) are reported in Table 6. The results of the disaggregated regional trade model (logistic, explicit panel, random effects and robust standard errors) are reported in Tables 7 through 10. Since the disaggregated model has a large number of trade variables, we only present trade results that are statistically significant at the ten percent level. Detailed lists of all trade results may be found in Appendix J.

Of our measures of value at risk, the livestock production index was selected as a measure of the development of a country's livestock industry. We found this to be negatively correlated with the probability of reporting disease outbreaks in both models. Countries in which agricultural productivity was rapidly increasing were less likely to experience FMD outbreaks than countries in which agricultural output was stagnating. Our other measures of value at risk were either uncorrelated with or did not significantly alter the odds of reporting an outbreak.

Of the measures that serve as proxies for the existence of wild reservoirs of FMD in a country — monitoring, the control of wild reservoirs, and zoning — all were positively correlated with the probability of an outbreak in both models, although their significance varied between models. In countries that actively pursue such control measures the disease is endemic in either wild or domesticated populations, and this presents a source pool of disease that may spread to commercial livestock. In countries

Table 6. Negative binomial estimates of exogenous and trade variables.

	Variable	IRR	p-value
	Agriculture value added	1.000*	0.071
	Livestock production index	0.993*	0.042
	Veterinarian density	0.001	0.191
	Existence of wild reservoirs	1.326	0.136
	Monitoring	1.377*	0.006
	Vaccinations practiced	1.200	0.152
	Vaccinations prohibited	0.568*	0.014
	Zoning	0.895	0.429
	Stocks (cattle, sheep, pigs)	1.000	0.752
Importing from:	Disease-free, no vaccination	0.999999*	0.054
	Disease-free, vaccination	1.000000	0.909
	Disease-free zones, no vaccination	1.000004	0.706
	Disease-free zones, vaccination	1.000003*	0.075
	Not disease-free	1.000002*	0.007
Exporting to:	Disease-free, no vaccination	0.999998*	0.088
	Disease-free, vaccination	0.997832*	0.014
	Disease-free zones, no vaccination	0.999997	0.190
	Disease-free zones, vaccination	1.000023*	0.047
	Not disease-free	1.000000	0.446
	Constant	-0.570	0.112
	N	761	
	Log-likelihood	-1875.90	
	AIC	3789.81	
	BIC	3877.86	

Note that the dependent variable is the number of new outbreaks. Estimates are reported as incidence rate ratios (IRRs). Due to nonlinearity in the maximum likelihood function, convergence of the negative binomial model is sensitive to correlation between independent variables and binary data (Allison and Waterman, 2002). Therefore, stocks of cattle, pigs, and sheep were aggregated into a single variable and the presence of border precautions was dropped from the analysis. Non-trade data and p-values are rounded to three decimal places; trade data are rounded to six. A single asterisk denotes significance at a 10% level.

Table 7. Logistic regression estimates of exogenous variables.

	no trade lag		*one-year trade lag*	
Variable	Odds ratio	p-value	Odds ratio	p-value
Agriculture value added	1.000*	0.036	1.000*	0.031
Livestock production index	0.970*	0.035	0.951*	0.001
Veterinarian density	0.000*	0.020	2.940E-10*	0.014
Existence of wild reservoirs	5.794*	0.002	5.282	0.111
Monitoring	2.601*	0.027	3.801*	0.004
Precautions at the border	0.607	0.404	0.586	0.316
Vaccinations practiced	2.083	0.181	0.922	0.895
Vaccinations prohibited	0.226*	0.024	0.197*	0.009
Zoning	10.004*	0.000	21.734*	0.000
Stocks, cattle	1.000	0.810	1.000	0.344
Stocks, pigs	1.000*	0.069	1.000*	0.000
Stocks, sheep	1.000	0.623	1.000*	0.005
Constant	2.903	0.441	14.540	0.103
N	1307		1298	
Psuedo log-likelihood	-290.194		-245.528	
AIC	800.039		707.057	
BIC	1369.343		1265.263	

Note that the dependent variable is a binary outbreaks/no outbreaks indicator. Odds ratios are rounded to three decimal places. A single asterisk denotes significance at a 10% level.

that actively pursue such control measures the disease is endemic in either wild or domesticated populations, and this presents a source pool of disease that may spread to commercial livestock. In countries that implement disease-free zones alongside wild reservoirs, the control and isolation of wild animals in which the disease is endemic is the primary goal of management (Jori et al., 2009).

Table 8. Logistic regression trade estimates from imports.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Importing from:	*Cattle*				
	Eastern Africa	-	-	1.0003	0.055
	Northern Africa	-	-	0.9965	0.033
	Southern Africa	-	-	0.9999	0.048
	Western Africa	0.9992	0.062	1.0022	0.005
	North America	1.0006	0.000	-	-
	Central America	0.9993	0.096	-	-
	Eastern Asia	0.9999	0.002	1.0003	0.001
	Southern Asia	1.0003	0.057	-	-
	Western Europe	0.9999	0.024	-	-
	Pacific Islands	1.0294	0.002	1.0734	0.005
	Pigs				
	Eastern Africa	-	-	1.0074	0.062
	North America	0.9991	0.014	-	-
	Caribbean	-	-	1.0934	0.047
	Central Asia	-	-	1.0160	0.015
	Eastern Asia	-	-	1.0001	0.000
	Southern Asia	-	-	1.3422	0.035
	Western Asia	1.0181	0.000	-	-
	Northern Europe	-	-	0.9997	0.054
	Southern Europe	0.9996	0.022	0.9984	0.095
	Western Europe	-	-	1.0002	0.024
	Australia and New Zealand	0.9907	0.039	0.9846	0.005
	Sheep				
	Eastern Africa	-	-	0.9999	0.019
	Southern Africa	0.9991	0.060	-	-
	South America	-	-	0.9999	0.060
	Central Asia	-	-	1.0035	0.053
	South-Eastern Asia	0.9961	0.001	0.9898	0.005
	Eastern Europe	-	-	1.0001	0.042
	Northern Europe	-	-	1.0007	0.033
	Southern Europe	0.9996	0.049	1.0009	0.079

P-values are rounded to three decimal places; trade data to four. A dash indicates an estimate not significant at the 10% level.

Table 9. Logistic regression trade estimates from exports.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Exporting to:	*Cattle*				
	Eastern Africa	1.0000	0.032	-	-
	Southern Africa	1.0006	0.068	-	-
	North America	1.0214	0.000	-	-
	Central Asia	0.9989	0.000	0.9978	0.004
	Eastern Asia	1.0001	0.032	-	-
	South-Eastern Asia	0.9999	0.002	0.9997	0.007
	Western Asia	1.0000	0.024	-	-
	Pigs				
	Eastern Africa	0.9979	0.005	-	-
	Southern Africa	-	-	0.9888	0.010
	Western Africa	-	-	1.0014	0.069
	Eastern Asia	-	-	0.9999	0.000
	Southern Asia	-	-	2.1892	0.041
	South-Eastern Asia	1.0000	0.030	1.0001	0.026
	Western Asia	1.0011	0.075	1.0021	0.059
	Southern Europe	-	-	0.9998	0.009
	Australia and New Zealand	-	-	0.1329	0.015
	Sheep				
	Southern Africa	1.0000	0.064	-	-
	Western Africa	-	-	1.0000	0.069
	Central America	0.9859	0.005	0.9604	0.037
	Caribbean	-	-	1.0288	0.035
	Central Asia	-	-	1.0011	0.079
	Eastern Asia	1.0004	0.012	0.9984	0.018
	Southern Asia	1.0006	0.000	1.0010	0.002
	South-Eastern Asia	0.9989	0.029	-	-
	Western Asia	-	-	1.0000	0.085
	Pacific Islands	1.5025	0.042	-	-

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A dash indicates an estimate not significant at the 10% level.

Table 10. Relative economic risks (RER) of trade (*no trade lag*).

	Variable	Odds ratio	Δ in odds	United Kingdom RER (lower) (million US$)	United Kingdom RER (upper) (million US$)
Importing from:	*Cattle*				
	North America	1.0006	0.0006	0.017	10.998
	Southern Asia	1.0003	0.0003	0.007	4.508
	Pigs				
	Western Asia	1.0180	0.0181	0.468	308.194
	Australia and New Zealand	0.9907	-0.0093	-0.241	-158.942
	Sheep				
	Southern Africa	0.9991	-0.0009	-0.024	-15.651
	Southern Europe	0.9996	-0.0004	-0.010	-6.477
Exporting to:	*Cattle*				
	Southern Africa	1.0006	0.0006	0.015	10.1098
	South-Eastern Asia	0.9999	-0.0001	-0.002	-1.317
	Pigs				
	Eastern Africa	0.9979	-0.0021	-0.054	-35.652
	Western Asia	1.0011	0.0011	0.029	19.024
	Sheep				
	Central America	0.9859	-0.0141	-0.365	-240.477
	Eastern Asia	1.0004	0.0004	0.011	7.155
	UK value of exports (million US$)			25.918	
	UK agriculture value added (billion US$)			17.077	

Relative economic risk (RER) is the product of the probability of FMD outbreak (change in the odds) and the magnitude of potential damages. We tested two measures of damages: the value of all exports of cattle, pigs, and sheep (lower bound), and the value of the agriculture sector (upper bound). RER is from the perspective of the United Kingdom in 2011.

We had expected precautionary biosecurity measures to be negatively correlated with disease outbreaks. We found a strong negative correlation between the density of veterinarians and FMD outbreaks, significant at the 5 per cent level in the more disaggregated model but only at the 20 per cent level in the more aggregated model. In the more disaggregated model, border precautions were essentially uncorrelated with FMD outbreaks. Also, we found that the prohibition of vaccination was associated with a substantial reduction in the probability of a country reporting an outbreak, while the practice of vaccination did not have a significant effect in either model. We discuss the implications of these findings later.

Our primary interest in the chapter is the relationship between trade and disease risk. The disease-free categories used by the OIE are also trade categories, since they are used in regulating which countries have access to certain markets. To get an overview of the impact of the OIE trade structure on disease risk, consider the more highly aggregated model reported in Table 6. These estimates show the association between the relative risk of reported FMD outbreaks and the volume of trade into and out of countries belonging to each of the OIE's main disease-free categories:

1. disease-free, without vaccination
2. disease free with vaccination
3. disease free zones without vaccination
4. disease free zones with vaccination
5. not disease free

We had expected that the risks of trade would be lowest for countries having disease-free status, and highest for those where the disease is endemic. Consistent with our expectations we found that imports from countries in the first two categories were risk reducing (although this was significant only for the first category), and that imports from the last three disease categories were risk increasing (significant for the last two categories). We also found that exports into countries in the first three disease categories were risk reducing (significant for the first two categories), and that exports into the last two categories were risk increasing (significant for the fourth category).

The more disaggregated model reported in Tables 7 to 9 provides an alternative perspective on the relation between trade and disease risks in the intermediate OIE disease categories. The results turned out to be more mixed. We had expected the probability of outbreaks to be increasing in imports of animals from regions in which FMD is known to be endemic and our results generally confirm this. Some geographical regions make safer trading partners than others. Imports from regions experiencing no outbreaks were generally negatively correlated with the probability of reported outbreaks. However, we also found anomalies. With the exception of the 1997 Taiwan outbreak and a 2011 outbreak in Bermuda, Eastern Asia, North America, and the Pacific islands were free of FMD over the study period. In fact, with the exception of Bermuda, the North American region has not had an FMD outbreak in over 50 years (Metcalf and McElvaine, 1995). Yet in both *no trade lag* and *one-year trade lag* models, imports from all three regions were positively correlated with the likelihood of FMD outbreaks in the importing country.

We also found a number of region-specific differences between species. For example, for imports with the *no trade lag* model, cattle brought in from Southern Asia were positively correlated with the probability of reported FMD outbreaks in importing countries, but cattle brought in from Central America and Western Europe were negatively correlated with reported outbreaks. Among pigs, imports from Western Asia were positively correlated with reported outbreaks, but imports from North America, Southern Europe, and Australia and New Zealand were all negatively correlated with reported outbreaks. For sheep, imports from Southern Africa, South-Eastern Asia, and Southern Europe were all negatively correlated with reported FMD outbreaks.

We had less well-defined expectations about the indirect effect of exports on disease risks. For many regions, exports were negatively correlated with FMD outbreaks in the exporting country. In the *no trade lag* model, examples include cattle to Central and South-Eastern Asia; pigs to Eastern Africa; sheep to Central America and South-Eastern Asia. However, we also found exports of cattle to Southern Africa, North America, and Eastern Asia to be positively associated with reported outbreaks. Similarly, exports of pigs to Western Asia and sheep to Eastern and Southern Asia, and the Pacific Islands were also all positively correlated with FMD outbreaks in the exporting country.

In general, a greater number of trade variables were associated with FMD outbreaks in the *one-year trade lag* model than the *no trade lag* model. This is particularly true for imports and exports of pigs and sheep. This may be due to differences in the conditions in which species are transported or the biology between species - all of which affect the length of time between when the virus and transported and when an outbreak is detected.[19] A lag may be more appropriate for trade in sheep and pigs than cattle. Nonetheless with the exception of several regions/species, overlapping estimates of risk are consistent between the two models. See, for example, imports of sheep from South-Eastern Asia and Southern Europe, or exports of pigs to South-Eastern and Western Asia.

Based on these results we then calculated the trade-related FMD risk by region, multiplying the relative probability of disease occurrence by the value at risk. Using the United Kingdom in 2011 as example, we present two potential values of the economic relative risk: the value of exports of livestock (sum of all cattle, sheep, pigs) and the contribution of the agricultural sector to GDP. These approximate the lower and upper bounds to risk. The results are reported in Figures 14 and 15 and Table 10.

Note that negative risk, in this context, implies that an increase in trade with a particular region will reduce the likelihood of disease outbreaks. That is, it implies the mitigation of risk. Positive risk, by contrast, implies that an increase in trade with a particular region will increase the likelihood of disease outbreaks. The risk as measured by foregone live animal export earnings (lower bound) is relatively minor. The risk as measured by output in the whole agriculture sector (upper bound) may be quite large.

Regardless of the time lag model, the greatest impact of imports and exports on relative economic risk are associated with low-income regions where biosecurity may be lax. However, the impact on risk of high-income regions where trade volumes are high can still be significant, e.g. North America and Eastern Asia.

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[19] Typically cattle are more susceptible and more readily exhibit symptoms of FMD than pigs or sheep (Alexandersen et al., 2003).

DISCUSSION

The disease risks of trade depend on the structure and volume of trade in live animals, the biosecurity measures undertaken by trading partners, and on the interactions between the two. As we had expected, we found a generally positive relationship between the volume of live animals *imported* from riskier countries and the probability of reported disease outbreaks. Globally, trade with disease-free countries is negatively associated with reported outbreaks; trade with countries experiencing outbreaks or where the disease is endemic amongst wild populations are positively associated with reported outbreaks. These are the most intuitive and transparent trade-related risks revealed by our models.

At the international scale, our findings on *imports* are broadly consistent with others (Berentsen et al., 1992; Garner and Lack, 1995; Hartnett et al., 2007; Martinez-Lopez et al., 2008; Miller et al., 2012; Schoenbaum and Disney, 2003) even though our methods are different. Berentsen et al. (1992), Garner and Lack (1995), and Schoenbaum and Disney (2003), for example, used simulations in a coupled epidemiological-economic framework. Hartnett et al. (2007), Martinez-Lopez et al. (2008), and Miller et al. (2012), grounded their analysis in data, as we do, but relied on simulations to determine the probability of introduction using a much smaller range of trading partners. Nevertheless our estimates of import risk often reach the same conclusions.

Perhaps counter-intuitively, we also found that *imports* of cattle from the North American region were positively associated with the probability of FMD introduction, yet the United States has not experienced an FMD outbreak since 1929

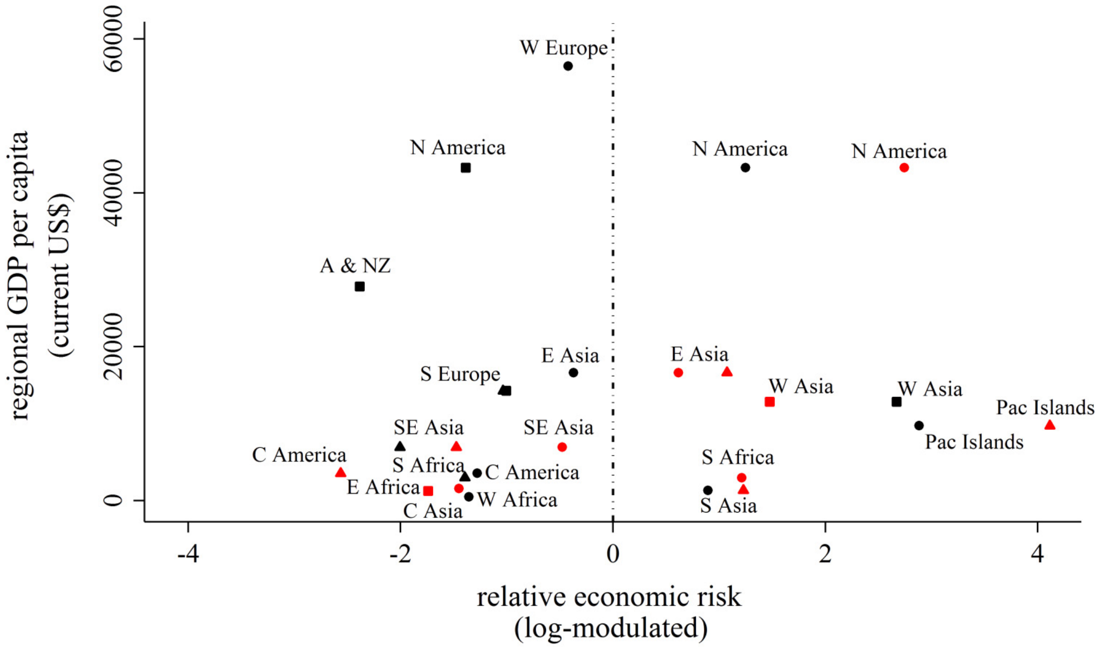

Figure 14. Regional GDP per capita versus relative economic risk calculated from the *no trade lag* model. Regional GDP is the average GDP per capita of all nations within a region averaged over the study period (1996-2011). Relative economic risks have been log-modulated. Marker color indicates imports (black) or exports (red), while the species is given by the marker shape (circle, cattle; square, pigs; triangle, sheep). Regions are labeled next to their corresponding marker. Zero relative economic risk of trade is plotted as the dot-dashed reference line.

(Sellers and Daggupaty, 1990). This is partly due to the geography of the FAO regions. Bermuda, part of the North America region, experienced an outbreak in 2011. But other have reached similarly counterintuitive conclusions from analyses conducted at the country level. Miller et al. (2012), for example, found the probability of FMD introduction to the United States from Canada to be positive (0.048%).

In two other respects our findings differ from those in the wider literature. The trade vehicles returning from infected areas as a source of risk. However, it has not previously been revealed as a general source of risk. We conjecture that it may include the risks associated with complex vessel itineraries. We found, for example, that the

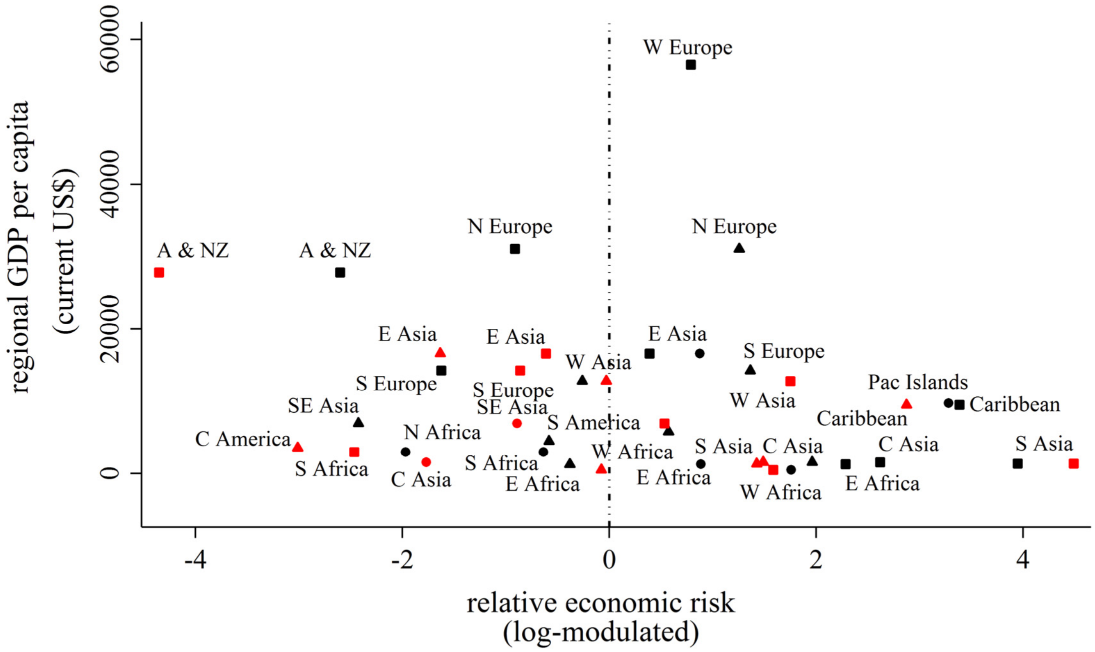

Figure 15. Regional GDP per capita versus relative economic risk calculated from the *one-year trade lag* model. Regional GDP is the average GDP per capita of all nations within a region averaged over the study period (1996-2011). Relative economic risks have been log-modulated. Marker color indicates imports (black) or exports (red), while the species is given by the marker shape (circle, cattle; square, pigs; triangle, sheep). Regions are labeled next to their corresponding marker. Zero relative economic risk of trade is plotted as the dot-dashed reference line.

first is that we found *exports* to be as strongly correlated with disease risk as *imports*. This is consistent with findings on African swine fever by Mur et al. (2012) that identify greatest export risks were associated with trade into regions characterized by high trade volumes and a complex trade network—North America and East Asia (Figures 14 and15, Tables 11 and 12).[20] This suggests that treating trade flows as unidirectional(considering

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[20] Alternatively a spatial model would capture direct and indirect sources of risk. A gravity model, for example, would incorporate all possible linkages between spatial locations into a single summary measure of disease exposure (Anderson, 2011; Thomas and Huggett, 1980).

only the propagule pressure associated with imports) may overlook a significant source of disease risk.

The second difference concerns countries with intermediate disease status at the OIE. At the extremes of the OIE spectrum, the conclusions from the disease status and regional models coincide. High-risk geographical regions (e.g. Western, Central, and South-Eastern Asia; Western and Eastern Africa) have disease endemic status, and the low-risk geographical regions have disease-free status (Figures 10 and 12). Our estimates of the risk of trade into and out of both geographical regions and OIE zones are consistent with this observation. Tables 11 and 12 present risk estimates for both trade aggregations.[21]

At intermediate disease designations, the ability of the disease-free grouping model to estimate risk is less clear. Although the direction of impact is as expected, the IRR estimates are not sufficiently precise to determine the sign of the effect. When aggregating trading partners by geographical region we found differences between the three main regions sharing intermediate designations: South America, Southern Africa, and South-East Asia. While trade with countries carrying intermediate disease was positively associated with FMD outbreaks in the disease-free grouping model, much of this was likely due to a large number of outbreaks in South America during the early 2000s (Figures 10, 12, and 13). Other countries implementing vaccination protocols, such as Botswana and Malaysia, had few or no outbreaks during the study period (Figures 10 and 12).

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[21] In order to compare the odds ratios of the logistic to relative risk estimates of the negative binomial, we convert odds ratios to the change in the odds. Since our odds ratios do not significantly deviate from one they should provide a reasonable approximation of relative risk (Cohen, 2000; Zhang and Yu, 1998).

Neither does the disease-free grouping capture the effect of different species on risk or regional differences in trade volumes that, by our analysis, are contributing risk factors. Different species have different degrees of susceptibility and infectivity to FMD (Alexandersen et al., 2003; Sutmoller et al., 2003), and we would expect animal husbandry standards and biosecurity measures to differ between types of livestock production.[22] In this respect there is added value in using a regional trade aggregation to evaluate the risks of trade.

Our findings on the relation between disease outbreaks and biosecurity measures were largely as expected. To interpret these, however, note that several of the measures tested are themselves evidence for the existence of wild FMD reservoirs in the country. The control of wild reservoirs, zoning, and monitoring are all activities that take place in countries where participation in the international live animal trade is conditional on maintaining disease-free compartments. Since the existence of wild reservoirs increases the risks to a country's trading partners, it is not surprising that these activities are positively and significantly related with disease outbreaks.

The two biosecurity measures tested, the density of veterinarians and precautions at the borders, were both expected to be increasing in the value at risk, and so to be negatively related to the probability of disease outbreaks. While the density of veterinarians was indeed negative, we found that the existence of protective measures at

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[22] Pigs tolerate proportionately larger dosages of virus compared to cattle and sheep before contracting the disease but infected pigs proportionately excrete the virus in larger quantities than cattle and sheep (see Alexandersen *et al.* (2003) for a review of this literature). At the same time, while cattle may have a lower excretion of the virus per unit body mass than pigs, their greater size may make them excrete greater quantities of the virus and so pose a larger risk (Sutmoller et al., 2003).

the border was uncorrelated with the probability of FMD outbreaks. Similarly, the practice of vaccination was not a significant factor in FMD disease risk. The prohibition

Table 11. Comparison of trade aggregations for imports.

	Variable	Odds ratio	p-value
Importing from:	*Cattle*		
	Western Africa	0.9992	0.062
	North America	1.0006	0.000
	Central America	0.9993	0.096
	Eastern Asia	0.9999	0.002
	Southern Asia	1.0003	0.056
	Western Europe	0.9999	0.024
	Pacific Islands	1.0294	0.002
	Pigs		
	North America	0.9991	0.014
	Western Asia	1.0180	0.000
	Southern Europe	0.9996	0.022
	Australia and New Zealand	0.9907	0.038
	Sheep		
	Southern Africa	0.9991	0.061
	South-Eastern Asia	0.9961	0.001
	Southern Europe	0.9996	0.049

	Variable	IRR	p-value
Importing from:	Disease-free, no vaccination	0.999999	0.054
	Disease-free, vaccination	1.000000	0.909
	Disease-free zones, no vaccination	1.000004	0.706
	Disease-free zones, vaccination	1.000003	0.075
	Not disease-free	1.000002	0.007

Note that odds ratios for the *no trade lag* model are presented for the regional trade aggregation.

Table 12. Comparison of trade aggregations for exports.

	Variable	Odds ratio	p-value
Exporting to:	*Cattle*		
	Southern Africa	1.0006	0.068
	North America	1.0214	0.000
	Central Asia	0.9989	0.000
	Eastern Asia	1.0001	0.032
	South-Eastern Asia	0.9999	0.002
	Pigs		
	Eastern Africa	0.9979	0.005
	Western Asia	1.0011	0.074
	Sheep		
	Central America	0.9859	0.005
	Eastern Asia	1.0004	0.013
	Southern Asia	1.0006	0.000
	South-Eastern Asia	0.9989	0.029
	Pacific Islands	1.5025	0.042

	Variable	IRR	p-value
Exporting to:	Disease-free, no vaccination	0.999998	0.088
	Disease-free, vaccination	0.997832	0.014
	Disease-free zones, no vaccination	0.999997	0.19
	Disease-free zones, vaccination	1.000023	0.047
	Not disease-free	1.000000	0.446

Note that the odds ratios for the *no trade lag* model are presented for the regional trade aggregation.

of vaccination, on the other hand, was strongly negatively correlated with the probability of reported outbreaks. There are two reasons for this. First, the prohibition of vaccination generally indicates the lack of any wild reservoir of the disease. Second, countries that prohibit vaccination are more cautious about what they trade and with whom.

Our analysis does have its limitations. While we identify correlations between observed outbreaks and factors that may be implicated in their occurrence, we are not able to assign causality.[23] Nor can we exclude the possibility that certain explanatory variables are biased. This creates a potential problem in identifying the true effect of our variables. The most likely sources of bias are: unobserved heterogeneity in the sample, omitted variables bias, and simultaneity (Kennedy, 2008). We take each of these in turn.

There is potential in both models that the errors are spatially correlated due to unobserved, time-varying events affecting the animal movement across borders of adjacent countries (e.g. conflict, famine, smuggling, natural disasters, etc.). This would lead to spatially correlated effects on reporting and/or the outcomes themselves. If present, however, this should be at least partially captured by country-level fixed effects.[24] Nor do our models account for bias in reporting outbreaks between countries

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[23] In economics, difference-in-differences, instrumental variables, and regression discontinuity design (RDD) experiments have been shown to be viable methods for establishing causation outside of randomized experiments (Lee and Lemieux, 2010). Difference-in-differences requires countries to experience the same trend in disease in the absence of a treatment (Card and Krueger, 1994; Angrist and Pischke, 2009). Given the nature of our data, this assumption is not likely to be met. Instrumenting for all potentially endogenous variables is not feasible given the large number of trade variables. Due to its relatively mild assumptions and credibility of causal inferences (Lee and Lemieux, 2010; Imbens and Lemieux, 2008; Hahn et al., 2001) we discuss applying a RDD experiment for our data in Appendix K.

[24] The logistic further assumes that the "choice" of the dependent variable is independent over time (Train, 2009). That is, past states have no influence on the current state and there is no lag in the response of the dependent variable to the independent variables. The *one-year trade lag* model should at least partially

("endogenous stratification"). While we expect differences in measurement and reporting between countries, the local involvement of the OIE in its member countries should help alleviate potential sampling bias. (Though see Shaw (1988), Englin and Shonkwiler (1995), and Richards et al. (2014) for techniques to account for endogenous stratification.)

So far as omitted variable bias is concerned, while we believe that we have accounted for the most relevant factors in the international spread of FMD, we cannot exclude the possibility that there are others. Live animals are not the only source of risk, and we lack detailed data on shipping routes and trade in other risk materials. The FMD virus is capable of persisting in the environment for extended periods of time ranging from weeks to months depending on the nature of the contaminated material (manure, bedding, fodder, clothing, equipment) and environmental conditions (temperature, humidity, pH) (Alexandersen et al., 2003; Callis, 1996; Paton et al., 2010; Ryan et al., 2008; Sutmoller et al., 2003). Therefore it would be useful to consider the trade in other risk materials that may potentially spread FMD, including meat, milk, hides, and skins.

For simultaneity, we expect trade responses to outbreaks to occur within the same year as the outbreak. To address this we time-lag the trade data. This should help alleviate the problem although there is a large degree of uncertainty about the mean length of the lag. Resistance, persistence, and infectivity varies significantly across species and environments (Alexandersen et al., 2003).

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account for potential autocorrelation of the dependent variable and endogeneity between our dependent and trade variables (Adamowicz, 1994).

Four other issues are worth mentioning. First, for the more disaggregated model the odds ratios provide less reliable approximations of relative risk as incidence rates increase or as the odds ratio deviates from one (Cohen, 2000; Zhang and Yu, 1998). Odds ratios less than one tend to underestimate relative risk; odds ratios greater than one overestimate it (Zhang and Yu, 1998). It is likely that our proxies for wild reservoirs (veterinarian density) overestimate (underestimate relative) risk, though we believe that we have correctly identified the direction of the effect.

Second, as with other parametric studies we assume a particular functional form for our models that does not explicitly account for the "tailed" nature of FMD outbreaks. Nonparametric methods exist to estimate the probability density function of continuous data, though they are less used in conventional statistics (Higgins, 2004). See Bean and Tsokos (1980), Cleveland and Devlin (1988), Izenman (1991), Racine and Li (2004), and Wolter (2016) for reviews and recent applications of this literature.

Third, aggregating trade by disease status or region loses a certain degree of spatial resolution. Our estimates are, from a global perspective, the change in probability that a country will have reported an outbreak given that it engaged in a particular biosecurity measure. This is different than an analysis on the effect of biosecurity on the probability of an outbreak within a single country. This potentially matters if the sanitary conditions and regulations pertaining to the surveillance and monitoring for disease are very different between the countries in a particular region. The risks undertaken by an importing or exporting country depend on biosecurity measures at the point of entry, which vary from country to country. The global risks of importing livestock is likely an overestimate for a country such as the United States, which has stringent protocols at the border, and an underestimate for developing countries whose border security is lax.

It would be helpful to have precise estimates of the different risks associated with biosecurity and trade for individual countries. Indeed, the Global FMD Disease Control Strategy relies heavily on increasing on increasing biosecurity, particularly the development of veterinary services and vaccination, in transitioning developing endemic countries to disease-free with vaccination status (World Organisation of Animal Health (OIE) and Food and Agriculture Organization (FAO), 2012).

Fourth, a long-term average estimate of risk will be appropriate for countries whose conditions remain relatively constant over the study period, but less appropriate for countries that experience short-term fluctuations in disease or trade. For instance, Eastern Asia, Northern Europe, and South America are often low risk areas - each region experienced a large number of reported outbreaks during the 1997 Taiwan and 2001 United Kingdom/Uruguay epidemics (Figure 13). We also observe marked changes in trade volumes around the 2007-2009 recession, when patterns of disease risk parallel those of trade (Figure 13).

In the future, we hope to explicitly account for changes in trade networks. The "natural" response by an importing country to a FMD outbreak is to impose trade bans on high risk products from the exporting country with FMD (Grubman et al., 2008), e.g. to cut off propagule pressure of risk materials. The World Trade Organization makes available information of the initialization, length, and termination of trade sanctions between countries in response to food and mouth outbreaks. However, we were unable to exploit such information in this paper.

CONCLUSION

To conclude, it is worth repeating our central finding that the indirect disease risks associated with exports may be as large or greater than those associated with imports, and that high-risk regions are characterized more by high trade volumes and complex trade networks than by lax biosecurity measures. Current risk assessments that consider only the risk posed by direct propagule pressure—the one-way threat posed by imports—may therefore overlook a potentially significant risk factor for the spread of FMD. Ignoring the indirect effects of exports means that the "natural" trade response to disease—banning imports—may prove less effective at mitigating risk than the many countries would like to believe. We also find that a country's disease-free status provides a reasonable approximation of the riskiness of trading with that country, but a regional grouping captures finer-scale and species-specific characteristics of risk. This can potentially inform targeting of trade actions to mitigate disease.

5 CONCLUSIONS

Common themes

My dissertation is a story about environmental risk, and how species dispersal mitigates or exacerbates environmental risk in ecological and social-ecological systems. Traditionally risk is measured as the probability of an event occurring multiplied by the magnitude of that event. A "high risk" event could be one with a high probability of occurring or whose damage is quite large. The inverse can be said for a "low risk" event.

In chapters 2 and 3 I look at the role of natural dispersal in mitigating environmental risk. Chapter 4 evaluates the role of anthropogenic dispersal via trade in exacerbating disease risk. Across all chapters I find that the risks associated with the spread of species depend on the biological and human components of the system, and the interaction between the two. For example, in a pure ecological system (chapter 2) species interactions and dispersal are the driving factors for the relative abundances of species in the system. Intermediate dispersal rates between locations provide the necessary source-sink effects to maximize biodiversity and the stability of productivity.

In a coupled social-ecological system (chapter 3) the risks associated with dispersal are less clear. The relationship between biodiversity and dispersal can be monotonically increasing or non-monotonic depending on the interaction between ecological and economic parts of the system - the competitive interactions between species, the set of relative prices for species harvest, and the distribution of those prices at each location across the system. Harvest places non-random pressure on the ecological system. It interacts with intra-specific species competition to determine the relative abundances of species. When human preferences over species differ between locations, natural dispersal can provide the necessary source-sink effects to maintain biodiversity in places where a single species would have otherwise dominated.

For foot and mouth disease spread (chapter 4) I find that the primary risk factors are a mix between human and wildlife components: the presence of wild disease reservoirs, the biosecurity measures in place in importing/exporting countries, and the volume of "risky" goods traded.

My dissertation is also a story of connectivity. Locations are connected by the species dispersing between them, where connections between some locations are riskier than connections between others. In my theoretical models, locations are symmetrically connected to each other - dispersal is a constant proportion of abundance. This implicitly assumes random, density independent dispersal in a homogeneous environment. The conclusions drawn from these studies may not hold in a heterogeneous environment where species disperse in a non-random way. Indeed, in my pure ecological system (chapter 2) structuring the system as a network of sources and sinks decreases biodiversity compared to the constant dispersal case (though productivity is still maintained).

For foot and mouth disease spread (chapter 4), the movement of animals is hardly a random, uniform process. It is an asymmetrically distributed trade network. The risks associated with each country ("node") in the network depend on the local biosecurity of each country and the volume of goods traded between them. I show that the bidirectional movement of animals is correlated with disease risk. I show that, for imports, certain regions make safer trading partners than others. For example, Thailand, Vietnam, India, and Iran are known for being high-risk countries while Australia and New Zealand is low risk. But indirect risks of exporting live animals may pose a potential source of risk for the exporting country. Several high-risk regions experienced few outbreaks but were associated with high trade volume. This indicates a role in trade structure (e.g. how a country is connected to others) in the disease risks associated with each country. Take, for example, two major FMD outbreaks in recent history: the 1997 Taiwan and 2001 United Kingdom outbreaks. Trade and travel are implicated in the introduction of FMD to each country (DEFRA, 2002; McLaws and Ribble, 2007). Both epidemics originated in the undocumented importation of contaminated meats. While neither country reported outbreaks, for a time there was a spreading disease reservoir. This made them risky to not only import from, but also export to - particularly if the biosecurity associated exports assumed no disease.

Implications for science

My research has implications for how we do science. First, as with other studies of anthropogenic environmental risk, it supports integration of the biological and human components of dynamic coupled systems. In ecology, many models consider only the biological component ignoring human behavior or taking it as static or exogenous (Costanza et al., 1993). Yet ecologists acknowledge that humans have affected virtually every ecosystem worldwide (Vitousek et al., 1997). My work extending the spatial insurance hypothesis joins numerous studies in resource economics that shows that human behavior strongly influences ecological dynamics (Clark, 2010; Conrad and Clark, 1987). Including human behavior changes the general conclusions of the spatial insurance hypothesis in a pure ecological system: specifically, it changes the non-monotonic relationship between biodiversity and ecosystem stability. Further, while resource economists often view the "world" as coupled social-ecological systems, they seldom consider the long-term effects of human on ecosystem properties (though see Brock et al. (2010)).

Second, my research promotes the interplay between theory and empirics, and correlative and causative studies. Theoretical models can be used to conduct "experiments" that would otherwise be impossible empirically. They generate hypotheses that, as new empirical methods become available, can be tested with data. Empirical studies support or reject the conclusions from theoretical studies. Where empirical studies reject the hypotheses generated by theory, new models/tests are designed and new hypotheses are developed. For example, the spatial insurance hypothesis is just one of several theories proposed to explain the relationship between biodiversity and ecosystem functioning. Others include overyielding (Lehman and Tilman, 2001; Tilman, 1999), statistical averaging (Cottingham et al., 2001; Doak et al., 1998; Isbell et al., 2009; Tilman et al., 1998), and compensatory dynamics (Gonzalez and Loreau, 2009; Lehman and Tilman, 2001). Empirical studies have been conducted for each and found mixed evidence across multiple ecosystems, scales and taxa (Aragon et al., 2011; Tilman et al., 1998; Valone and Barber, 2008). This led to the conclusion that large-scale functioning is a combination of these mechanisms (Loreau, 2010a). My research extends the theory of the spatial insurance hypothesis to more complex systems that can again be tested empirically.

There is a similar feedback between correlative and causative studies. Causation is more difficult to establish than correlation. Correlation can be used to direct researchers to areas where further research is justified - where to focus to establish causation. For foot and mouth disease, I find several regions with low disease history are positively correlated with disease risk, and that they are characterized by high trade volume. But while trade structure and volume are associated with risk, a more detailed analysis of the international trade network and the biosecurity in each associated country will be required to establish causation.

A fine scale understanding of the problem allows development of fine scale management instruments. At the international level the primary policy response to an FMD outbreak is to ban the export of potentially infected material from the entire infected country or allow exports only from particular zones or compartments within the country that meet acceptable biosecurity standards (Grubman et al., 2008; Leforban, 1999; Ratananakorn and Wilson, 2011; Sugiura and Murray, 2011; Sutmoller et al., 2003). This is a blunt management instrument and may cause significant economic damages (Knight-Jones and Rushton, 2013). A fine scale instrument, such as one targeting a specific industry or institution, could be more efficient and less costly.

Policy recommendations for FMD management

As an importer or exporter, current policies on whether to engage in trade with a partner country rely on the OIE's disease-free designation (World Organisation of Animal Health (OIE), 2015). However, I show that while a country's disease-free designation provides a good first approximation of risk, further scrutiny may be warranted. A country's designation captures some of the biosecurity and sanitary conditions of a country, but it does not capture the risks associated with trade structure. My research demonstrates that prior to trade a complete risk analysis should evaluate a country's disease history, the biosecurity measures in place to prevent and control a disease outbreak, the presence the endemic wild reservoirs, and who, what, and how much a partner country trades with.

The current global strategy to mitigate the global spread of FMD is outlined in the World Organization of Animal Health's Global FMD control strategy (World Organisation of Animal Health (OIE) and Food and Agriculture Organization (FAO), 2012). It focuses efforts on improving biosecurity and sanitary conditions in developing countries with low/intermediate disease-free designation countries. The goal is to reduce the global risk of FMD by transitioning endemic countries to disease-free (zones) with vaccination. It is established that the unregulated movement of animals across country borders is an obstacle hindering the control of FMD in parts of Africa and the Middle East (Di Nardo et al., 2011). On a broader scale my research joins a suite of papers advocating the allocation of resources to biosecurity in the trade sector (Rich et al., 2005b).

Future directions

My research is an example of how the manner in which locations are connected and the state of each location matters for the stability of the whole system. In theoretical systems, evaluating the role of network structure, the mechanisms of how organisms move, and the interactions between species on stability is an important step to be considered in future work. Indeed, my conclusions drawn from systems with constant, symmetric dispersal may not hold in a more structured network. A highly connected location often poses greater risk than an isolated one. Density-dependent dispersal will alter the source-sink dynamics that are the foundation for the stabilizing effect of dispersal. And altering the nature of species interactions (e.g. competition, mutualism, parasitism, predation) or trophic structure can dramatically change the long-term outcome in ecological systems (Gotelli, 1995) and optimal harvest in coupled social-ecological ones (Clark, 2010).

For disease risk in empirical systems, finer scale information on the trade network and how countries manage disease would be invaluable for policy. In my analysis I present proxies for a country's sanitary conditions and biosecurity measures in place to manage disease. For a small subset of countries the OIE makes available *Performance of Veterinary Service* reports - highly detailed evaluations of veterinary services that identifies the strengths and gaps in a country's ability to meet OIE standards (http://www.oie.int/). Similarly, I present proxies for the trade linkages between countries. While I show that disease risk is correlated with bidirectional trade more work is needed to establish causation. A detailed description of the trade network - specifically second or third "degrees of separation" - would allow us to establish causation for the indirect risks of trade.

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APPENDIX A

ECOLOGICAL MODEL ASSUMPTIONS

The ecological model depends on several assumptions. First, we assumed that communities initially contained the same set of species and differed only in environmental variation as defined by the phase parameter, x_j (Figure A1a). Second, we assumed that species differed only in their consumption rates, which varied by community as a function of H_i and x_j (Figure A1b). This implies that species are similar in their ecological function and exist within a single trophic level. Third, we assumed that species competed for a single limiting resource whose natural influx and loss rates are constant and independent across time and space. Fourth, we assumed that species competition arose solely from resource consumption. The system is equivalent to a Holling type I predator response where species have the same conversion efficiency but different consumption (predation) rates. There is no direct interaction between individuals within and across patches (e.g. local competition for light or nutrients in plant systems). Finally, we assumed that dispersal was density-independent and occurred at a constant rate. This implicitly assumes a spatially homogeneous environment where all patches are equally connected. These assumptions, while restrictive, simplify the analysis while providing a structure for analyzing competition over a range of environmental conditions, and the effect of harvest on species composition and resource availability. For a detailed analysis and extension of the Loreau model, see Loreau et al. (2003), Gonzalez et al. (2009), Urban (2006), and Shanafelt et al. (2015). Table A1 reports the ecological parameters used in our analysis.

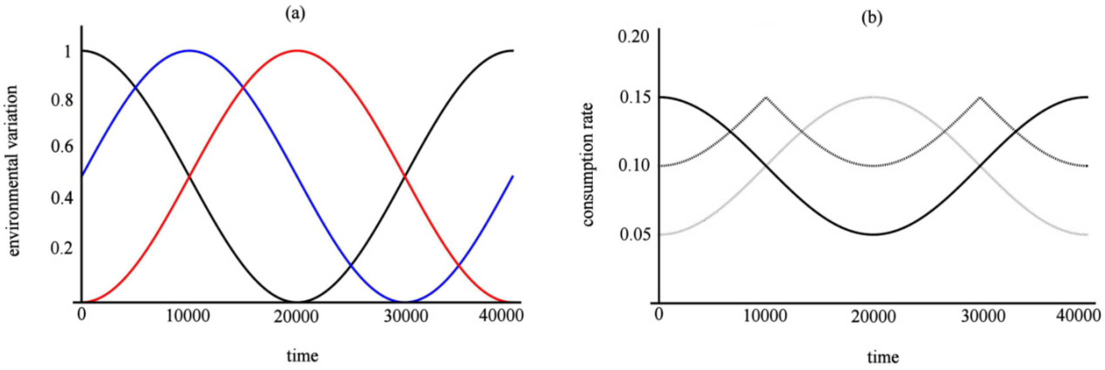

Figure A1. Community environmental variation (a) and species consumption (b) curves over time. In (a), color denotes community number: black (community 1, $x_1 = \pi/2$), blue (community 2, $x_2 = 0$), red (community 3, $x_3 = -\pi/2$). The phase parameter, x_j, shifts environmental variation along its x-axis. In (b), species consumption rates are for community 1 and species is 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 by the species competition parameter and environmental variation.

Table A1. Ecological and economic model parameters.

Ecological parameters

Variable	Value	Interpretation
S	3	Total number of species
M	3	Total number of patches (communities)
$c_{ij}(t)$	variable [0, 0.15]	Species consumption rate of resource biomass
e	0.2	Resource to species biomass conversion efficiency
m	0.2	Natural mortality rate
I	165	Patch resource influx
l	10	Rate of resource loss
a	variable [0, 1]	Species dispersal rate
H_i	variable 1, 1/2, 0	Species competition parameter
x_j	variable 1, 0, -1	Environmental phase parameter
T	25	Period of environmental variation

Economic parameters

Variable	Value	Interpretation
p_{ij}	variable 14, 15, 16 25, 5, 1	Price per unit species harvested
q	0.2	Efficiency of harvest effort
w	variable 45, 65	Cost per unit of species harvest
α_{ij}	variable [0, 1.5]	Marginal social benefits of species abundance
β_j	variable [0, 50]	Social benefits of biodiversity
δ	0.01	Discount rate
τ	100	Terminal time

Note that "*ij*" indicate species i on patch j where $i = 1,2,3$ and $j = 1,2,3$.

APPENDIX B

OPTIMAL HARVEST DERIVATION

Optimal levels of harvest effort were solved by the maximum principle (Clark, 2010). We defined the current-value Hamiltonian, hereafter the Hamiltonian. Suppressing time arguments the Hamiltonian is:

[A10] $$\tilde{H} = \sum_{i=1}^{S}\left(p_{ij}qE_{ij}N_{ij} - wqE_{ij} + \alpha_{ij}N_{ij}\right) + \beta_j\left(1-\sum_{i=1}^{S}\left(\frac{N_{ij}}{N_j}\right)^2\right) + \sum_{i=1}^{S}\lambda_{ij}\dot{N}_{ij} + \mu_j\dot{R}_j$$

where λ_{ij} and μ_j represent the shadow value of species and resource biomass respectively. By converting the units of the equations of motion (biomass*time^{-1}) into the units of the objective function, they define the social value of a marginal change in species or resource biomass.

The Hamiltonian is linear in harvest effort, therefore the optimal control rule must include a most rapid approach path (Conrad and Clark, 1987). From [A10] the marginal impact of harvest effort on the i^{th} species depends on the size of the stock of species i:

[A11] $$\frac{\partial\tilde{H}}{\partial E_{ij}} = p_{ij}qN_{ij} - wq - \lambda_{ij}qN_{ij}$$

The associated adjoint equations describe the evolution of shadow prices along any arbitrary trajectory (Clark, 2010; Fenichel and Abbott, 2014):

[A12] $$\begin{aligned}\dot{\lambda}_{ij} - \delta\lambda_{ij} = -\frac{\partial H}{\partial N_{ij}} = \mu_j R_j c_{ij} + \lambda_{ij}\left(m - ec_{ij}R_j + qE_{ij} + a\right) - p_{ij}qE_{ij}\\ -\alpha_{ij} - \frac{2\beta_j\left(\sum_{k\neq i}N_{kj}^2 - N_{ij}\sum_{k\neq i}N_{kj}\right)}{\left(\sum_{k=1}^{S}N_{kj}\right)^3}\end{aligned}$$

[A13] $$\dot{\mu}_j - \delta\mu_j = -\frac{\partial H}{\partial R_j} = \mu_j\left(l + \sum_{i=1}^{S}c_{ij}N_{ij}\right) - \sum_{i=1}^{S}\lambda_{ij}N_{ij}ec_{ij}$$

where species consumption rates, c_{ij}, is taken as exogenous following exogenous changes in $F_j(t)$. From [A11], assuming the optimality of the singular solution, the shadow value of an extra unit of species biomass is increasing in the social marginal net benefit of harvest effort - the difference between the marginal revenue and marginal cost per unit of harvested species.

[A14] $$\lambda_{ij} = p_{ij} - \frac{w}{N_{ij}}$$

The ecological models of the spatial insurance hypothesis are concerned with the behavior of the system at equilibrium, and specifically with the effect of species dispersal on long run equilibrium productivity, stability, and diversity (Gonzalez et al., 2009; Loreau et al., 2003; Mouquet and Loreau, 2003; Shanafelt et al., 2015). To address the long-run equilibrium properties of the social-ecological system we solved for the optimal harvest at equilibrium. An alternative full analytical derivation of optimal harvest is derived in Appendix C. We then verified that our results matched those obtained from the full analytical solution at equilibrium in Appendix C. Evaluating [A12] and [A13] at equilibrium[25] we can see that:

$$[A15] \quad \mu_j = \frac{\sum_{i=1}^{S} \lambda_{ij} N_{ij} e c_{ij}}{l + \sum_{i=1}^{S} c_{ij} N_{ij} + \delta}$$

That is, the value of an extra unit of resource at the steady state is the ratio of the marginal value of the biomass of all species it induces to the marginal opportunity cost of the resource. By substituting λ_{ij} and μ_j into [A12], we may solve for the singular harvest effort directed at species i in terms of the model parameters.

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[25] In our model, equilibria are characterized by non-constant, cyclical fluctuations in species and resource biomass. This behavior is caused by variation in environmental conditions.

APPENDIX C

FULL-ANALYTICAL DERIVATION OF OPTIMAL HARVEST

The full analytical derivation of optimal harvest follows that of Fenichel et al. (2010a), Fenichel et al. (2015), Horan and Fenichel (2007), and Horan et al. (2011).

First, it is useful to focus on the case with zero dispersal. Differentiating the single-patch equivalent of [A14] with respect to time yields:

[A16] $$\dot{\lambda}_i = \frac{w}{N_i}\left(ec_iR - m - qE_i\right)$$

Then, by substituting [A14] and [A16] into [A12], one can solve for:

[A17] $$\mu = \frac{1}{Rc_i}\left(\frac{w\delta}{N_i} - p_i\left(m - ec_iR + \delta\right) + \alpha_i + 2\beta\left[\frac{\sum_{k\neq i} N_k^2 - N_i\sum_{k\neq i} N_k}{\left(\sum_{i=1}^{S} N_i\right)^3}\right]\right)$$

For simplicity, define the Simpson's index (B) and its associated first and second derivatives as:

[A18] $$B = \beta\left(1 - \sum_{i=1}^{S}\frac{N_i}{N}\right)$$

[A19] $$\partial B/\partial N_i = \frac{2\beta\left(\sum_{k\neq i} N_k^2 - N_i\sum_{k\neq i} N_k\right)}{\left(\sum_{i=1}^{S} N_i\right)^3}$$

[A20]

$$\partial^2 B/\partial N_i\partial t = 2\beta\left[\frac{2\left(\sum_{k\neq i} N_k\dot{N}_k - N_i\sum_{k\neq i}\dot{N}_k - \dot{N}_i\sum_{k\neq i} N_k\right)}{\left(\sum_{i=1}^{S} N_i\right)^3} + \frac{3\left(N_i\sum_{k\neq i} N_k - \sum_{k\neq i} N_k^2\right)\sum_{i=1}^{S}\dot{N}_i}{\left(\sum_{i=1}^{S} N_i\right)^4}\right]$$

Taking the derivative of [A17] with respect to time allows us to solve for the equation describing how the resource shadow value changes over time:

[A21]

$$\begin{aligned}\dot{\mu} &= \frac{-\dot{R}}{c_iR^2}\left(\frac{w\delta}{N_i} - p_i(m - ec_iR + \delta) + \alpha_i + {}^{\partial B}\!\big/_{\partial N_i}\right) + \frac{1}{c_iR}\left(-\frac{w\delta}{N_i^2}\dot{N} + p_iec_iR + {}^{\partial^2 B}\!\big/_{\partial B\partial t}\right)\\ &= \frac{-\dot{R}}{R}\mu + \frac{1}{c_iR}\left(-\frac{w\delta}{N_i^2}\dot{N}_i + p_iec_iR + {}^{\partial^2 B}\!\big/_{\partial B\partial t}\right)\end{aligned}$$

Substituting [A14], [A17], and [A21] into [A13] allows one to solve for the optimal path of harvest per species:

$$E_i^* = \frac{Rc_i\left(\mu\left(l+\sum_{i=1}^{S}c_iN_i+\delta+\frac{\dot{R}}{R}\right)+\sum_{i=1}^{S}\lambda_iN_iec_i\right)-p_iec_i\dot{R}+\frac{w\delta ec_iR}{N_i}-\frac{w\delta m}{N_i} +2\beta\left(\frac{N_i\sum_{k\neq i}\dot{N}_k-2\sum_{k\neq i}N_k\dot{N}_k+\left(N_iec_iR-N_im\right)\sum_{k\neq i}N_k}{\left(\sum_{i=1}^{S}N_i\right)^3}\right) +\frac{6\beta\left(N_i\sum_{k\neq i}N_k-\sum_{k\neq i}N_k^2\right)\left(N_im-N_iec_iR-\sum_{k\neq i}\dot{N}_k\right)}{\left(\sum_{i=1}^{S}N_i\right)^4}}{\frac{w\delta q}{N_i}-\frac{6\beta\left(N_i\sum_{k\neq i}N_k-\sum_{k\neq i}N_k^2\right)qN_i}{\left(\sum_{i=1}^{S}N_i\right)^4}+\frac{2\beta N_i\sum_{k\neq i}N_k}{\left(\sum_{i=1}^{S}N_i\right)^3}} \tag{A22}$$

Note that [A22] is a function of the harvest efforts of the other species in the patch. In order to solve for the full solution, one must solve [A22] for each species simultaneously - a system of three equations and three unknowns.

To solve the full system with dispersal, note that equations [A16] and [A17] become:

$$\dot{\lambda}_{ij} = \frac{w}{N_{ij}}\left(ec_{ij}R_j-m-qE_{ij}-a\right)+a\frac{w}{N_{ij}^2}\sum_{k\neq j}N_{ik} \tag{A23}$$

$$\mu_j = \frac{1}{R_jc_{ij}}\left(\begin{array}{c} p_{ij}\left(ec_{ij}R_j-m-a-\delta\right)+\frac{w}{N_{ij}}\left(\delta+\frac{1}{N_{ij}}\frac{a}{2}\sum_{k\neq j}N_{ik}\right) \\ +\alpha_{ij}+2\beta\left[\frac{\sum_{k\neq i}N_{kj}^2-N_{ij}\sum_{k\neq i}N_{kj}}{\left(\sum_{i=1}^{S}N_{ij}\right)^3}\right] \end{array}\right) \tag{A24}$$

where subscripts i and j denote species and patch respectively. Following the procedure above it can be shown that E_{ij}^* is an equation that is a function of the harvest efforts of all species within patch j and the harvest effort of all species i on patch k where $k \neq j$. The harvest efforts of all species in the system must be solved simultaneously - a system of $i*j$ equations with $i*j$ unknowns.

APPENDIX D

RELAXATION OF EQUILIBRIUM HARVEST ASSUMPTION

Define optimal harvest assuming equilibrium (Appendix B) and the full analytical solution (Appendix C) as E^*_{EQ} and E^*_{FA} respectively. In order to calculate the trajectories of the biological system to equilibrium, optimal harvest rates are substituted into the equations of motion for species and resource biomass and the resulting system of differential equations solved (Fenichel et al., 2010a; Horan and Fenichel, 2007; Horan et al., 2011). However, even under constant species consumption, benefits only from harvest, and zero dispersal the system is highly nonlinear. Evaluating of the trajectories analytically is mathematically intractable.[26]

Instead we calculated the steady states of the system and their stability under E^*_{EQ} and E^*_{FA}. We held species consumption rates constant, and assumed benefits only from harvest and zero dispersal. We found the same steady state values under E^*_{EQ} and E^*_{FA} though the stability of the fixed points varied (Table A2). Under E^*_{FA} it is likely that harvest will shift the equilibrium away from the stable resource-only fixed point to a saddle that includes one or more species and the resource. Given the assumption that all species are positively valued for harvest, the full coexistence saddle point is a feasible long-run equilibrium point.

Extensions to include non-consumptive benefits and species dispersal are left for future work.

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[26] Analysis was conducted in Mathematica 10.4 using analytical and numerical differential equation solvers. We explored multiple methods for solving nonlinear systems of equations.

Table A2. Steady states and stability under E^*_{FA} and E^*_{EQ}.

equilibrium assumption, E^*_{EQ}

steady states (N_1*[t], N_2*[t], N_3*[t], R*[t])				eigenvalues				stability of fixed point
0.000	0.000	0.000	16.500	-10.000	0.010	0.010	0.010	saddle
39.785	0.000	0.000	10.333	-14.533	-2.641	0.010	0.010	saddle
0.000	48.744	0.000	11.093	-14.610	-0.529	0.010	0.010	saddle
0.000	0.000	108.866	10.684	-15.321	-0.253	0.010	0.010	saddle
39.681	0.385	0.000	10.319	-14.568	-2.621	-0.010	0.010	saddle
39.719	0.000	0.690	10.317	-14.567	-2.626	-0.010	0.010	saddle
0.000	47.364	4.910	11.013	-14.735	-0.496	-0.010	0.010	saddle
39.614	0.386	0.693	10.303	-14.602	-2.606	-0.010	-0.010	stable node

full analytical solution, E^*_{FA}

steady states (N_1*[t], N_2*[t], N_3*[t], R*[t])				eigenvalues				stability of fixed point
0.000	0.000	0.000	16.500	-10.010	-10.010	-10.009	-10.000	stable node
39.785	0.000	0.000	10.333	-247.637	-15.978	-15.978	247.647	saddle
0.000	48.744	0.000	11.093	-107.225	-14.884	-14.884	107.235	saddle
0.000	0.000	108.866	10.684	-77.362	-15.453	-15.453	77.372	saddle
39.681	0.385	0.000	10.319	-246.737	-16.001	16.001	246.747	saddle
39.719	0.000	0.690	10.317	-246.917	-16.002	16.002	246.927	saddle
0.000	47.364	4.910	11.013	-103.440	-14.992	14.992	103.450	saddle
39.614	0.386	0.693	10.303	-246.009	16.025	16.025	246.019	saddle

Steady states and stability are evaluated assuming that species consumption rates are constant such that $c_1(t) = 0.15$, $c_2(t) = 0.10$, and $c_3(t) = 0.05$. Benefits are obtained solely through harvest such that $p_1 = 25$, $p_2 = 5$, $p_3 = 1$, and $w = 65$. All other parameters are reported in Table A1.

APPENDIX E

EFFECT OF ALTERNATIVE SPECIES COMPETITION PARAMETERS AND ENVIRONMENTAL CONDITIONS

We tested the behavior of our model under other species competition parameters. Specifically we tested the boundary species competition parameters of Loreau et al. (2003) and Gonzalez et al. (2009) ($H_i = 1$ and $H_i = 0$). Compared to $H_i = 1/2$, the corresponding consumption rate curves were lower on average and reached a maximum only once (Figure A1b). With these competition parameters we did not observe the suppression of the least valuable species. We found similar, but asynchronous, harvest regimes for each species (Figures A2-A4). Effort was staggered such that the most valuable species was most abundant.

Environmental variation did not qualitatively affect our results. The phase parameter x_j shifts species consumption rate curves forwards or backwards in time. It affects where in the phase we end our simulations but not the behavior of the bioeconomic model.

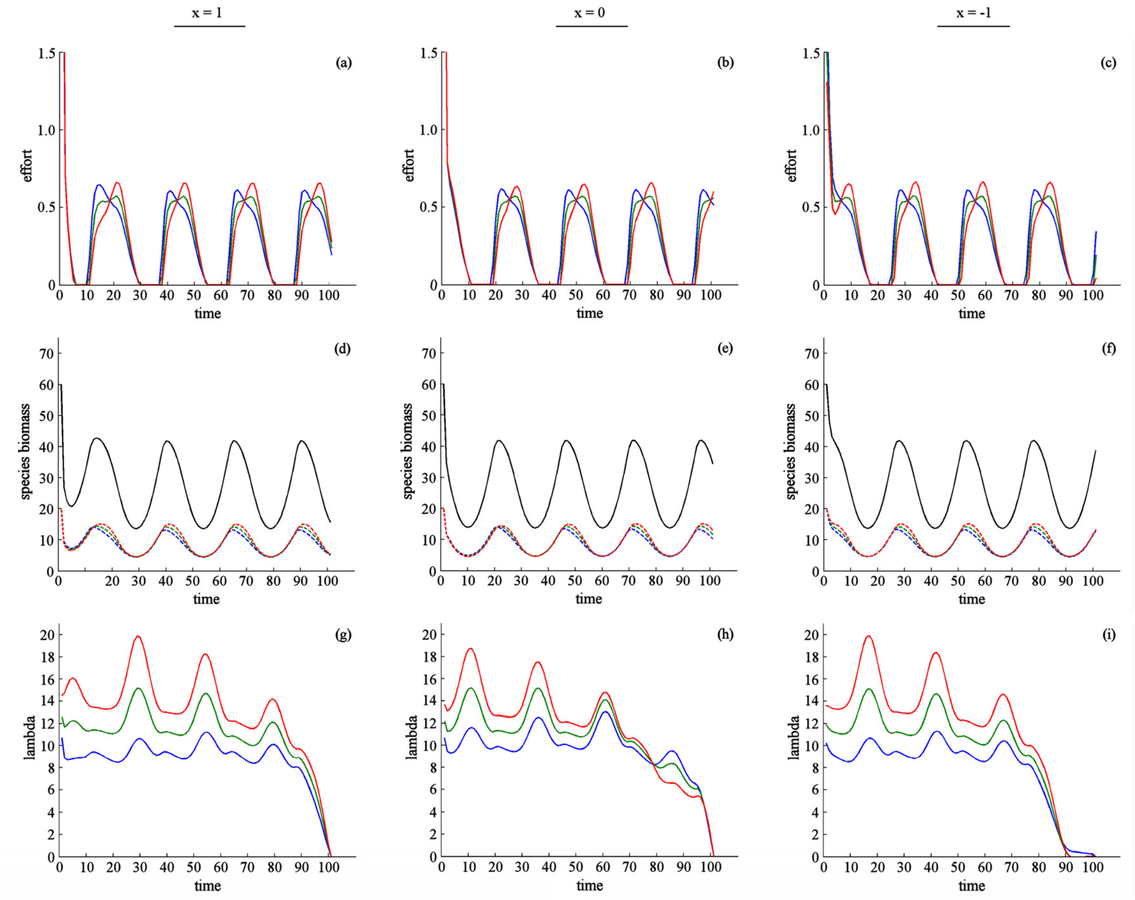

Figure A2. Effect of alternative species competition parameters ($H_i = 1$ for all i) in different environmental conditions: $x_j = 1$ (a, d, g), $x_j = 0$ (b, e, h), and $x_j = 0$ (c, f, i). Harvest effort (a-c); species biomass (d-f); lambda (g-i). Color indicates species: species 1 (blue, lowest harvest price), species 2 (green), species 3 (red, greatest harvest price). In (d-f), dashed lines denote values of individual species biomass; the solid, black line is the aggregate level of biomass across all species. In (h, i) the "flip" of the curves is due to constraining the final value to zero. Results are in a closed system with zero dispersal.

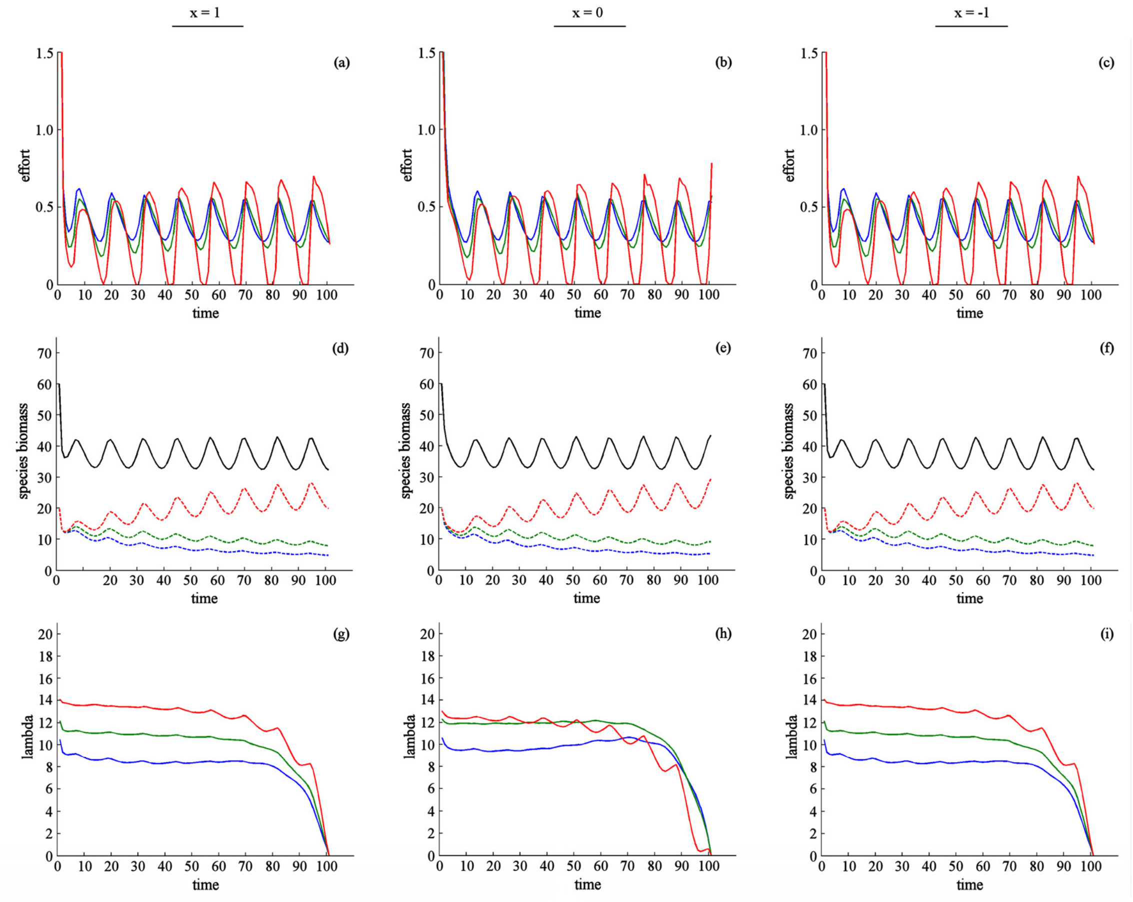

Figure A3. Effect of alternative species competition parameters ($H_i = 1/2$ for all *i*) in different environmental conditions: $x_j = 1$ (a, d, g), $x_j = 0$ (b, e, h), and $x_j = 0$ (c, f, i). Harvest effort (a-c); species biomass (d-f); lambda (g-i). Color indicates species: species 1 (blue, lowest harvest price), species 2 (green), species 3 (red, greatest harvest price). In (d-f), dashed lines denote values of individual species biomass; the solid, black line is the aggregate level of biomass across all species. In (h) the "flip" of the curves is due to constraining the final value to zero. Results are in a closed system with zero dispersal.

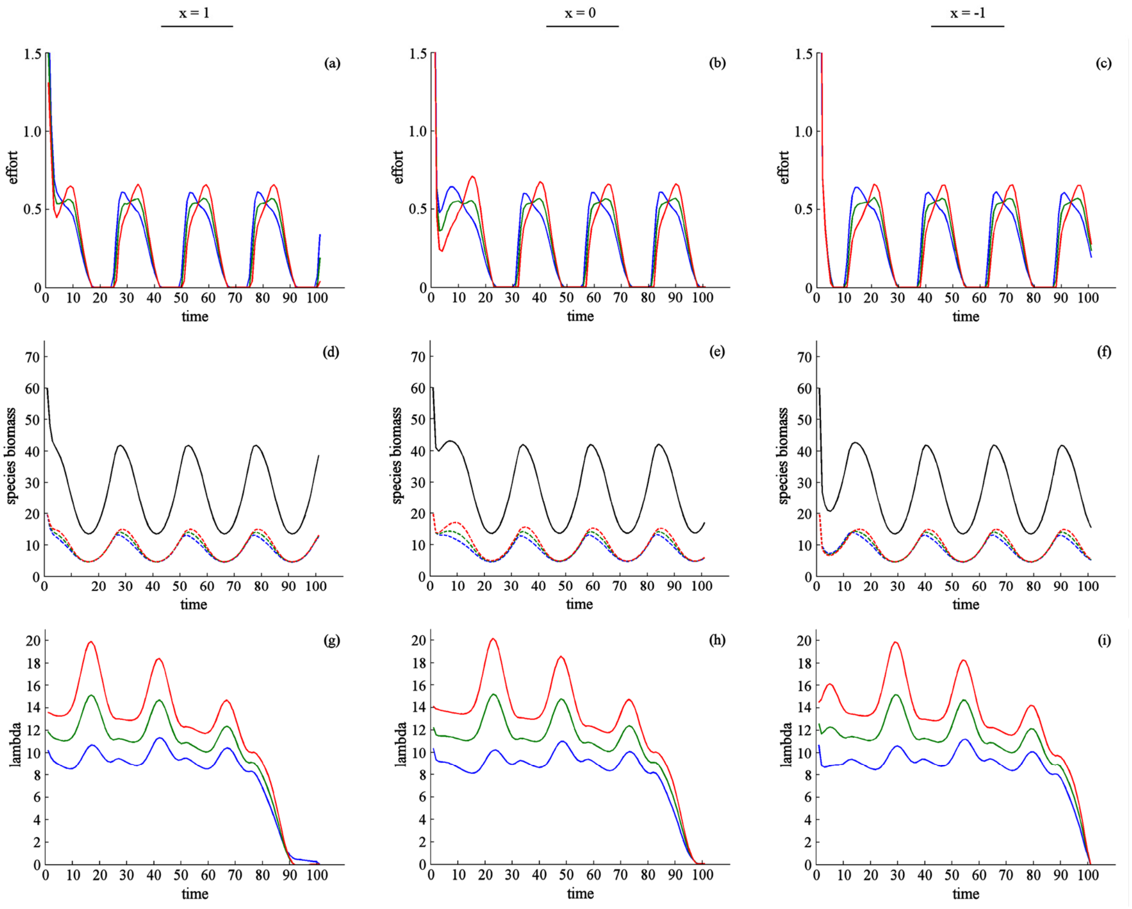

Figure A4. Effect of alternative species competition parameters ($H_i = 0$ for all i) in different environmental conditions: $x_j = 1$ (a, d, g), $x_j = 0$ (b, e, h), and $x_j = 0$ (c, f, i). Harvest effort (a-c); species biomass (d-f); lambda (g-i). Color indicates species: species 1 (blue, lowest harvest price), species 2 (green), species 3 (red, greatest harvest price). In (d-f), dashed lines denote values of individual species biomass; the solid, black line is the aggregate level of biomass across all species. In (g) the "flip" of the curves is due to constraining the final value to zero. Results are in a closed system with zero dispersal.

APPENDIX F

EFFECT OF NEGATIVE PRICE ON HARVEST EFFORT AND SPECIES BIOMASS

We assumed that species were functionally identical, managers obtained benefits solely from harvest, there was no dispersal, and that harvest price was initially positive for all species. In order to test the sensitivity of the economic model to changes in model price, we varied the price of the most valued species (holding all others constant). We found that the suppression of the least valued species varied inversely with harvest price (Figure A5). As price decreased the level of initial suppression increased. This held for negative prices (e.g. pest species).

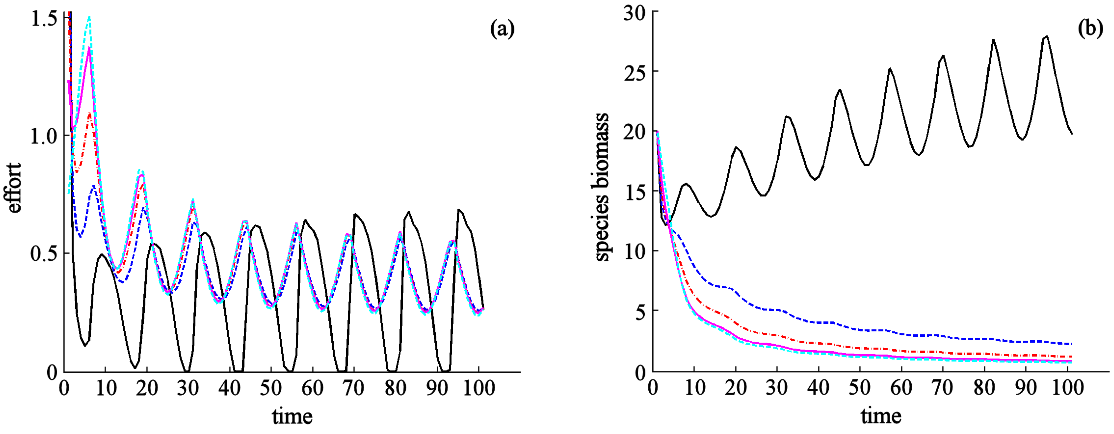

Figure A5. Effect of price per unit species harvested on harvest effort and species biomass when benefits are obtained through the direct consumption of species. Results are in the absence of dispersal. (a) Harvest effort; (b) species biomass (b). Color and style indicate the price per unit species harvested for a single species (prices for other species are held at $p_2 = 14$ and $p_3 = 15$): black, solid ($p_1 = 16$); blue, dashed ($p_1 = 10$); red, dot-dashed ($p_1 = 5$); magenta, solid ($p_1 = 0$); cyan, dashed ($p_1 = -5$).

APPENDIX G

ADDITIONAL FIGURES FOR BIOECONOMIC ANALYSIS

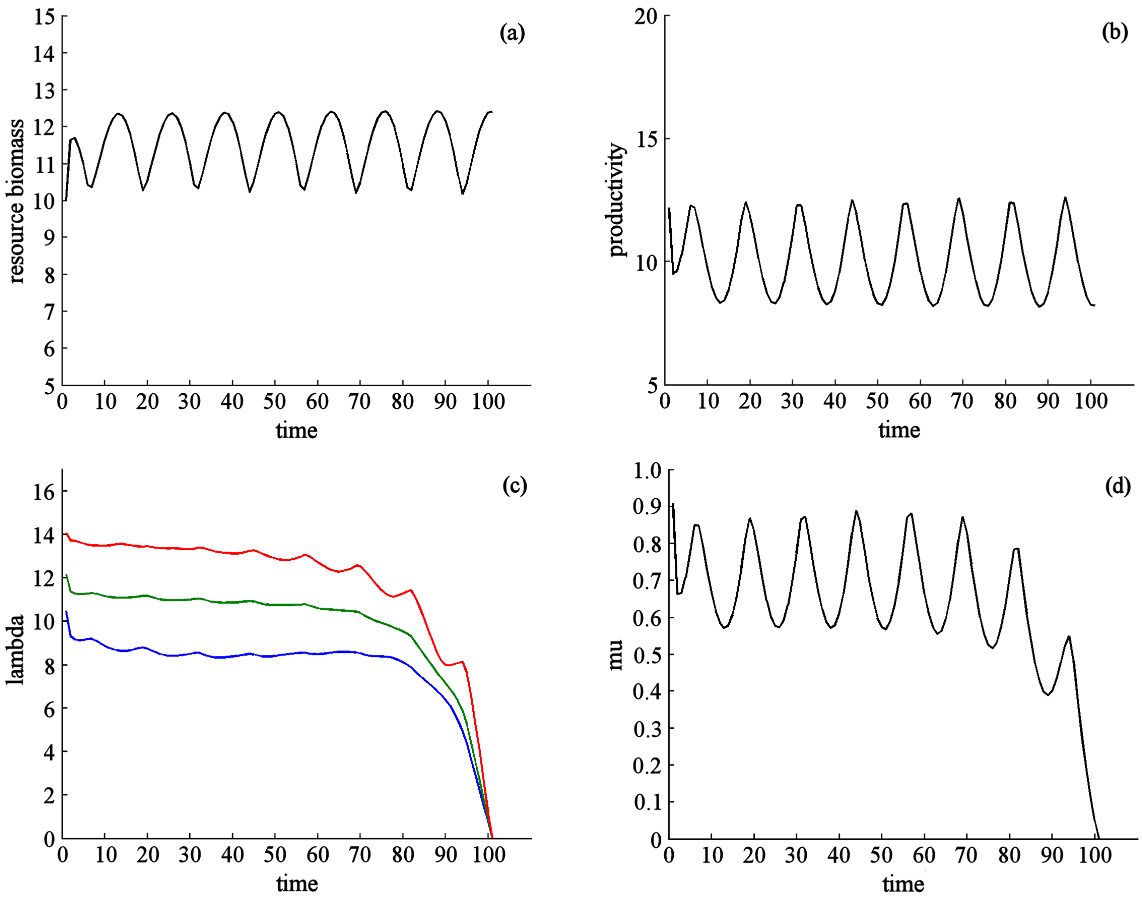

Figure A6. Effect of harvest price when benefits are obtained from harvest only. Resource biomass (a), productivity (b), lambda (c), and mu (d). In (c) color indicates species: species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price).

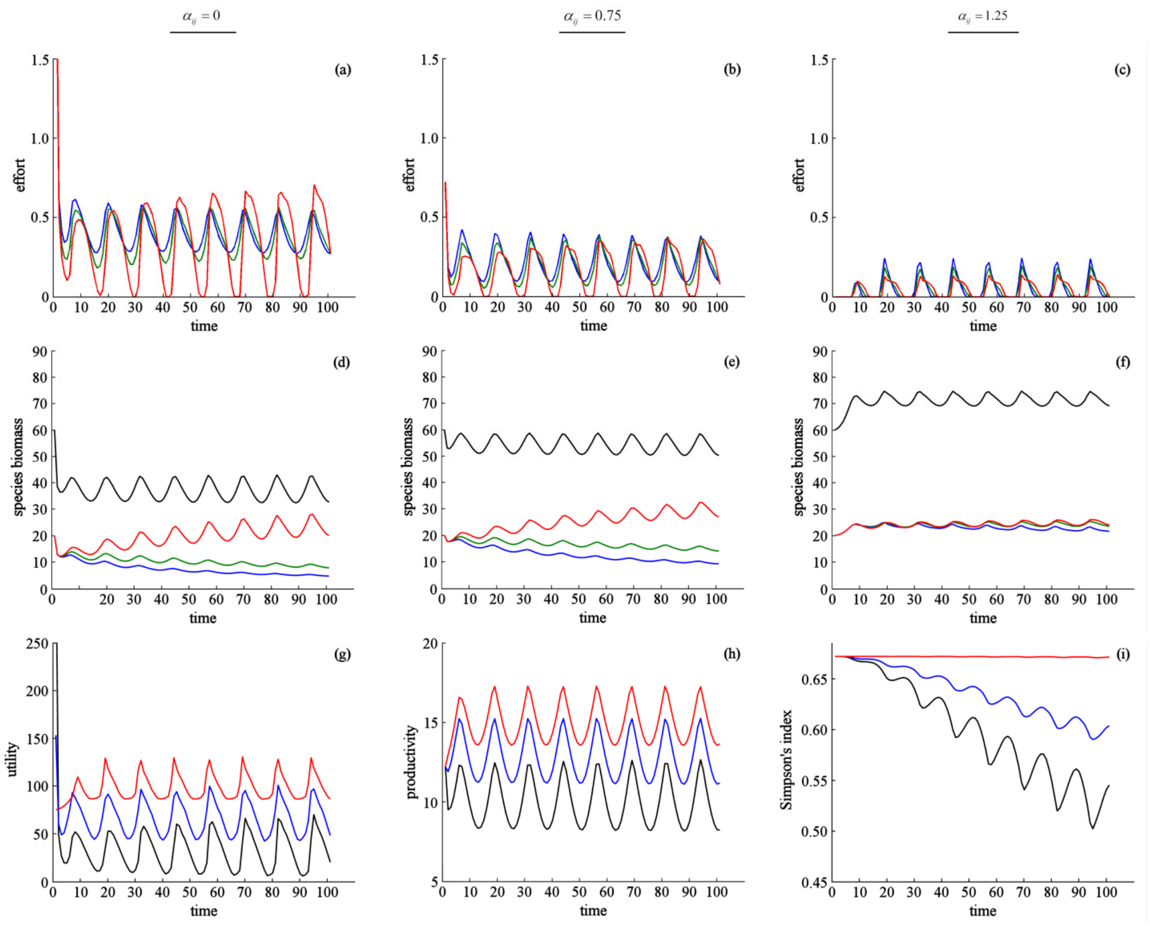

Figure A7. Effect of harvest price when benefits are obtained through harvest and species abundance. The non-consumptive benefits, α_{ij}, are the same for all species: $\alpha_{ij} = 0$ (a, d), $\alpha_{ij} = 0.75$ (b, e), and $\alpha_{ij} = 1.25$ (c, f). Harvest effort (a-c); species biomass (d-f); utility (g); productivity (h); biodiversity (i). In (a-f) color indicates harvest and species biomass: species 1 (red, highest harvest price), species 2 (green), species 3 (blue, lowest harvest price). The black line is the aggregate level of biomass across all species. In (g-i) color indicates the level of non-consumptive benefits: $\alpha_{ij} = 0$ (black), $\alpha_{ij} = 0.75$ (blue), and $\alpha_{ij} = 1.25$ (red). Values of α_{ij} were chosen to illustrate the qualitative shift in the harvest regiment.

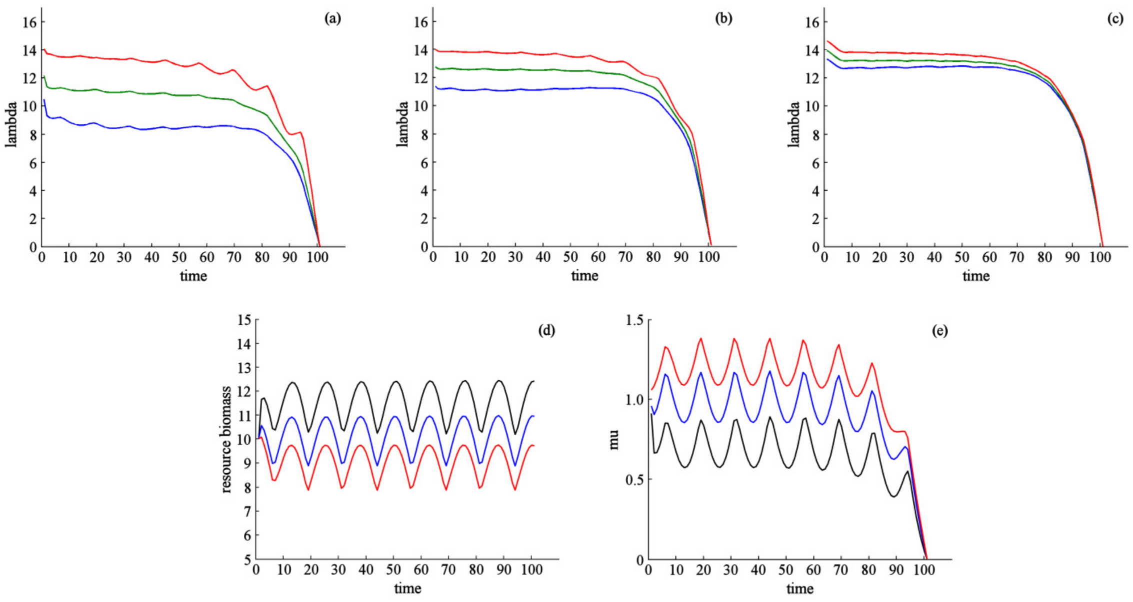

Figure A8. Effect of harvest price when benefits are obtained through harvest and species abundance. Lambda (a-c); resource biomass (d); and mu (e). In (a-c) color indicates the shadow prices (lambdas) for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). The level of non-consumptive benefits are given by column: $\alpha_{ij} = 0$ (a), $\alpha_{ij} = 0.75$ (b), and $\alpha_{ij} = 1.25$ (c). In (d-e) color indicates the level of non-consumptive benefit: $\alpha_{ij} = 0$ (black), $\alpha_{ij} = 0.75$ (blue), and $\alpha_{ij} = 1.25$ (red).

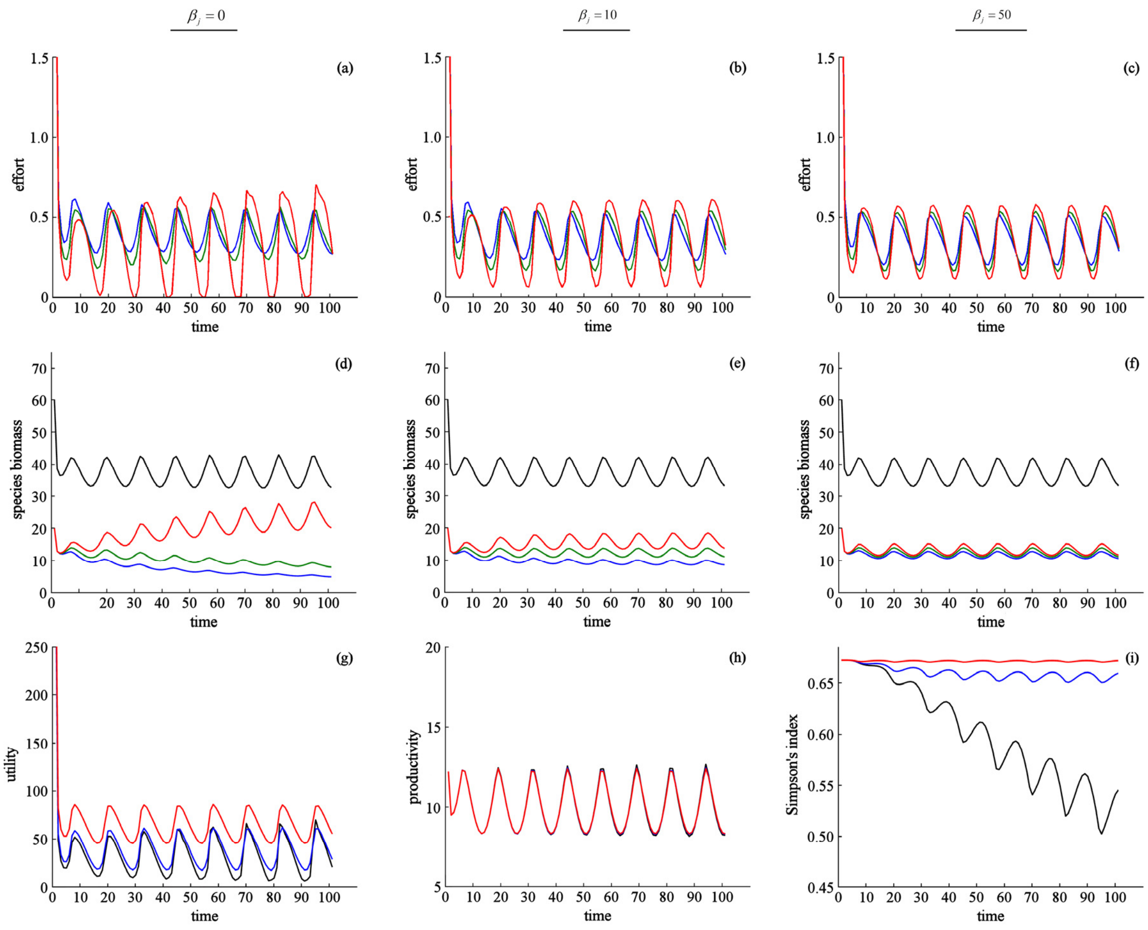

Figure A9. Effect of harvest price when benefits are obtained through harvest and species biodiversity: $\beta_j = 0$ (a, d); $\beta_j = 10$ (b, e); $\beta_j = 50$ (c, f). Harvest effort (a-c); species biomass (d-f); utility (g); productivity (h); biodiversity (i). In (a-f) color indicates harvest and species biomass: species 1 (red, highest harvest price), species 2 (green), species 3 (blue, lowest harvest price). The black line is the aggregate level of biomass across all species. In (g-i) color indicates the level of benefits of biodiversity: $\beta_j = 0$ (black); $\beta_j = 10$ (blue); $\beta_j = 50$ (red). Values of β_j were selected to illustrate the qualitative changes in the distribution of harvest as β_j increases.

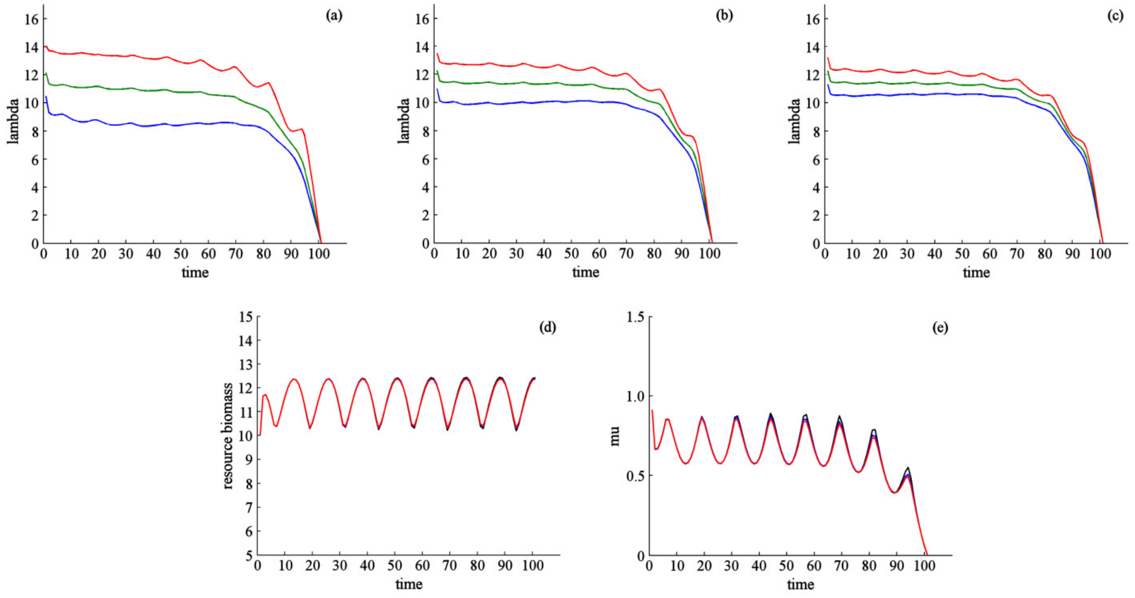

Figure A10. Effect of harvest price when benefits are obtained through harvest and species biodiversity. Lambda (a-c); resource biomass (d); and mu (e). In (a-c) color indicates the shadow prices (lambdas) for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). The benefits of biodiversity are given by column: $\beta_j = 0$ (a), $\beta_j = 10$ (b), and $\beta_j = 50$ (c). In (d-e) color indicates the level of biodiversity benefits: $\beta_j = 0$ (black), $\beta_j = 10$ (blue), and $\beta_j = 50$ (red).

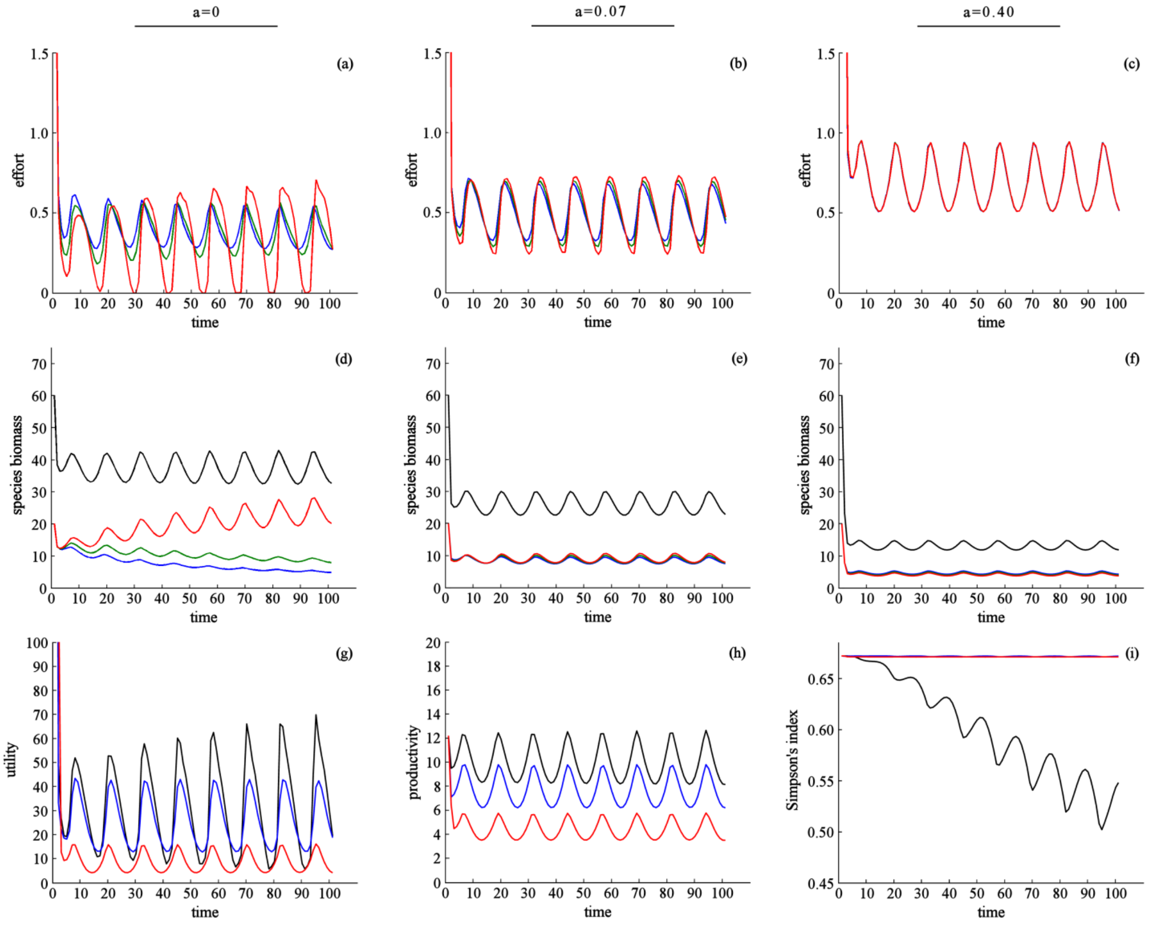

Figure A11. Effect of dispersal when all species possess *identical* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species are *identical* between patches. Environmental conditions are the *same* across patches. Harvest effort (a-c); species biomass (d-f); utility (g); productivity (h); biodiversity (i). In (a-f) column indicates dispersal rate: $a = 0$ (a, d), $a = 0.04$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates dispersal rate: $a = 0$ (black), $a = 0.04$ (blue), and $a = 0.70$ (red).

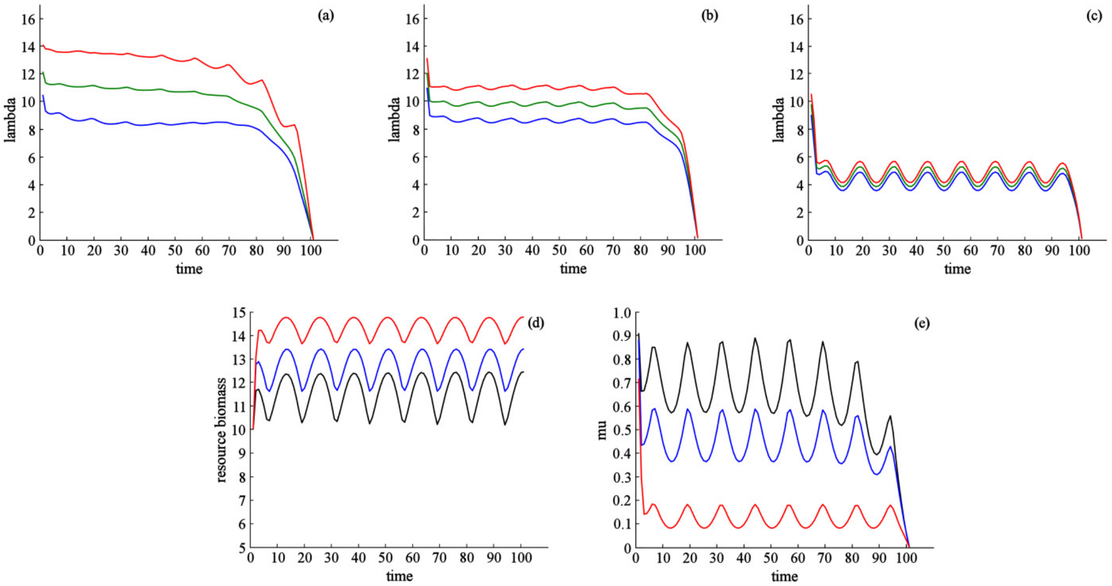

Figure A12. Effect of dispersal when all species possess *identical* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species are *identical* between patches. Environmental conditions are the *same* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates the shadow prices (lambdas) for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Dispersal rate given by column: $a = 0$ (a), $a = 0.04$ (b), and $a = 0.70$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.04$ (blue), and $a = 0.70$ (red).

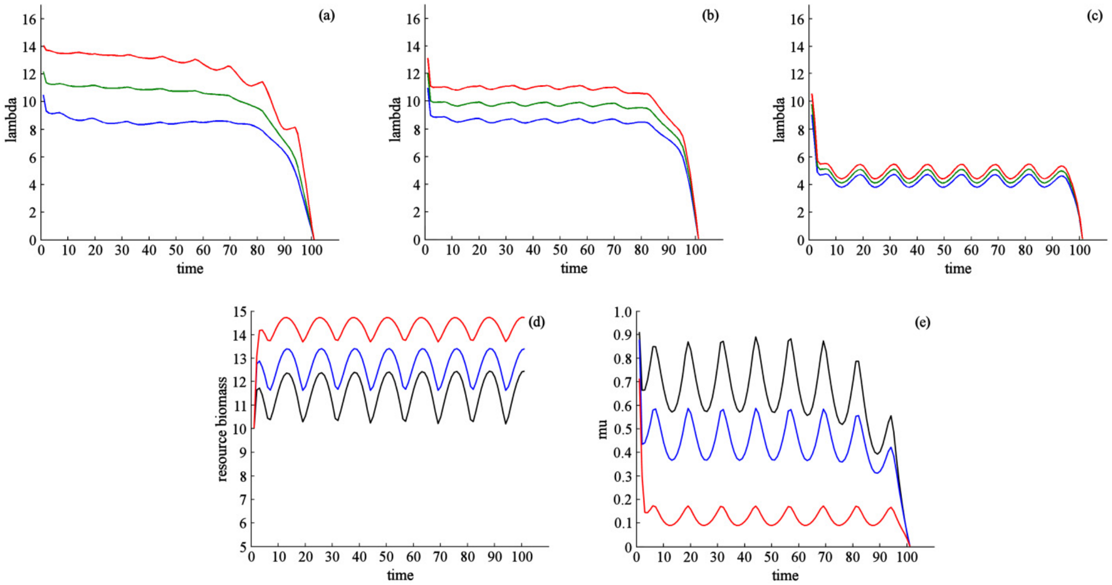

Figure A13. Effect of dispersal when all species possess *identical* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species are *identical* between patches. Environmental conditions *differ* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.07$ (b), and $a = 0.40$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.07$ (blue), and $a = 0.40$ (red).

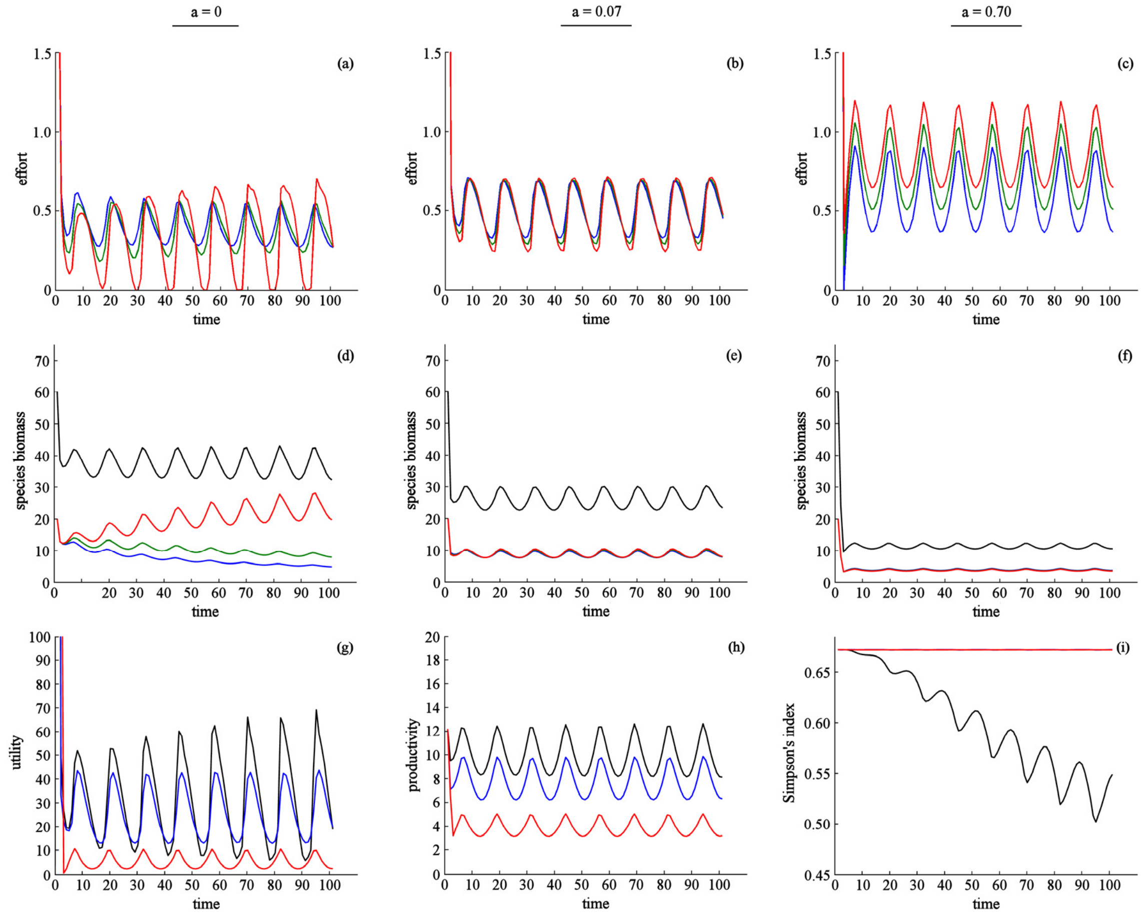

Figure A14. Effect of dispersal when all species possess *identical* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species *differ* between patches. Environmental conditions are the *same* across patches. Harvest effort (a-c); species biomass (d-f); utility (g); productivity (h); biodiversity (i). In (a-f) column indicates dispersal rate: $a = 0$ (a, d), $a = 0.07$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Black shows aggregate species biomass. In (g-i) color indicates dispersal rate: low (black), intermediate (blue), and high (red).

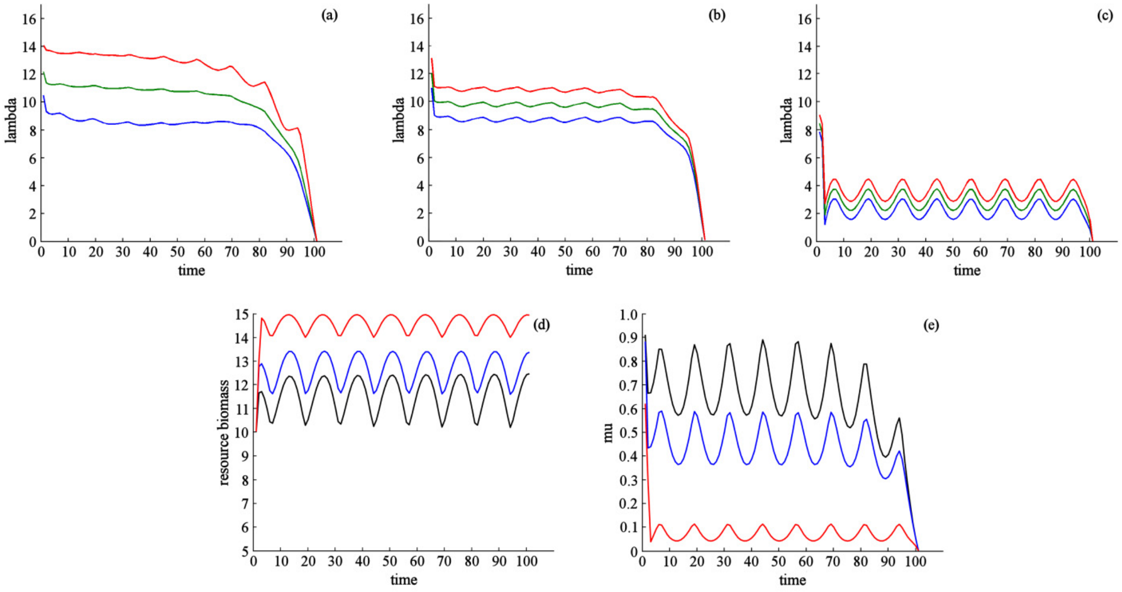

Figure A15. Effect of dispersal when all species possess *identical* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species *differ* between patches. Environmental conditions are the *same* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.07$ (b), and $a = 0.70$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.07$ (blue), and $a = 0.70$ (red).

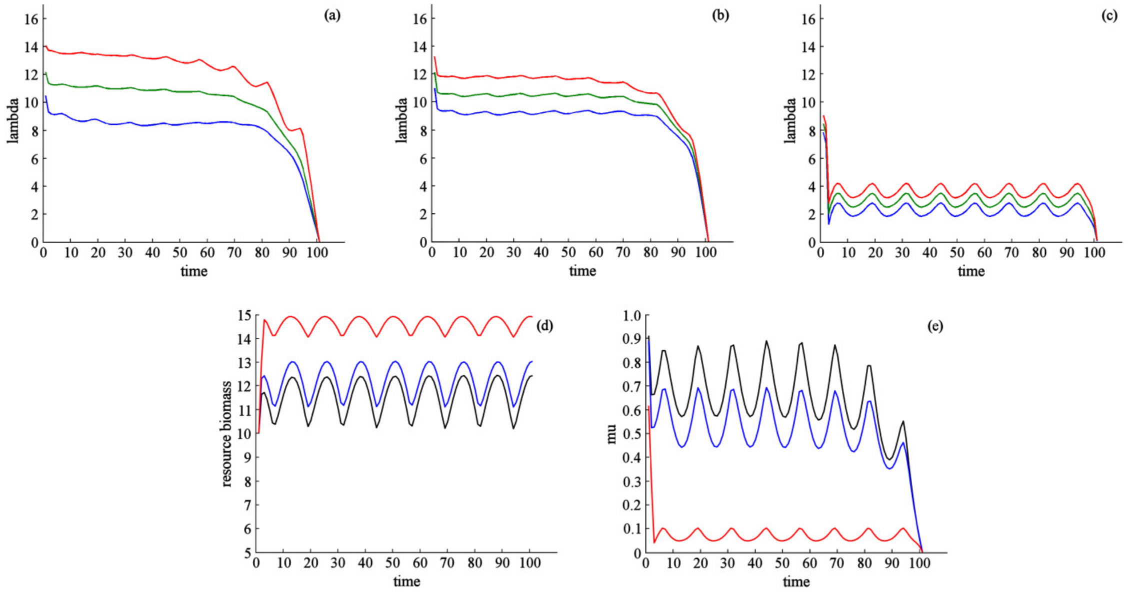

Figure A16. Effect of dispersal when all species possess *identical* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species *differ* between patches. Environmental conditions *differ* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, highest harvest price), species 2 (green), and species 3 (blue, lowest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.04$ (b), and $a = 0.70$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.04$ (blue), and $a = 0.70$ (red).

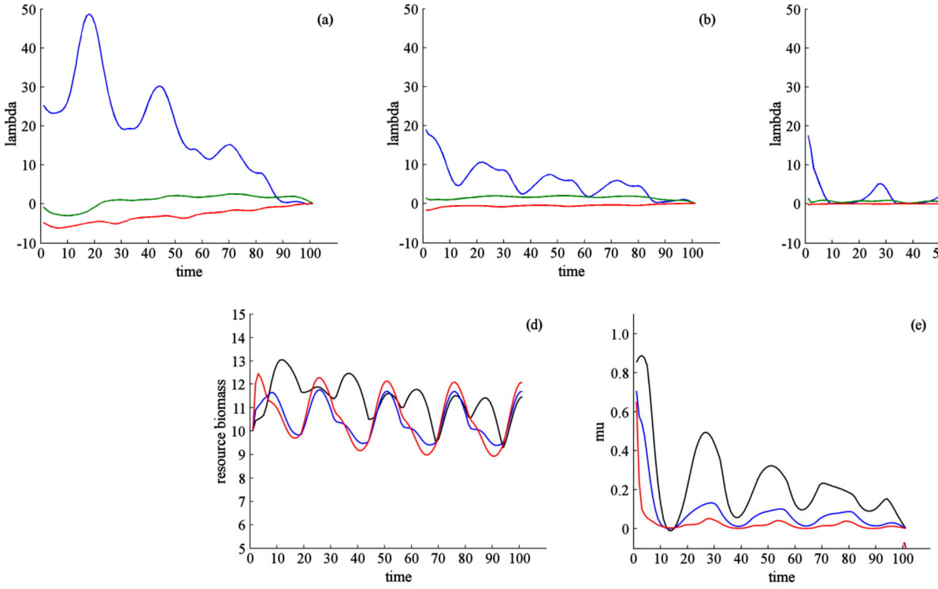

Figure A17. Effect of dispersal when species possess *different* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species are *identical* between patches. Environmental conditions are the *same* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, lowest harvest price), species 2 (green), and species 3 (blue, highest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.07$ (b), and $a = 0.40$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.07$ (blue), and $a = 0.40$ (red).

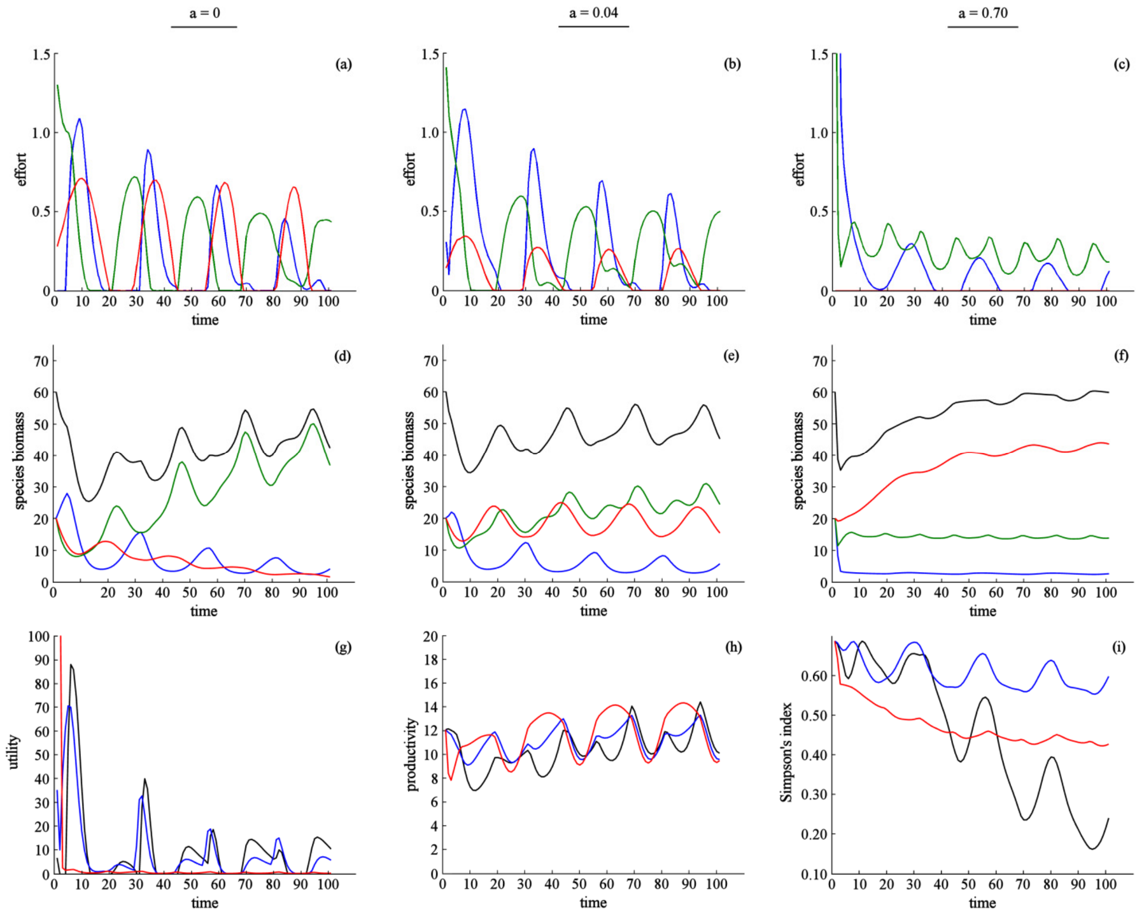

Figure A18. Effect of dispersal when species possess *different* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species are *identical* between patches. Environmental conditions *differ* across patches. Harvest effort (a-c); species biomass (d-f); utility (g); productivity (h); biodiversity (i). In (a-f) dispersal rate is indicated by column: $a = 0$ (a, d), $a = 0.04$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, lowest harvest price), species 2 (green), and species 3 (blue, highest harvest price). Black shows aggregate species biomass. In (g-i) color indicates dispersal rate: $a = 0$ (black), $a = 0.04$ (blue), and $a = 0.70$ (red).

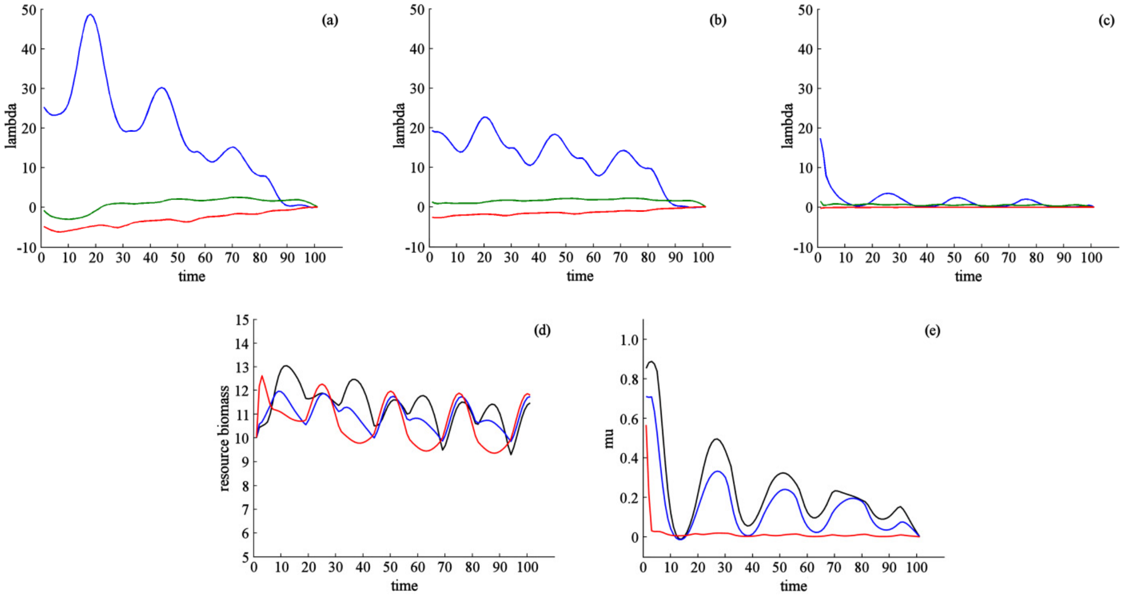

Figure A19. Effect of dispersal when species possess *different* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species are *identical* between patches. Environmental conditions *differ* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, lowest harvest price), species 2 (green), and species 3 (blue, highest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.04$ (b), and $a = 0.40$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.04$ (blue), and $a = 0.40$ (red).

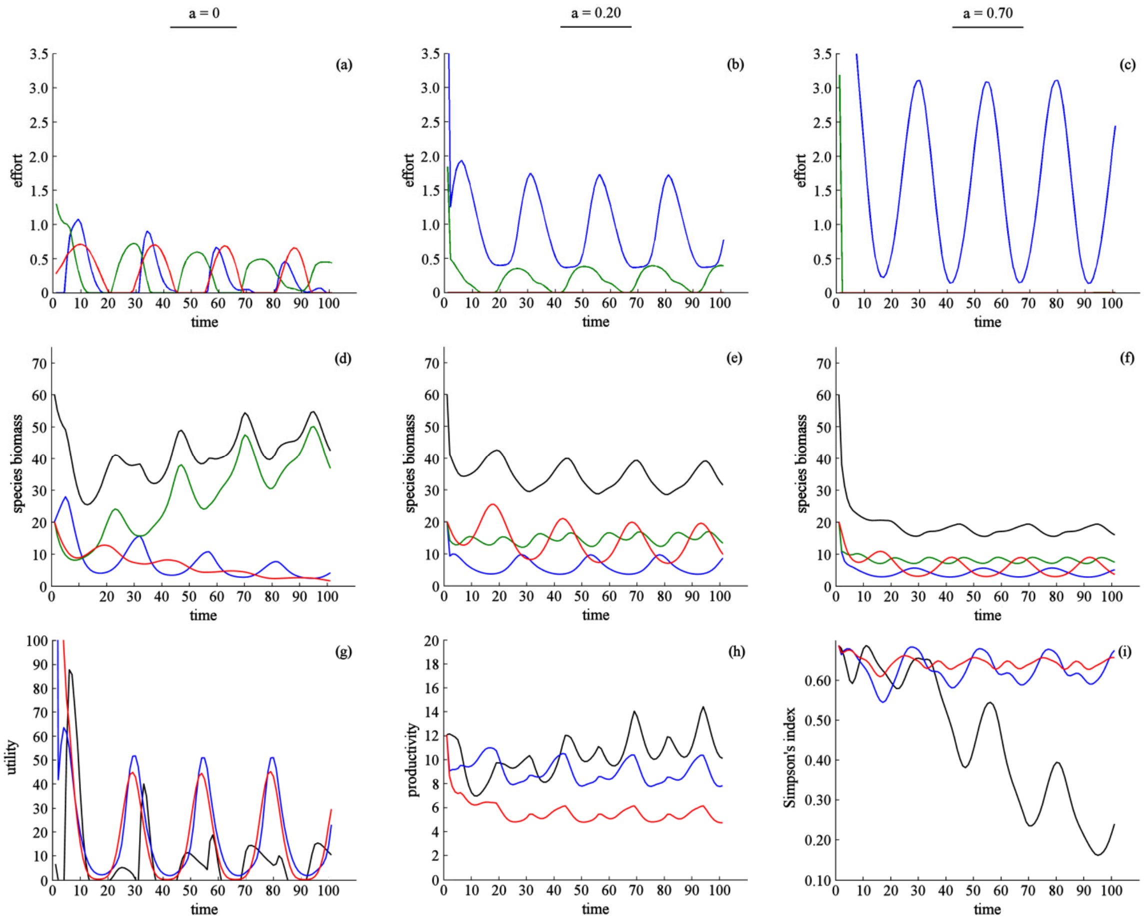

Figure A20. Effect of dispersal when species possess *different* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species *differ* between patches. Environmental conditions are the *same* across patches. Harvest effort (a-c); species biomass (d-f); utility (g); productivity (h); biodiversity (i). In (a-f) column indicates dispersal rate: $a = 0$ (a, d), $a = 0.20$ (b, e), and $a = 0.70$ (c, f). Color indicates harvest effort and species biomass for species 1 (red, lowest harvest price), species 2 (green), and species 3 (blue, highest harvest price). Black shows aggregate species biomass. In (g-i) color indicates dispersal rate: $a = 0$ (black), $a = 0.20$ (blue), and $a = 0.70$ (red).

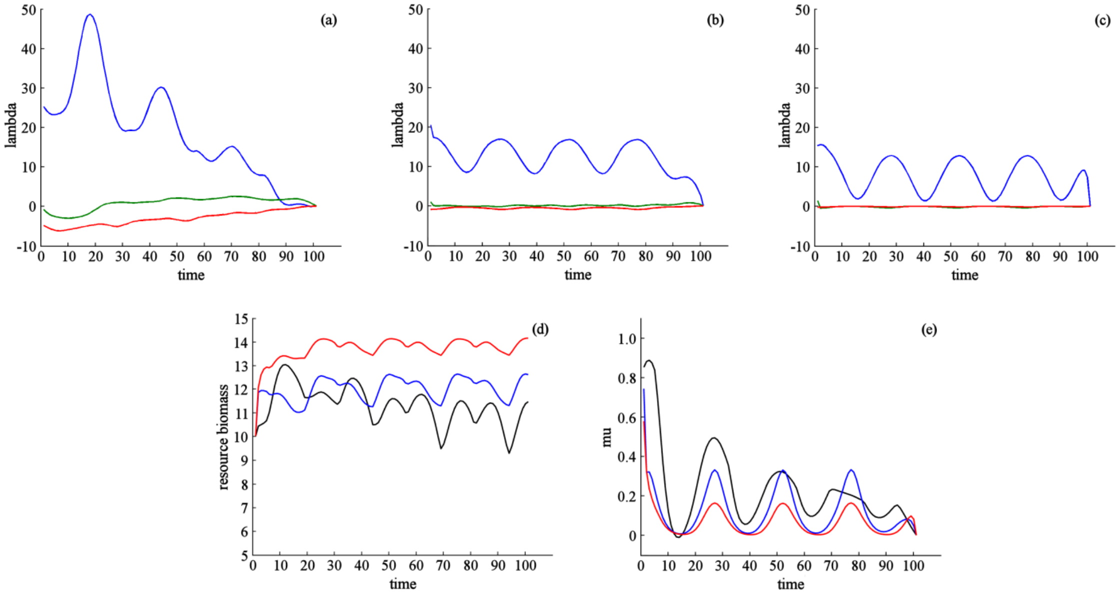

Figure A21. Effect of dispersal when species possess *different* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species *differ* between patches. Environmental conditions are the *same* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, lowest harvest price), species 2 (green), and species 3 (blue, highest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.20$ (b), and $a = 0.70$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.20$ (blue), and $a = 0.70$ (red).

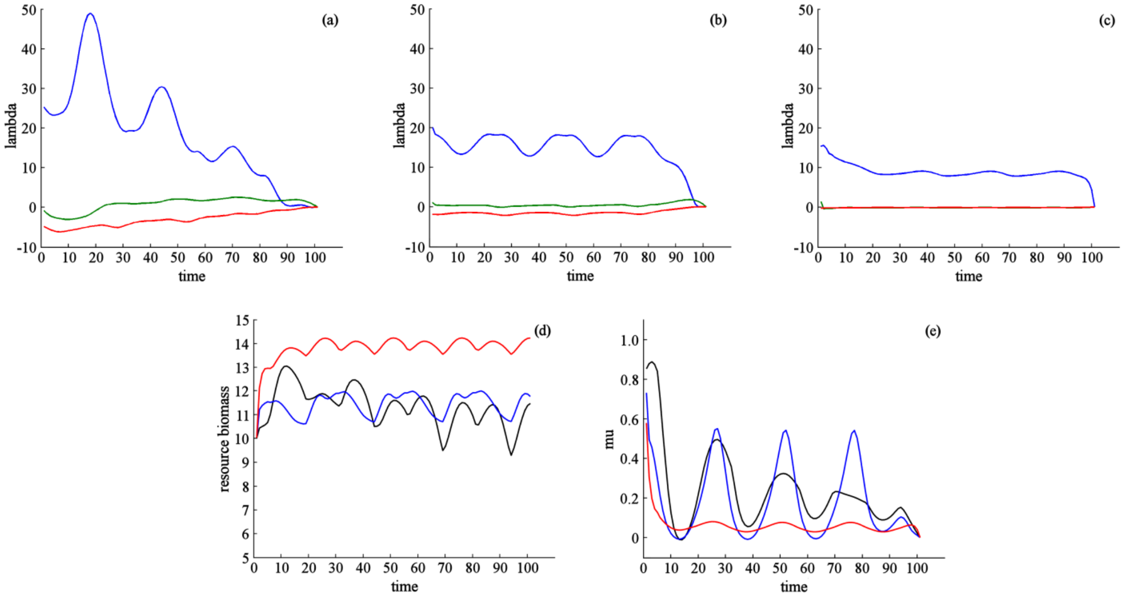

Figure A22. Effect of dispersal when species possess *different* ecological competition parameters, benefits are obtained through the direct consumption of species, and preferences for species *differ* between patches. Environmental conditions *differ* across patches. Lambda (a-c), resource biomass (d), and mu (e). In (a-c) color indicates shadow prices (lambdas) for species 1 (red, lowest harvest price), species 2 (green), and species 3 (blue, highest harvest price). Dispersal rate is given by column: $a = 0$ (a), $a = 0.10$ (b), and $a = 0.70$ (c). In (d-e) color indicates dispersal rate: $a = 0$ (black), $a = 0.10$ (blue), and $a = 0.70$ (red).

APPENDIX H

DETAILED TRADE DATA BY DISEASE-FREE CATEGORY

Table A3. Aggregate imports by disease-free, no vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	20,064,192	0	6	0	2,226,239
1997	17,542,230	2,506	94	0	1,906,428
1998	21,107,862	2,020	203	146	2,631,229
1999	22,446,030	2,244	401	416	1,387,416
2000	25,115,918	1	34,684	299	164,822
2001	16,048,212	0	201	156	6,498,031
2002	26,601,374	0	3,335	300	255,153
2003	27,790,668	0	16,786	327	187,627
2004	29,393,039	387	20,443	451	1,079,036
2005	32,345,965	449	8,875	4,119	57,937
2006	36,637,626	418	6,998	399	24,904
2007	40,046,609	835	10,325	3,475	20,891
2008	39,948,050	460	13,491	2,690	7,094
2009	39,799,253	429	15,655	2,542	13,223
2010	41,786,422	260	5,694	6,960	9,145
2011	41,163,047	35	211	19,274	68,025

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A4. Aggregate exports by disease-free, no vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	20,524,759	0	318	0	12,111,132
1997	17,581,013	136,789	1,502	0	18,753,391
1998	21,155,749	15,755	2,053	6,062	10,083,655
1999	21,127,562	44,945	1,171	112,311	14,783,355
2000	25,034,769	177	917	193,592	9,762,490
2001	16,986,901	5	107,777	624	11,789,193
2002	26,842,807	0	125,342	3,211	9,817,912
2003	29,871,470	0	98,315	2,209	9,093,117
2004	31,047,154	1,449	185,683	2,567	9,742,559
2005	33,938,948	2,568	142,564	6,732	4,872,216
2006	37,224,112	1,337	188,906	3,036	5,077,206
2007	40,555,387	901	205,708	2,316	4,671,545
2008	40,726,525	407	185,083	5,923	5,560,761
2009	44,009,689	135	236,767	3,283	5,489,216
2010	45,617,416	294	226,884	580,382	4,830,154
2011	43,393,590	22	172,097	967,191	4,692,144

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A5. Aggregate imports by disease-free zones, no vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	0	0	0	0	0
1997	636,189	16,668,170	0	0	1,158,726
1998	81,258	2,145,100	0	6,363	117
1999	32,255	18	0	392	51
2000	261	0	0	266	14
2001	2	0	0	34	222
2002	0	0	134	405	0
2003	0	0	0	0	0
2004	231	0	1,190	359	0
2005	145	1	0	2,866	0
2006	135	55	798	514	0
2007	51	0	0	372	0
2008	96	4	0	325	0
2009	105	1	0	511	0
2010	0	0	0	0	0
2011	0	0	0	0	0

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A6. Aggregate exports by disease-free zones, no vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	0	0	0	0	0
1997	4,062	86,064	834	0	96,028
1998	8,535	2,610	1,623	22,190	12,859
1999	0	0	0	14,488	56,560
2000	26	0	0	32,986	103
2001	0	0	0	0	17
2002	0	0	0	10,528	0
2003	0	0	0	0	0
2004	397	0	774	750	632,212
2005	830	1	1,415	4,403	287,122
2006	433	64	140	2,982	611,815
2007	833	330	1,608	44,475	408,822
2008	481	0	0	104,058	165,231
2009	472	0	8	51,052	309,009
2010	0	0	0	0	0
2011	0	0	0	0	0

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A7. Aggregate imports by disease-free, vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	273	0	25	0	218
1997	3,570	715	84,686	0	6,480
1998	971	261	57,303	1,572	6,336
1999	3,252	62	38,186	174	3,037
2000	964	0	44,737	8	3,868
2001	93,736	0	4,880	0	31,605
2002	125,510	0	11	603	12,914
2003	632	0	5,620	199	3,483
2004	254,084	783	149	340	12,413
2005	131,033	1,383	53	91	308
2006	231,320	105	93	95	73,246
2007	179,814	1,591	4,383	687	10,403
2008	161,121	157	6,294	518	57,095
2009	155,159	0	4,014	220	50,696
2010	202,816	18	4,897	2,318	45,087
2011	164,475	0	65	182	111,749

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A8. Aggregate exports by disease-free, vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	0	0	0	0	0
1997	1,837	0	624,079	0	37,950
1998	148	0	1,807,813	9	148,334
1999	389	0	243,833	39	17,786
2000	404	0	293,007	2	10,903
2001	276	0	6,136	0	836,945
2002	6,883	56	3	207	808,711
2003	33,035	0	812,315	685	27,418
2004	20,912	265	115	479	40,892
2005	10,544	0	101	28	2,905
2006	6,848	2,775	126	541	13,172
2007	15,759	0	831	52	9,194
2008	23,599	4	2,909	55	7,576
2009	12,846	0	299	137	33,198
2010	8,897	0	13	107	81,816
2011	249	0	233	142	112,735

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A9. Aggregate imports by disease-free zones, vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	0	0	0	0	0
1997	0	0	0	0	0
1998	112,461	28,709	0	0	99
1999	129,318	15,686	8	0	4,510
2000	193,452	36,701	4	0	45
2001	679	10	0	0	40,442
2002	3,310	38,428	178	4	20
2003	2,728	0	557	751	209
2004	2,083	802	537	67	225
2005	6,538	2,169	18	601	32
2006	1,989	3,135	562	383	74
2007	2,133	47,702	30	4,733	7
2008	2,594	83,725	49	6,091	6
2009	3,697	84,990	136	6,319	13
2010	304,077	82,568	102	6,757	134
2011	1,012,852	165,807	135	13,157	746,725

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A10. Aggregate exports by disease-free zones, vaccination countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	0	0	0	0	0
1997	0	0	0	0	0
1998	155	549	283	0	3,064
1999	210	1,128	5	0	7,009
2000	268	36	18	0	778
2001	273	13	0	0	1,272
2002	287	390	603	755	1,754
2003	297	0	198	380	3,488
2004	469	339	351	114	269,812
2005	4,302	2,805	160	648	250,619
2006	361	498	133	233	511,516
2007	4,492	434	213	4,642	581,292
2008	3,961	335	223	5,893	427,207
2009	2,588	475	2,309	5,480	535,250
2010	6,953	829	307	11,847	943,203
2011	1,828	3,146	339	17,599	446,474

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A11. Aggregate imports by not disease-free countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	5,117,268	0	38,535	0	6,878,131
1997	4,464,673	40,448	29,307	0	6,312,744
1998	4,142,247	1,131	92,850	76	8,744,182
1999	3,885,796	2,155	10,502	1,381	5,199,130
2000	4,504,725	13	10,850	2,408	10,006,715
2001	6,853,884	106	42,006	1,454	8,264,575
2002	5,137,380	0	476	2,006	10,489,904
2003	4,218,747	0	22,141	4,925	10,861,548
2004	2,406,721	545,415	70,007	214,364	12,136,692
2005	3,496,470	342,287	27,668	236,860	12,258,375
2006	3,455,688	782,616	12,104	429,869	11,575,985
2007	3,542,806	379,941	28,862	432,258	13,309,281
2008	2,483,643	89,848	5,159	448,341	8,751,498
2009	3,664,959	297,775	93,707	595,933	10,358,243
2010	3,480,758	71,088	64,870	899,200	10,161,907
2011	3,455,768	43,240	95,199	494,429	11,399,893

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

Table A12. Aggregate exports by not disease-free countries with countries in each disease-free designation.

year	DF, no vaccination	DFZ, no vaccination	DF, vaccination	DFZ, vaccination	Not disease-free
1996	2,365,482	0	367	0	5,650,685
1997	972,557	1,480	5,295	0	7,375,149
1998	978,171	5	7,626	2,300	5,112,289
1999	1,422,810	23	605	3,080	5,239,426
2000	113,285	0	21	718	4,637,486
2001	5,245,652	229	336	46,077	6,827,189
2002	120,303	0	928	3,112	8,965,030
2003	14,824	0	3,913	677	5,291,682
2004	23,910	3	10,267	693	8,147,576
2005	24,828	4	1,265	569	6,588,645
2006	10,667	1	1,096	255	7,922,047
2007	26,728	5	7,567	45	6,923,573
2008	5,425	16	64,937	9	9,004,199
2009	38,469	0	118,733	9	6,584,555
2010	6,773	0	133,469	48	6,552,578
2011	42,222	0	109,767	763,046	7,042,625

"DF" and "DFZ" indicate "disease-free" and "disease-free zones" respectively. Units are aggregate heads of livestock of all cloven hoofed animals available from the Food and Agriculture Organization (http://faostat3.fao.org/home/E).

APPENDIX I

TEST FOR COLLINEARITY BETWEEN IMPORTS AND EXPORTS

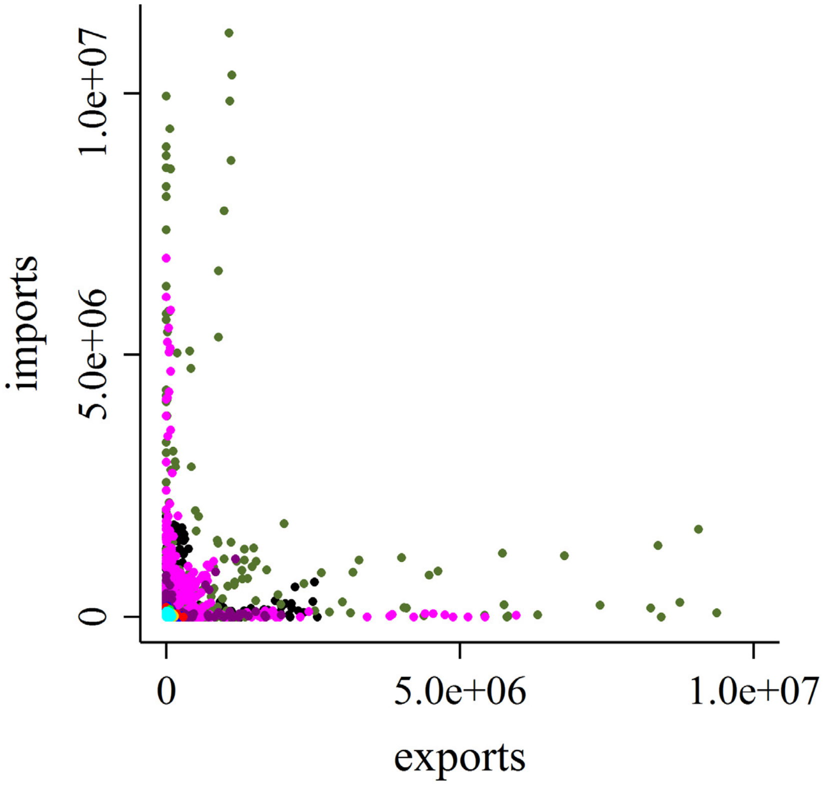

Figure A23. Annual imports versus annual exports. Each data point represents a country and year in my study. Color indicates the species traded: asses (green), buffaloes (yellow), camels (red), cattle (black), goats (purple), mules (cyan), pigs (forest green), and sheep (magenta).

APPENDIX J

FULL LOGISTIC TRADE REGRESSION ESTIMATES

Table A13. Full logistic regression trade estimates from imports of cattle.

	Variable	*no trade lag* Odds ratio	*no trade lag* p-value	*one-year trade lag* Odds ratio	*one-year trade lag* p-value
Importing from:	Eastern Africa	1.0001	0.372	1.0003*	0.055
	Central Africa	1.0002	0.472	0.9999	0.738
	Northern Africa	0.9993	0.524	0.9965*	0.033
	Southern Africa	1.0000	0.874	0.9999*	0.048
	Western Africa	0.9992*	0.062	1.0022*	0.005
	North America	1.0006*	0.000	1.0001	0.596
	Central America	0.9993*	0.096	0.9991	0.420
	Caribbean	0.9947	0.370	1.0014	0.430
	South America	1.0000*	0.034	1.0000	0.414
	Central Asia	0.9749	0.523	0.9890	0.646
	Eastern Asia	0.9999*	0.002	1.0003*	0.001
	Southern Asia	1.0003*	0.057	1.0007	0.107
	South-Eastern Asia	1.0000	0.499	1.0000	0.469
	Western Asia	1.0001	0.875	0.9983	0.124
	Eastern Europe	1.0000	0.733	0.9999	0.232
	Northern Europe	0.9997	0.503	1.0000	0.983
	Southern Europe	1.0002	0.164	0.9996	0.276
	Western Europe	0.9999*	0.024	1.0000	0.823
	Australia and New Zealand	1.0000*	0.007	1.0000	0.740
	Pacific Islands	1.0295*	0.002	1.0734*	0.005

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A single asterisk indicates significance at a 10% level.

Table A14. Full logistic regression trade estimates from imports of pigs.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Importing from:	Eastern Africa	0.9969	0.183	1.0074*	0.062
	Central Africa	1.0062	0.253	0.9915	0.260
	Northern Africa	1.0000	(omitted)	0.7972	0.210
	Southern Africa	1.0001	0.692	1.0003	0.135
	Western Africa	0.9938	0.258	1.0008	0.902
	North America	0.9991*	0.014	1.0002	0.702
	Central America	1.0074	0.919	0.8342	0.175
	Caribbean	1.0604	0.330	1.0934*	0.047
	South America	1.0003	0.476	0.9997	0.482
	Central Asia	1.0010	0.787	1.0160*	0.015
	Eastern Asia	1.0000	0.352	1.0001*	0.000
	Southern Asia	1.1146	0.278	1.3422*	0.035
	South-Eastern Asia	1.0000	0.187	1.0000	0.339
	Western Asia	1.0181*	0.000	1.0285	0.126
	Eastern Europe	1.0000	0.512	1.0000	0.885
	Northern Europe	1.0000	0.253	0.9997*	0.054
	Southern Europe	0.9996*	0.022	0.9984*	0.095
	Western Europe	1.0000	0.170	1.0002*	0.024
	Australia and New Zealand	0.9907*	0.039	0.9846*	0.005
	Pacific Islands	1.0000	(omitted)	1.0000	(omitted)

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A single asterisk indicates significance at a 10% level.

Table A15. Full logistic regression trade estimates from imports of sheep.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Importing from:	Eastern Africa	1.0000	0.473	0.9999*	0.019
	Central Africa	0.9999	0.307	1.0001	0.217
	Northern Africa	1.0000	0.830	1.0000	0.127
	Southern Africa	0.9991*	0.060	1.0001	0.160
	Western Africa	1.0000	0.789	1.0000	0.456
	North America	1.0002	0.416	1.0001	0.527
	Central America	0.9986	0.842	0.9992	0.913
	Caribbean	0.9671	0.232	0.9324	0.105
	South America	1.0000	0.347	0.9999*	0.060
	Central Asia	1.0024	0.323	1.0035*	0.053
	Eastern Asia	1.0001	0.673	1.0001	0.539
	Southern Asia	1.0001	0.861	1.0002	0.532
	South-Eastern Asia	0.9961*	0.001	0.9898*	0.005
	Western Asia	1.0000	0.998	1.0000*	0.068
	Eastern Europe	1.0000	0.565	1.0001*	0.042
	Northern Europe	1.0001	0.268	1.0007*	0.033
	Southern Europe	0.9996*	0.049	1.0009*	0.079
	Western Europe	0.9998	0.339	0.9999	0.571
	Australia and New Zealand	1.0000	0.758	1.0000	0.764
	Pacific Islands	1.0000	(omitted)	1.0000	(omitted)

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A single asterisk indicates significance at a 10% level.

Table A16. Full logistic regression trade estimates from exports of cattle.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Exporting to:	Eastern Africa	1.0000*	0.032	1.0000	0.660
	Central Africa	1.0000	0.938	1.0005	0.251
	Northern Africa	1.0000	0.482	1.0000	0.707
	Southern Africa	1.0006*	0.068	1.0000	0.782
	Western Africa	1.0000	0.254	1.0000	0.551
	North America	1.0214*	0.000	0.9955	0.709
	Central America	1.0003	0.644	1.0001	0.927
	Caribbean	0.9780	0.107	1.0644	0.139
	South America	1.0000	0.117	1.0000	0.743
	Central Asia	0.9989*	0.000	0.9978*	0.004
	Eastern Asia	1.0001*	0.032	0.9998	0.110
	Southern Asia	0.9984	0.677	0.9835	0.403
	South-Eastern Asia	0.9999*	0.002	0.9997*	0.007
	Western Asia	1.0000*	0.024	1.0000	0.272
	Eastern Europe	1.0002	0.368	1.0006	0.556
	Northern Europe	0.9994	0.280	0.9996	0.574
	Southern Europe	1.0000	0.414	1.0000	0.876
	Western Europe	0.9999	0.337	1.0002	0.256
	Australia and New Zealand	0.9447	0.190	1.1043	0.197
	Pacific Islands	0.8777	0.289	1.2464	0.123

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A single asterisk indicates significance at a 10% level.

Table A17. Full logistic regression trade estimates from exports of pigs.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Exporting to:	Eastern Africa	0.9979*	0.005	1.0013	0.329
	Central Africa	1.0055	0.444	0.9972	0.754
	Northern Africa	0.9993	0.916	0.9899	0.234
	Southern Africa	1.0002	0.897	0.9888*	0.010
	Western Africa	0.9997	0.620	1.0014*	0.069
	North America	0.9743	0.126	0.9748	0.119
	Central America	1.0000	(omitted)	0.1473	0.108
	Caribbean	0.5562	0.264	0.5055	0.158
	South America	1.0004	0.430	1.0007	0.227
	Central Asia	0.9956	0.418	0.9939	0.511
	Eastern Asia	1.0000	0.404	0.9999*	0.000
	Southern Asia	1.0567	0.396	2.1892*	0.041
	South-Eastern Asia	1.0000*	0.030	1.0001*	0.026
	Western Asia	1.0011*	0.075	1.0021*	0.059
	Eastern Europe	0.9999	0.219	0.9998	0.153
	Northern Europe	1.0000	0.525	1.0007	0.132
	Southern Europe	1.0000	0.741	0.9998*	0.009
	Western Europe	1.0000	0.311	0.9999	0.448
	Australia and New Zealand	1.0127	0.973	0.1329*	0.015
	Pacific Islands	0.9708	0.671	1.0000	(omitted)

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A single asterisk indicates significance at a 10% level.

Table A18. Full logistic regression trade estimates from exports of sheep.

		no trade lag		*one-year trade lag*	
	Variable	Odds ratio	p-value	Odds ratio	p-value
Exporting to:	Eastern Africa	1.0001	0.526	0.9999	0.628
	Central Africa	1.0001	0.622	1.0000	0.984
	Northern Africa	0.9999	0.145	1.0001	0.245
	Southern Africa	1.0000*	0.064	1.0000	0.793
	Western Africa	1.0000	0.424	1.0000*	0.069
	North America	1.0003	0.894	1.0011	0.760
	Central America	0.9859*	0.005	0.9604*	0.037
	Caribbean	1.0082	0.493	1.0288*	0.035
	South America	1.0000	0.860	1.0000	0.488
	Central Asia	1.0003	0.168	1.0011*	0.079
	Eastern Asia	1.0004*	0.012	0.9984*	0.018
	Southern Asia	1.0006*	0.000	1.0010*	0.002
	South-Eastern Asia	0.9989*	0.029	0.9999	0.826
	Western Asia	1.0000	0.807	1.0000*	0.085
	Eastern Europe	1.0001	0.191	1.0000	0.659
	Northern Europe	0.9995	0.455	0.9993	0.196
	Southern Europe	1.0000	0.317	1.0000	0.126
	Western Europe	1.0001	0.132	0.9999	0.785
	Australia and New Zealand	0.9988	0.704	1.0030	0.374
	Pacific Islands	1.5025*	0.042	1.0081	0.878

P-values are rounded to three decimal places; trade data are rounded to four decimal places. A single asterisk indicates significance at a 10% level.

APPENDIX K

IMPLEMENTING A REGRESSION DISCONTINUITY DESIGN (RDD) EXPERIMENT

The basic idea behind a regression discontinuity design (RDD) experiment is to exploit a discontinuity in the data ("threshold effect") due to a particular treatment (Anderson and Magruder, 2012; Hahn et al., 2001). The discontinuity arises as a break in the dependent variable at an exogenously determined threshold of an indicator or "assignment" variable. By measuring the change in the dependent variable on either side of the discontinuity one may measure the effect of the treatment. See Imbens and Lemieux (2008), Lee and Lemieux (2010), and Jacob et al. (2012) for reviews of this literature.

Though mild compared to difference-in-differences and instrumental variable approaches, an RDD experiment makes several key assumptions that are of particular concern (Jacob et al., 2012; Lee and Lemieux, 2010). First, there exists a clear structural break in the data, specifically solely in the assignment variable. Discontinuities in other covariates lead to problems in the identification of the treatment effect. Second, participants in the experiment have an equal chance of being on either side of the discontinuity. That is, they have no control in their placement around the discontinuity and (all else equal) the treatment is the driving factor in determining the value of their assignment variable.

We would expect a country's disease-free designation to be an appropriate assignment variable for a RDD experiment. It captures observed and unobserved characteristics that determine the number of outbreaks within a country. Regressing across disease-free categories should aid in removing endogeneity associated with unobserved heterogeneity between countries. We find a distinct difference in the number of reported outbreaks for countries within each disease-free designation (Figure A24a).

However, the use of disease-free designation is problematic for several reasons. Countries have a certain degree of control over their designation. Low designation countries can improve biosecurity and sanitary conditions to obtain a higher status. Indeed, this is the goal of the global food and mouth disease control strategy (World Organisation of Animal Health (OIE) and Food and Agriculture Organization (FAO), 2012).

Further, disease-free designation is a discrete categorical variable. RDD experiments compare data on either side of the discontinuity to estimate the effect of a treatment (Imbens and Lemieux, 2008). With a categorical variable the data is physically on the structural break leading to problems with identification of the treatment effect. We constructed a new assignment variable based on a country's binary control variables:

$$\begin{aligned} assign_{it} = {} & 1.37R_{it} + 1.16Cr_{it} + 0.89M_{it} + 1.43Qf_{it} + 1.09Qi_{it} + 4.04S_{it} \\ & + 0.45Sp_{it} + 1.31Su_{it} + 1.04Te_{it} + 0.36V_{it} + 5.44Vp_{it} + 1.53Z_{it} \end{aligned} \quad \text{[A25]}$$

where the binary variables for country i at time t are given by: R (legal obligation to report a disease outbreak), Cr (presence of wild reservoirs), M (disease monitoring), Qf (precautions at the borders), Qi (movement control inside the country), S (stamping out of all sick and contaminated animals), Sp (modified stamping out, e.g. practicing a subset of stamping out procedures), Su (continuous surveillance of a given population),

Te (screening), V (vaccinations practiced), Vp (vaccinations prohibited), and Z (zoning).

The weight associated with each variable is the ratio of the percentage of occurrences for all observations in countries with any disease-free designation over that of countries with no disease-free designation. For example, countries with any disease-free designation were required to report an outbreak 80.23% of the time; countries without a designation were required to report an outbreak 58.40% of the time (1.37=80.23/58.40). A higher value of the assignment variable indicates a safer country. Due to the zero-inflated nature of the data we did not observe a clear break in the data (Figure A24b). This suggests that a RDD experiment may not be appropriate for this type of study.

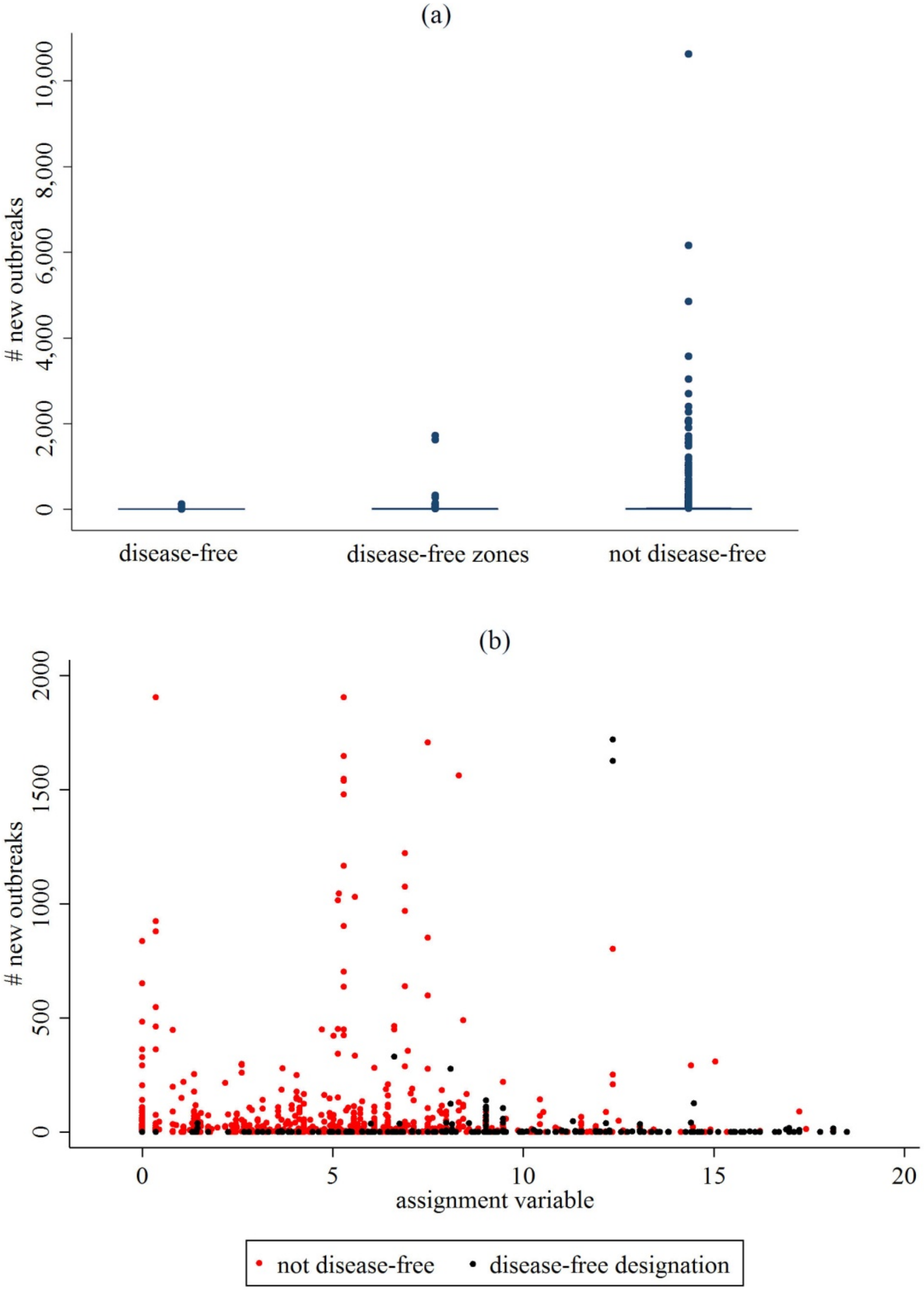

Figure A24. Number of new outbreaks by disease-free designation (a) and assignment variable (b). In (a) disease-free designations are aggregated into two categories: disease-free (vaccination and no vaccination) and disease-free zones (vaccination and no vaccination). In (b) we aggregated all countries possessing a disease-free designation into a single category.