THE STRUCTURE AND FUNCTIONING OF METACOMMUNITIES IN CHANGING ENVIRONMENTS

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This work is dedicated to my family.
To my parents, Sharon and James, who fostered my love of nature.
To my brother, Niobe, who showed me what was possible.
And to my wonderful partner, Maia, who inspires me to be my best.

ABSTRACT

Landscape fragmentation limits the ability of species to disperse between habitats and shift their distributions in response to changing environmental conditions. Because of habitat fragmentation, many species will be unable to keep pace with climate change, and this is expected to greatly impact the diversity, functioning, and stability of future ecosystems. Conserving habitat connectivity is expected to mitigate some of these impacts. But there are also concerns that the complexity of ecological responses will compromise our ability to predict future community structure and functioning. The spatial insurance hypothesis extends connectivity science to show how dispersal between local habitats maintains biodiversity and ecosystem functioning when environmental conditions are changing. However, complex issues remain, such as whether dispersal can simultaneously provide stability for the full range of ecosystem functions produced by a community, and how regional climate warming will impact the strength of spatial insurance provided by biological diversity.

In this thesis, I extend research on the spatial insurance hypothesis with a combination of field surveys, experimentation, and theoretical simulations. I first conducted a field survey to determine how the composition and function of pond zooplankton communities was structured by the local environmental conditions of ponds on Mont St. Hilaire, QC. I found that measures of zooplankton functional and phylogenetic diversity outperformed species richness in explaining variation in two types of zooplankton ecosystem functions. Furthermore, the composition of these communities was determined by the local environmental conditions in the ponds, suggesting that dispersal could potentially provide spatial insurance if these conditions were to change. I then tested this experimentally, asking whether dispersal could preserve diversity and provide stability to metacommunities under ambient and warmed conditions. I found that dispersal preserved biodiversity and stabilized metacommunity biomass in ambient conditions, but that this benefit was lost with warming. This suggests that the stabilizing effects of dispersal may be eroded by directional environmental change, such as climate warming. I then returned to the spatial insurance model, extending the theory by incorporating multiple ecosystem functions. I showed that changing the rate at which species disperse dramatically alters the number, identity, and stability of functions that are produced both locally and regionally. Intermediate dispersal rates result in the greatest simultaneous production of functions across spatial scales and stabilize the temporal production of each function at the regional scale. However, this results in great local variability of each function, which differs from the stabilizing effect previously reported when only one function is considered. Finally, I used a theoretical simulation to test how biotic interactions and the rate of species dispersal interact to affect the predictability of multispecies range shifts under directional climate change. I showed how biotic interactions result in differences in the ability of species to track changes in climate, resulting in novel and unpredictable community compositions. Yet, when dispersal rates are not limiting, these differences are minimized and species track changes in climate at the same speed as their neighbours, leading to predictable range shifts.

As a whole, my thesis tests and extends the spatial insurance hypothesis, demonstrating the conditions under which dispersal maintains the composition, functioning, stability, and predictability of ecological communities. These findings give support to the strategy of managing landscapes to maintain connectivity as a way to mitigate the joint impacts of habitat fragmentation and climate change.

RÉSUMÉ

La fragmentation du paysage limite la capacité des espèces à se disperser d'un habitat à l'autre et à modifier leurs distributions en fonction des variations dans les conditions environnementales. En raison de la fragmentation des habitats, plusieurs espèces seront incapables de suivre le rythme des changements climatiques, ce qui pourrait entraîner des conséquences importantes au niveau de la diversité, du fonctionnement, et de la stabilité des écosystèmes futurs. Bien que la conservation de la connectivité des habitats devrait permettre de mitiger certains de ces impacts, notre capacité à prévoir la structure et le fonctionnement des communautés futures pourrait être compromise par la complexité des réponses écologiques. L'hypothèse d'assurance spatiale approfondit la science de la connectivité en démontrant comment la dispersion entre les habitats locaux maintient la biodiversité et le fonctionnement de l'écosystème lors de changements dans les conditions environnementales. Néanmoins, certains enjeux complexes persistent : la dispersion des espèces peut-elle simultanément stabiliser l'éventail complet des fonctions écosystémiques générées par une communauté, et comment les changements climatiques régionaux influenceront-ils la force de l'assurance spatiale engendrée par la diversité biologique?

Cette thèse approfondit la recherche au sujet de l'hypothèse d'assurance spatiale à travers une combinaison d'études de terrain, d'expérimentation, et de simulations théoriques. Premièrement, j'ai réalisé une étude de terrain afin de déterminer comment les conditions environnementales locales ont structuré la composition et le fonctionnement des communautés de zooplancton dans des étangs du Mont St-Hilaire, QC. Mes résultats démontrent que les mesures de diversités fonctionnelle et phylogénétique du zooplancton étaient plus performantes que celles de diversité des espèces pour expliquer la variation dans deux types de fonctions des écosystèmes de zooplancton. De plus, la composition de ces communautés était déterminée par les conditions environnementales locales des étangs, ce qui suggère que la dispersion pourrait potentiellement offrir une assurance spatiale si ces conditions devaient changer. J'ai ensuite testé ce constat de façon expérimentale en examinant si la dispersion permettait de préserver la diversité et d'assurer la stabilité de métacommunautés sous conditions ambiantes et sous une hausse de température.

Mes résultats démontrent que la dispersion préserve la biodiversité et stabilise la biomasse de la métacommunauté sous conditions ambiantes, mais que cet avantage se perd avec une hausse de température. Ceci suggère que les effets stabilisateurs de la dispersion pourraient être érodés par un changement environnemental directionnel, tel que le réchauffement climatique. En portant un second regard sur le modèle de l'assurance spatiale, j'ai approfondi la théorie en y incorporant plusieurs fonctions écosystémiques. J'ai démontré que lorsque la fréquence de dispersion des espèces varie, le nombre, l'identité, et la stabilité des fonctions produites de façon locale et régionale sont altérés considérablement. Une fréquence de dispersion intermédiaire entraîne la plus grande production simultanée de fonctions dans l'ensemble des échelles spatiales et stabilise la production temporelle de chaque fonction à l'échelle régionale. En contrepartie, ceci entraîne une grande variabilité locale de chaque fonction, ce qui contraste avec l'effet stabilisateur rapporté auparavant lorsqu'une seule fonction est considérée. Finalement, j'ai utilisé une simulation théorique afin de tester comment les interactions biotiques et la fréquence de dispersion des espèces interagissent et affectent la prévisibilité des déplacements multiespèces des aires de répartition en réponse à un changement climatique directionnel. J'ai démontré comment les interactions biotiques entraînent des différences dans la capacité des espèces à suivre les changements climatiques, ce qui entraîne de nouvelles compositions de communautés imprévisibles. Pourtant, lorsque les fréquences de dispersion ne sont pas limitantes, ces différences sont minimisées et les espèces suivent les changements climatiques à la même vitesse que leurs voisins, entraînant ainsi des déplacements prévisibles des aires de répartitions.

Dans son ensemble, ma thèse teste et approfondit l'hypothèse d'assurance spatiale en démontrant les conditions sous lesquelles la dispersion maintient la composition, le fonctionnement, la stabilité et la prévisibilité des communautés écologiques. Ces résultats se portent à l'appui d'une stratégie de gestion des paysages visant à maintenir la connectivité dans le but de mitiger les impacts conjoints de la fragmentation des habitats et des changements climatiques.

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PREFACE

THESIS FORMAT

This thesis is presented in manuscript-based format, with connecting statements between the chapters. All manuscripts have been published, submitted for review, or are in preparation for submission to a peer reviewed scientific journal. Each manuscript chapter has therefore been written to stand-alone. I start with a general introduction proving the background rationale for the research and outlining how the thesis chapters are linked. This is followed by four manuscript chapters:

2. **Ecosystem functions across trophic levels are linked to functional and phylogenetic diversity.** This chapter has been published by Patrick L. Thompson, T. Jonathan Davies, & Andrew Gonzalez (2015) *PLoS ONE* 10(2): e0117595.
3. **Warming induces synchrony and destabilizes experimental pond zooplankton metacommunities.** This chapter has been published by Patrick L. Thompson, Beatrix E. Beisner, & Andrew Gonzalez (2015) *Oikos*. Online early view.
4. **Spatial insurance extends to multiple ecosystem functions across metacommunities.** This chapter is in preparation for submission to an academic journal: Patrick L. Thompson & Andrew Gonzalez. *Proceedings of the Royal Society of London B*.
5. **Connectivity makes future communities more predictable under climate change.** This chapter is in preparation for submission to an academic journal: Patrick L. Thompson & Andrew Gonzalez. *Nature Climate Change*.

A sixth chapter serves as a synthesis of the thesis, suggests future directions for research, and provides general conclusions of the thesis. References throughout the thesis follow the format from the journal *Ecology*.

AUTHOR CONTRIBUTIONS

I am the first author on all manuscript chapters. I led all aspects of each project including: the conception, study design, fieldwork, data collection, mathematical simulations, statistical analyses, and writing. Andrew Gonzalez provided supervision throughout each project, contributing in the design and implementation of the projects, providing advice on the simulations and statistical analyses, and providing guidance in the preparation and writing of the manuscripts. T. Jonathan Davies, provided guidance in the data analysis, and writing of Chapter 2. Beatrix Beisner provided guidance in the design, analysis, and writing of Chapter 3, and contributed materials and equipment to the study.

STATEMENT OF ORIGINALITY

In Chapter 2, I show how functional and phylogenetic diversity indices outperform species richness in explaining variation in the functioning of natural pond zooplankton communities. Previous studies on this topic have focused almost exclusively on experimental communities consisting only of plants. In addition, I use variation partitioning as a novel way of considering how functional, phylogenetic, and taxonomic diversity measures explain unique and overlapping variation in ecosystem functioning.

In Chapter 3, I provide the one of the first empirical test of the spatial insurance hypothesis in the context of regional climate warming. Several researchers have demonstrated the stabilizing effect of dispersal experimentally, but this is the first test of this theory in the context of directional climate warming. My results suggest that the stabilizing effects of dispersal may be eroded when warming is directional and regional.

In Chapter 4, I use metacommunity theory to formalize the relationship between biodiversity and multiple ecosystem functions from local to regional scales. Empirical studies have observed that this relationship is scale dependent, but surprisingly, few studies have addressed the theoretical expectations of the biodiversity-multifunction relationship. I demonstrate that in variable environments, the relationship between biodiversity and the number of functions that are simultaneously produced is mediated by the rate at which species disperse.

In Chapter 5, I show how biotic interactions and dispersal interact to affect the predictability of multispecies range shifts under climate change. Biotic interactions and dispersal limitation are widely acknowledged to create uncertainty in range shift predictions, but so far they have been largely considered independently. My results suggest that the amount of uncertainty caused by biotic interactions depends on species dispersal rates so that future ecosystems are most predictable in connected landscapes.

1. INTRODUCTION

The Millennium Ecosystem Assessment (2005) defines an ecosystem as “a dynamic complex of plant, animal, and microorganism communities and the nonliving environment interacting as a functional unit.” Within this functional unit, species produce a variety ecosystem functions (e.g. primary productivity, nitrogen fixation, and pollination)(Hector and Bagchi 2007), which sustain the ecosystem services that humans rely on (Costanza et al. 1997). The composition, and therefore the functioning, of an ecosystem depends on the complex interplay of the abiotic (nonliving) environment, the interactions between species, and the movement of organisms to and from other ecosystems (Hutchinson 1957, Leibold et al. 2004). In ecosystems across the globe, human activities are now altering this interplay (Vitousek et al. 1997, Sala et al. 2000, Pereira et al. 2010). Climate change is modifying the abiotic environment (IPCC 2013), while habitat destruction and the resulting landscape fragmentation are restricting the movement of species between ecosystems (Haddad et al. 2015). Biodiversity is expected to decline because many species will not be able to disperse fast enough to track their climate niches (Loarie et al. 2009), and those that do survive will be present in new habitats, interacting with species that they were not previously in contact with (Williams and Jackson 2007). Through these changes in biodiversity and community composition, the anthropogenic stresses of climate change and landscape fragmentation will have consequences for the functioning of ecosystems and the services that we derive from them (Cardinale et al. 2012, Hooper et al. 2012, Mitchell et al. 2013).

With this thesis, I seek to further our understanding of how climate change and landscape fragmentation interact to affect the composition of ecological communities, and how this in turn affects their functioning, stability, and predictability at local and regional scales. This focus on scale is important because the way that these ecosystem properties change will depend on the spatial scale at which they are considered (Chase and Leibold 2002). Landscapes are composed of mosaics of local habitats varying in spatial composition and configuration (Fig. 1-1) and connected by fluxes of nutrients and energy and the movement of organisms (Loreau et al. 2003b). Therefore, when the connectivity of a region is altered, it affects the diversity and composition of each local community, and this has consequences for the functioning and stability at both local and regional scales (Holt 1993, Chase and Ryberg 2004). Because of this spatial interdependence, large-scale environmental change, such as climate change and land use change will affect dynamics of the region as a whole as well as each of the component communities. For example, local biodiversity may decline, but if different species are lost in each community, regional biodiversity will be unaffected (Mouquet and Loreau 2003). In this thesis, I consider three spatial scales, local (i.e. individual habitat patches; Fig. 1-1a), regional (Fig. 1-1b), and landscape (Fig. 1-1c). Patches within a region will vary in their local environmental conditions, but all patches in the region experience the same climatic conditions. In contrast, the larger landscape scale spans climatic gradients, and patches at higher elevation and latitude tend to be cooler than patches at lower elevation and latitude (Loarie et al. 2009). An understanding of how climate change and landscape fragmentation will interact to affect ecosystems across spatial scales is needed if we are to manage landscapes to preserve biodiversity and ecosystem functioning.

CLIMATE CHANGE AND LANDSCAPE FRAGMENTATION

Since 1880, global temperatures have risen by an average of 0.85°C, and forecasts estimate that we can expect an additional increase of as much as 4.8°C by 2100 (IPCC 2013). In addition to warming temperatures and changing patterns of precipitation, the frequency and magnitude of extreme weather events are expected to increase. These changes are already affecting natural ecosystems, as species respond to warming temperatures by shifting their phenologies and geographic distributions (Walther et al. 2002, Parmesan and Yohe 2003). Species must disperse by an average of 0.42 km each year to keep pace with climate change, and many will be unable to do so (Loarie et al. 2009). Estimates suggest that 15 to 37 % of species may be committed to extinction as a result of climate change (Thomas et al. 2004), making it one of the primary threats to biodiversity (Sala et al. 2000, Pereira et al. 2010). Overall, climate change is expected to greatly disrupt the composition of ecosystems, creating no-analogue communities, comprised of species that do not currently co-occur (Williams and Jackson 2007).

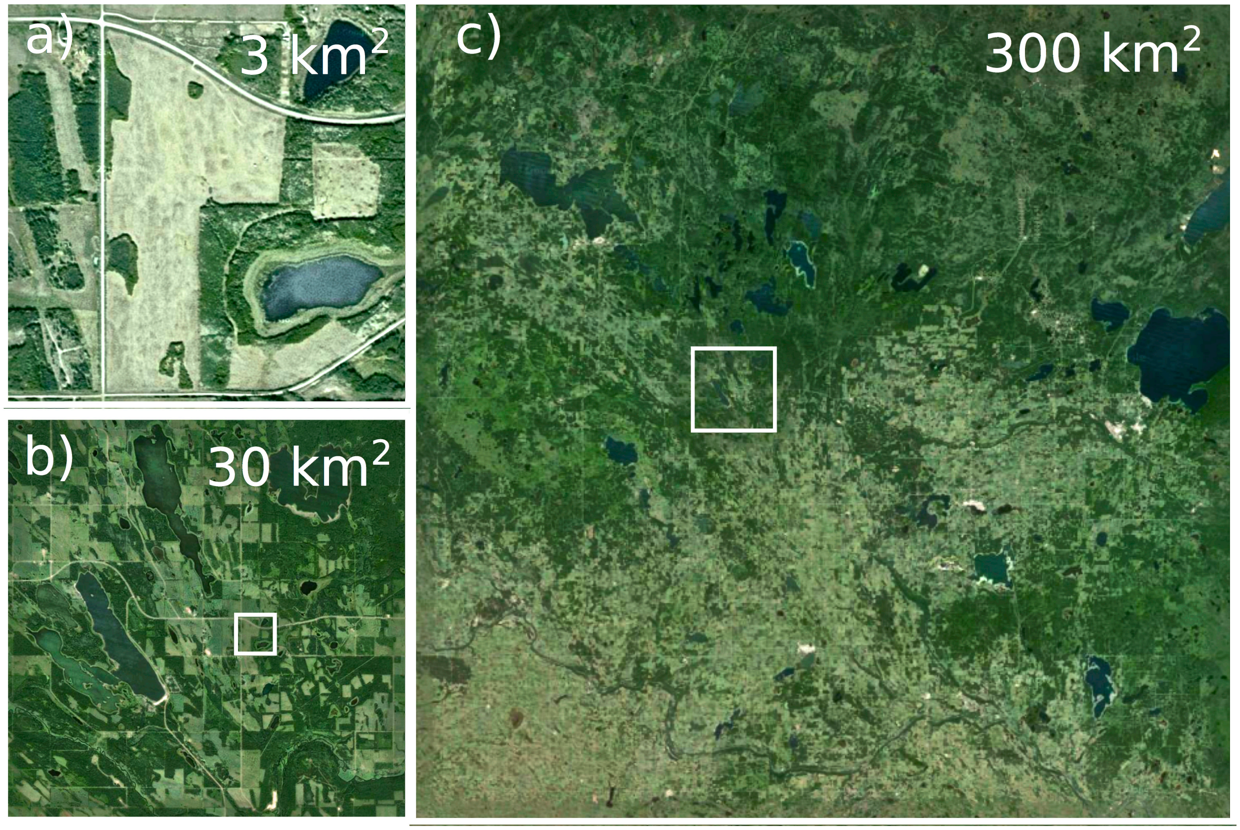

Figure 1-1. Illustration of the scale dependency of habitat and landscape connectivity. Individual habitat patches (lakes and forest patches that are visible in panel a) together form regional (b) and landscape (c) scales. The areas shown in panels a and b correspond to the boxes in panels b and c respectively.

As well as directly causing biodiversity loss, habitat destruction fragments landscapes by dividing and isolating habitat that was previously continuous (Fahrig 2003). Loss of habitat around the globe is the primary cause of biodiversity loss (IUCN 2014) and has resulted in widespread fragmentation: 70% of the world's remaining forests are now within 1km of the forest edge (Haddad et al. 2015). Landscape fragmentation has complex effects on biodiversity because it simultaneously results in reduced fragment size and fragment isolation (Didham et al. 2012). Habitat isolation reduces the movement of organisms between fragments, which results in changes in biodiversity, community composition, and thus ecosystem function in both the individual fragments and in the region as a whole (Ibáñez et al. 2014, Haddad et al. 2015).

In combination, climate change and landscape fragmentation have even greater consequences for biodiversity and ecosystem functioning (Brook et al. 2008). Fragmentation restricts the ability of species to track their climate niches (Collingham and Huntley 2000), increasing the number of species that are expected to go extinct (Thomas et al. 2004) and the likelihood of no-analogue communities (Urban et al. 2012). Yet, this synergy between ecological stressors offers an opportunity to manage landscapes to be resilient to climate change. Maintaining landscape connectivity in order to preserve biodiversity in changing climates is a widely accepted strategy (Heller and Zavaleta 2009); it is the impetus for programs such as the Yellowstone to Yukon Conservation Initiative (www.y2y.net). However, this strategy is largely based on the common sense reasoning that connectivity will allow species to shift their ranges in response to change (Heller and Zavaleta 2009). Research is needed to understand how different levels of landscape connectivity will affect the way ecosystems respond to climate change in space and time.

THE METACOMMUNITY FRAMEWORK

Metacommunity theory offers a framework for understanding the effects of the interaction between landscape fragmentation and climate change on biodiversity and ecosystem functioning. Metacommunities, an extension of the metapopulation concept (Levins 1969, Hanski 1994), consist of communities of interacting species that occupy habitat patches connected in space by dispersal (Tilman et al. 1994, Leibold et al. 2004). By considering a region or landscape as a network of connected local habitats (Fig. 1-1), the metacommunity framework allows us to consider how the interactive effects of climate change and landscape fragmentation affect the composition, stability, functioning, and predictability of ecosystems, at both local and regional scales.

Metacommunity models provide insight into the effects of landscape fragmentation by asking how changing the rate at which species disperse between patches affects community structure and ecosystem functioning (Mouquet and Loreau 2003). When the local environments in a metacommunity are heterogeneous and fluctuate independently, dispersal can provide spatial insurance, preserving biodiversity and stabilizing community productivity (Loreau et al. 2003a, Gonzalez et al. 2009). By dispersing between patches, species are able to persist and remain productive as they track their environmental niches through time and space. This facilitates stabilizing compensatory dynamics, whereby species exhibit differential responses to environmental fluctuations so that the overall biomass and productivity of the community varies less than that of its component species (Gonzalez and Loreau 2009). By preserving local biodiversity and ensuring high and stable productivity in each patch, spatial insurance also ensures that these properties are maintained at the regional, metacommunity scale. The effects of spatial insurance are strongest when dispersal rates are intermediate but decrease when dispersal is either too low or too high (Loreau et al. 2003a). Low dispersal rates are not sufficient to allow species to track local changes in the environment, while high dispersal rates homogenize the metacommunity, through source sink effects, and productivity and biodiversity decline because species are present in patches that are unsuitable to growth. Therefore, changing the rate at which species disperse between habitats alters the ability of metacommunities to maintain biodiversity, ecosystem functioning, and stability in changing environments.

Habitat fragmentation and metacommunity theory is relevant to both terrestrial and aquatic ecosystems (Haddad et al. 2015). Deforestation is an obvious example that results in the fragmentation of the remaining forest patches, within a matrix of converted land. Similarly, the conversion of natural grasslands into farmland results in a fragmented metacommunity of remnant grassland. Freshwater ponds and lakes form natural metacommunities with discrete boundaries, and human activities, such as the damming of rivers, are resulting in the further fragmentation of these ecosystems as well (Nilsson et al. 2005). Another type of aquatic fragmentation occurs when water removal and increased evaporation reduce water levels, isolating water bodies that were previously connected (Bond et al. 2008). Regardless of the type of ecosystem, metacommunity theory is useful for understanding how these changes in landscape connectivity will affect the ecosystems in changing environments.

The empirical chapters of my thesis, chapters 2 and 3, were conducted using the regional scale pond zooplankton metacommunity in the Gault Nature Reserve, Mont St. Hilaire, Quebec. Pond communities are ideal for testing metacommunity theory because plankton have short generation times and respond dynamically to changes in their environments (Leibold and Norberg 2004). Many aquatic insects have areal life stages, allowing them to move easily between waterbodies. Plankton are also known disperse readily between nearby waterbodies (Havel and Shurin 2004, Vanschoenwinkel et al. 2008). Many zooplankton produce resting stages that are resistant to desiccation; these resting stages are easily dispersed by the wind or on the feathers and fur of birds and animals that move between ponds. Pond communities can be replicated in mesocosm tanks by adding sediment, water, and live organisms. Although these communities differ somewhat from their natural counterparts, they allow us to experimentally test metacommunity theories. The interaction between climate change and landscape fragmentation can be tested by manipulating the abiotic environments in the mesocosms and contrasting the response of communities over a gradient of dispersal rates, facilitated by physically exchanging organisms between communities.

GAPS IN OUR KNOWLEDGE AND THESIS OVERVIEW

In the following chapters, I employ a combination of empirical and theoretical approaches to study the synergy between climate change and landscape fragmentation. The chapters address different aspects of this topic but are linked in their focus on the effect of these environmental stressors on the composition, functioning, stability, and predictability of ecological communities (Fig. 1-2).

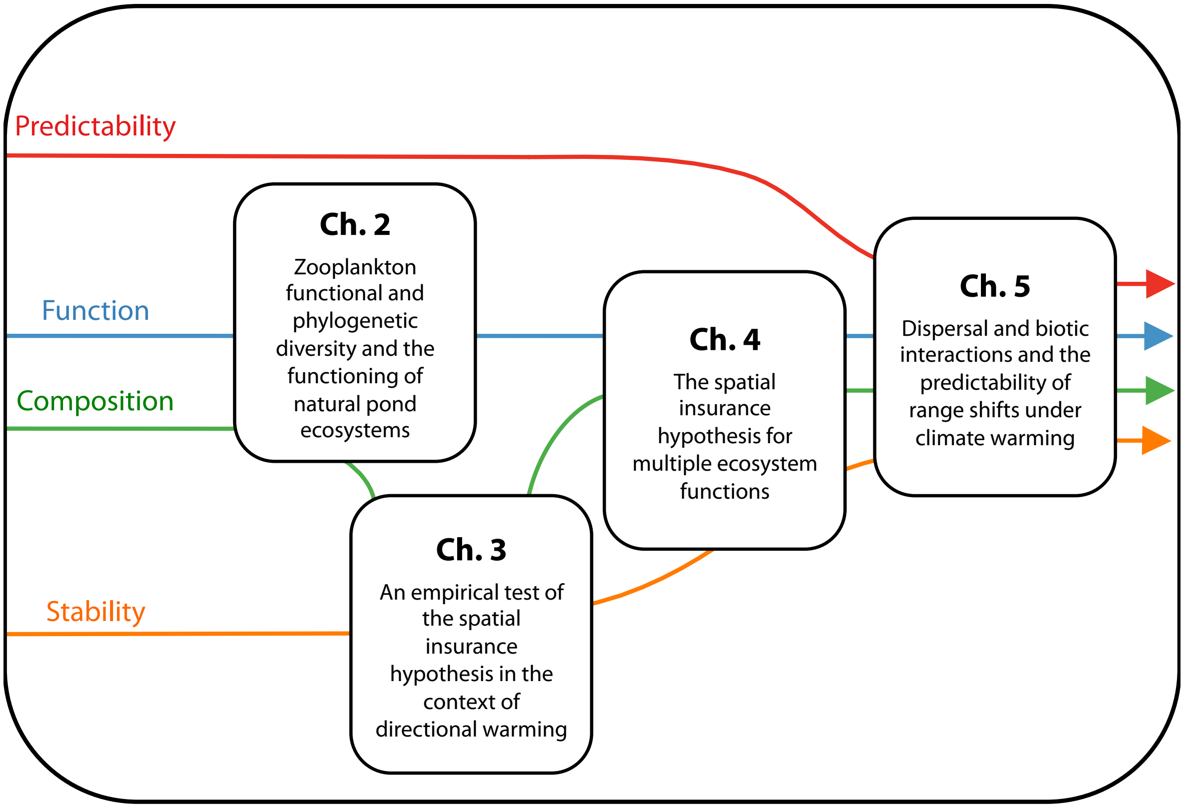

Figure 1-2. Conceptual diagram of the thesis chapters and the themes linking them. The four coloured arrows represent how the chapters are linked by the ecosystem properties that are considered.

The positive relationship between biodiversity and ecosystem functioning has been well established by two decades of experiments (Cardinale et al. 2011, 2012, Hooper et al. 2012). More diverse communities tend to produce greater ecosystem function because they have a greater chance of having a highly productive species, the “selection effect,” or because of resource partitioning, the “complementarity effect” (Loreau and Hector 2001). For these reasons, measures of biodiversity that reflect the functional differences between species, either based on traits or phylogeny, often outperform measures of species richness in explaining variation in ecosystem functioning and stability (Cadotte et al. 2009, Flynn et al. 2011, Cadotte et al. 2012) (but see Venail et al. 2015). However, the vast majority of studies that have used these measures to explain variation in ecosystem functioning have done so in experiments and in plant communities (Cadotte et al. 2008, Flynn et al. 2011, Srivastava et al. 2012, Clark et al. 2012). In Chapter 2, I apply these biodiversity measures to the natural pond communities of Mont St. Hilaire in order to test the hypothesis that **the functioning of these zooplankton communities are related to their phylogenetic and functional diversity.** This chapter considers how diversity, community composition, and the local environment affect multiple types of ecosystem functions, a theme I return to in Chapter 4. While Chapter 2 does not consider the effect of dispersal or environmental change on these communities, it serves as an introduction to the pond zooplankton metacommunity used in Chapter 3. In particular, this field survey allowed me to identify how the composition and functioning of the metacommunity are determined by the local environmental conditions and the spatial arrangement of the ponds.

Chapter 3 provides an empirical test of the spatial insurance hypothesis, involving realistic types of environmental change. Howeth and Leibold (2010) and Steiner et al. (2011, 2013) demonstrated spatial insurance in empirical systems where they forced local conditions to vary asynchronously, thereby creating the ideal conditions for spatial insurance. However, environmental variation in natural systems is rarely perfectly asynchronous. For example, fluctuations in weather tend to be spatially autocorrelated (Moran 1953) but differences in community composition (β-diversity) are maintained because of spatial variation in other abiotic variables (e.g. soil composition) and biotic interactions (Whittaker 1960). Therefore, local communities may respond differently to synchronous fluctuations in the environment, and dispersal may potentially provide spatial insurance, *but this has yet to be empirically demonstrated.*

Climate change is causing changes to the mean temperatures and precipitation (IPCC 2013), and the spatial insurance hypothesis, in its current form, does not consider this type of directional change. Two experiments have demonstrated how dispersal from a regional species pool can buffer biodiversity and ecosystem function against directional change that affects a single habitat patch (Thompson and Shurin 2012, Symons and Arnott 2013). This type of localized change is realistic for point source stresses, such as eutrophication and salinization. However, climate change is expected to result in warming across all communities in a region, and this has the potential to synchronize populations and communities, which may weaken spatial insurance effects. *An open question, therefore, is whether spatial insurance can preserve biodiversity and stabilize the productivity of metacommunities when environmental change is directional.*

In Chapter 3, I use the Mont St. Hilaire pond zooplankton communities to conduct a mesocosm experiment to test the hypothesis that **spatial insurance can provide stability to regional metacommunities experiencing synchronous environmental fluctuations, but that directional warming will reduce the strength of spatial insurance by synchronizing metacommunities.**

A current limitation of the spatial insurance hypothesis is that it assumes that all species contribute equally to a single ecosystem function (Loreau et al. 2003a, Gonzalez et al. 2009). In reality, species produce multiple ecosystem functions in varying amounts (Hector and Bagchi 2007, Gamfeldt et al. 2008, Isbell et al. 2012)(Chapter 2). Therefore, greater biodiversity is required for ecosystem multifunctionality—the simultaneous production of multiple ecosystem functions—than is required to produce a single function (Hector and Bagchi 2007, Gamfeldt et al. 2008). Experiments have also shown that ecosystem multifunctionality varies with scale: because local communities generally contain only a subset of the regional diversity of species, local communities generally produce only a subset of the ecosystem functions that are produced within a region (Zavaleta et al. 2010). We know dispersal mediates the diversity of metacommunities and their response to environmental change (Loreau et al. 2003a, Gonzalez et al. 2009), but we do not understand how this affects the production of multiple ecosystem functions. In Chapter 4, **I augment the spatial insurance hypothesis to include multiple ecosystem functions. This lead to new predictions about how environmental variability and dispersal interact to affect multifunctionality at local and regional scales.**

The way species respond to climate change and landscape fragmentation also depends on their interactions with other species. Biotic interactions alter the response of species to environmental change (Ives and Cardinale 2004) and affect their ability to colonize new habitats (Gilman et al. 2010, Svenning et al. 2014). This results in the rearrangement of species on the landscape, creating no-analogue communities as species track changes in climate (Davis et al. 1998, Williams and Jackson 2007, Urban et al. 2013). Dispersal can alter the outcome of biotic interactions by determining where species are on the landscape and, therefore, the species with which they come into contact (Urban et al. 2012, Norberg et al. 2012). Despite this, models used to predict the distributions of species in future climates rarely incorporate biotic interactions or realistic dispersal scenarios because they are difficult to estimate (Heikkinen et al. 2006, Brooker et al. 2007, Araújo and Luoto 2007). In Chapter 5, **I use a metacommunity model to test the hypothesis that biotic interactions and dispersal interactively affect the predictability of multispecies range shifts under climate change.** Like Chapter 3, Chapter 5 considers how dispersal affects the response of ecological communities to directional environmental change, but at a larger landscape scale.

This thesis addresses key gaps in our understanding of how climate change and landscape fragmentation synergistically affect ecological communities across spatial scales. In combination, the chapters suggest that managing landscapes to preserve connectivity may help minimize the changes in ecosystem structure and function, even as species and community distributions shift with climate change. This is especially critical given the current rates of landscape fragmentation (Haddad et al. 2015), which threaten biodiversity and the viability of ecosystems in future climates (Newbold et al. 2015).

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2. ECOSYSTEM FUNCTIONS ACROSS TROPHIC LEVELS ARE LINKED TO FUNCTIONAL AND PHYLOGENETIC DIVERSITY

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ABSTRACT

In experimental systems, it has been shown that biodiversity indices based on traits or phylogeny can outperform species richness as predictors of plant ecosystem function. However, it is unclear whether this pattern extends to the function of food webs in natural ecosystems. Here we tested whether zooplankton functional and phylogenetic diversity explains the functioning of 23 natural pond communities. We used two measures of ecosystem function: (1) zooplankton community biomass and (2) phytoplankton abundance (*Chl a*). We tested for diversity-ecosystem function relationships within and across trophic levels. We found a strong correlation between zooplankton diversity and ecosystem function, whereas local environmental conditions were less important. Further, the positive diversity-ecosystem function relationships were more pronounced for measures of functional and phylogenetic diversity than for species richness. Zooplankton and phytoplankton biomass were best predicted by different indices, suggesting that the two functions are dependent upon different aspects of diversity. Zooplankton community biomass was best predicted by zooplankton trait-based functional richness, while phytoplankton abundance was best predicted by zooplankton phylogenetic diversity. Our results suggest that the positive relationship between diversity and ecosystem function can extend across trophic levels in natural environments, and that greater insight into variation in ecosystem function can be gained by combining functional and phylogenetic diversity measures.

INTRODUCTION

After two decades of biodiversity-ecosystem function research, there is now consensus that the functioning of a biological community is mediated by the diversity of its component species (Hooper et al. 2005, Cardinale et al. 2011). Most experiments reveal that ecosystem function has a positive but saturating relationship with species richness (Cardinale et al. 2011). However, in experimental data, species richness typically accounts for between 30 to 73 percent of the variance of a given ecosystem function (Cardinale et al. 2006). This wide range has prompted ecologists to look for measures of diversity that more reliably explain variation in ecosystem function, including estimates of functional and phylogenetic diversity (Reiss et al. 2009, Cadotte et al. 2011, Naeem et al. 2012).

Measures of functional diversity are typically based on a subset of traits of the component species that are known to be important for ecosystem functions (Petchey and Gaston 2006). In general, such measures require careful *a priori* consideration of which traits to include, and whether or not traits should receive different weights. Despite these complications, functional diversity measures often better explain variation in ecosystem function than species richness and other taxonomic diversity measures (Petchey et al. 2004, Flynn et al. 2011).

Another approach has been to relate the phylogenetic diversity—a measure of the evolutionary relatedness of species in a community— to ecosystem function (Srivastava et al. 2012). This relies on the hypothesis that closely related species are more functionally similar than distantly related species, and therefore a more phylogenetically diverse community will have greater functional complementarity. While this will not be the case if functional traits show convergence in the phylogeny, two recent studies found phylogenetic diversity to be a better predictor of ecosystem function than species richness, and an equal or better predictor than indices incorporating functional traits (Cadotte et al. 2009, Flynn et al. 2011). An advantage of using phylogenetic diversity is that it can capture functional differences due to unmeasured or immeasurable traits, and is more readily applicable to groups such as microbes, where traits are less often measured (Srivastava et al. 2012).

To date, studies relating functional and phylogenetic diversity to ecosystem function have been largely limited to experimental settings (Cadotte et al. 2009, Flynn et al. 2011, Clark et al. 2012) (but see Ye et al. 2013). Therefore, it is unclear whether these diversity measures will still be strong predictors of ecosystem function in natural communities, where environmental conditions are not controlled as they are in experiments.

Furthermore, the use of functional and phylogenetic diversity measures for predicting ecosystem function has been focused on productivity in plant communities(Srivastava et al. 2012) (but see Best et al. 2012, Ye et al. 2013, Leduc et al. 2013). However, we expect that these measures should also improve our understanding of the functioning of higher trophic levels (Dinnage et al. 2012, Griffin et al. 2013). Experimental evidence suggests that more species-rich herbivore assemblages are 1) able to exert stronger top-down control on plant biomass, and 2) able to produce greater herbivore biomass (Cardinale et al. 2006, Duffy et al. 2007). This effect may be because communities with more herbivore species are likely to graze on a variety of plant types. If the ability, or preference, to graze on certain plant types is linked to traits, then measures of the functional and phylogenetic diversity of herbivores should explain more variation in the strength of top-down control compared to species richness. Of course, plant biomass may also be influenced by bottom up effects, such as nutrient availability, which may obscure the top down effect of grazer diversity (McQueen et al. 1986). Regardless of these complications, testing whether functional and phylogenetic diversity measures are predictive of the functioning of herbivores in complex natural communities is an obvious next step.

To address whether functional and phylogenetic diversity are useful predictors of ecosystem function for food webs in natural communities, we examined the explained variance in the functioning of natural pond communities across two trophic levels. We used two measures of ecosystem function, (1) zooplankton community biomass and (2) phytoplankton abundance (*Chl a*), to test for diversity-ecosystem function relationships within and across trophic levels. We predicted that more diverse zooplankton communities would have higher biomass and would exert stronger top-down control, suppressing phytoplankton abundance. Furthermore, because diet complementarity is likely related to the diversity of functional traits or phylogenetic relatedness, we predicted that both functional and phylogenetic diversity would overlap in the variation in ecosystem function explained, but each might explain additional variation beyond that captured by species richness alone (Fig. 2–1). Detecting these relationships is complicated by the fact that environmental conditions are not constant across ponds, and this can affect both diversity and ecosystem function. Therefore, we used structural equation modelling to explore the direct and indirect effect of environmental gradients on the diversity-ecosystem function relationships (Cardinale et al. 2009).

MATERIAL AND METHODS

Pond Zooplankton Survey

We conducted a survey of 23 ponds in the Gault Nature Reserve (GNR), Quebec, Canada (45° 32’ 10” N, 73° 09’ 10”, W) on May 23-27, 2011. GNR is a UNESCO Biosphere Reserve, and one of the few remaining examples of primeval forest in the region. Permission for conducting this survey was given by the director of the GNR. This study did not involve endangered or protected species, or any vertebrate species. The ponds were a mix of ephemeral and permanent, and were scattered around the 1000-hectare reserve (Fig. A–1). They ranged in size from 0.0006 to 0.136 hectares and from 0.11 to 0.60 meters deep, and spanned an elevation gradient of 204 to 415 meters above sea level. All ponds were surrounded by similar forest habitat, and had low observed macrophyte abundance. The benthic habitat of these ponds was characterized by very loose sediment, so that the sediment water interface was not well defined.

Our survey determined zooplankton community composition, phytoplankton abundance (*Chl a*), and relevant abiotic variables in each pond. All samples for water chemistry, zooplankton, and phytoplankton were collected from the centre of the pond using a 4L horizontal VanDorn water sampling bottle (Wildco, USA). The process of collecting the samples from such shallow ponds inevitably caused mixing of the water column so that the samples contained water, zooplankton, and phytoplankton from all depths.

Total phosphorous (TP), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC)

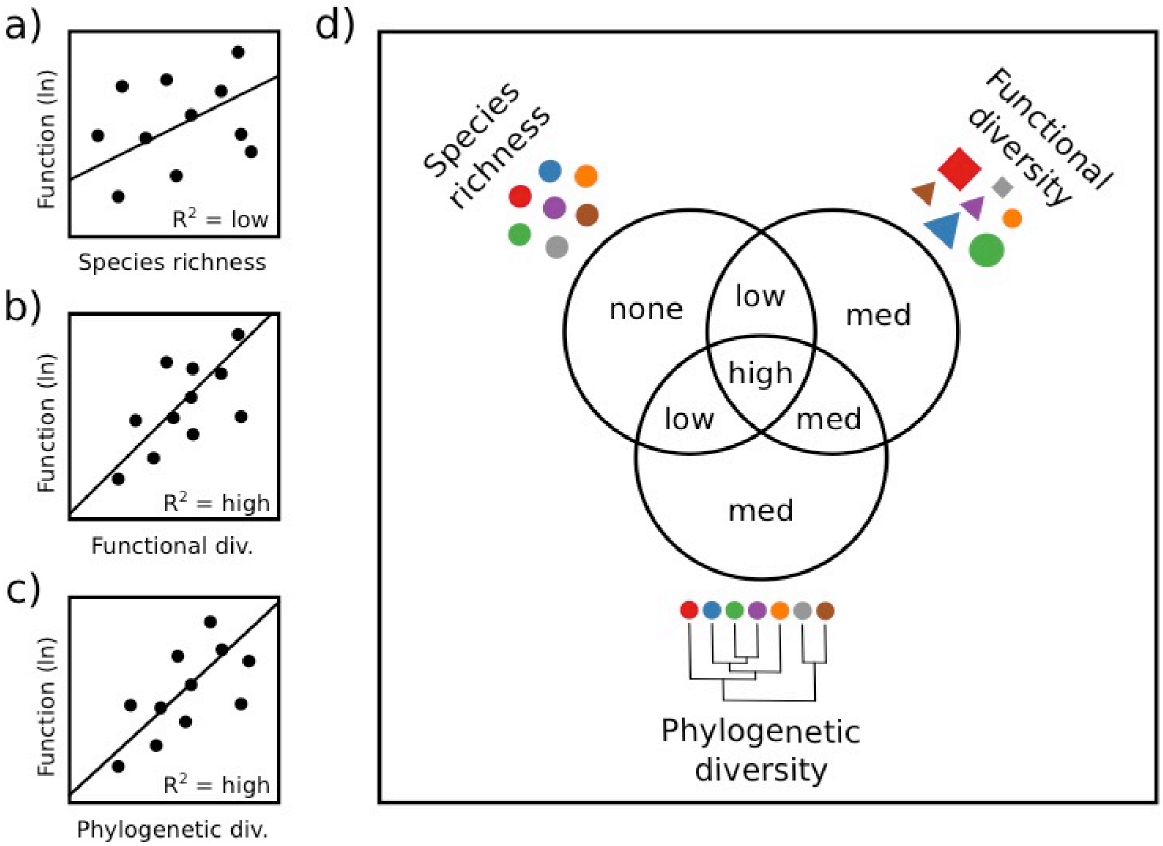

Figure 2-1. Hypothesized relationships between ecosystem function and species richness (a), functional diversity (b), and phylogenetic diversity (c). We predict a stronger relationship with ecosystem function, and thus a higher R^2, for functional diversity (b) and phylogenetic diversity (c) than for species richness (a) because the former two measures incorporate information about the traits, or the evolutionary similarity of the different species in the community. Panel (d) depicts the results of variation partitioning, indicating our hypothesis that functional and phylogenetic diversity will explain all of the variation explained by species richness, as well as additional variation, both overlapping and unique.

concentrations were analysed by the GRIL Aquatic Analytical Laboratory (UQAM, Montreal). Dissolved oxygen (DO), and pH were measured using a handheld probe (YSI, USA). Elevation and pond surface area were measured using a handheld GPS (Garmin, USA). Depth was measured in the centre of each pond using a meter stick. Canopy cover was estimated visually. Pond permanence was estimated as the number of days after sampling that the ponds retained water, to a maximum of six months. This measure of permanence was based on temperature sensors, placed at the bottom of each pond, taking measurements every 30 minutes. Temperature time series were inspected visually, and the pond was assumed dry when the amplitude of the daily temperature fluctuations increased by at least twice. These measurements were corroborated with monthly visits to the ponds. We measured conductivity but we were unable to include it in our analysis because our probe was malfunctioning and did not provide readings for all of our ponds.

Zooplankton samples were collected by passing 8-16 L of water through a 75 μm Nitex sieve. Higher volumes were sampled when zooplankton appeared to be in low abundance. Zooplankton were anesthetized using carbonated water and preserved in 95% ethanol.

Crustacean zooplankton were enumerated and identified using a dissecting microscope at 60x magnification (Leica, Germany). Entire samples were counted for all species (mean of 1116 and median of 690 individuals per sample), and identifications were performed using a compound microscope (Leica, Germany) when necessary. All organisms were identified to the highest possible taxonomic resolution, generally species, according to Haney (2010). For our analyses, we used genus level distinctions, to maintain consistency across all taxa, with the exception of harpacticoid copepods, which were left as a group because their identification is challenging. None of our genera contained more than one identified species and so this taxonomic resolution appears to be an accurate representation of the diversity within these ponds. It remains possible that we may have classified multiple species together when we were unable to identify to species level (e.g., the harpacticoid copepods), but based on the morphological similarity of individuals, we expect this underestimation of diversity to have been minimal. We were unable to identify copepod nauplii to species, but we included them in our estimates of community biomass.

Biomass was estimated using average measured body lengths and length-weight regressions (McCauley 1984), multiplied by the number of individuals and divided by the volume of water sampled.

Ecosystem Functions

Zooplankton community biomass was calculated as the summed biomass of all taxa per litre of sampled pond water. The top down effect of zooplankton on phytoplankton abundance was estimated as the relationship between zooplankton diversity and chlorophyll *a*; thus the highest zooplankton function occurs when chlorophyll *a* is lowest. Chlorophyll *a* concentrations were estimated by filtering at least 250 mL of water, through a GF/F filter paper. Chlorophyll concentrations (μg L^{-1}) were analysed spectrophotometrically after cold extraction in ethanol using the acidified method (Wetzel and Likens 1979). It was not possible to directly sample for periphyton because of the loose sediment water interface, but observations suggest that it was not abundant. Therefore, it is unlikely that disturbance of periphyton during sampling would have contaminated our phytoplankton samples.

Diversity Indices

Three taxonomic diversity measures, species richness (SR), Shannon diversity (Shan), and Simpson diversity (Simp), were calculated using the *vegan* package (Oksanen et al. 2011) in R version 3.0.2 (R Development Core Team 2014). Rarefaction curves were produced using the *vegan* package to evaluate whether our estimate of SR was affected by the number of zooplankton in our samples, and thus variation in the abundance of zooplankton across the ponds. There are a variety of indices for calculating functional and phylogenetic diversity, each emphasizing a different aspect of the diversity of a community (summarized in Petchey et al. 2009, Cadotte et al. 2010). Therefore, using multiple complementary indices can provide insight into how ecosystem function is dependent upon different aspects of community diversity.

We chose to use a set of three independent functional diversity measures that each capture one of the three primary components of functional diversity: richness (FRic), evenness (FEve), and divergence (FDiv)(Villeger et al. 2008). These were calculated using four zooplankton traits (body length, feeding type, habitat preference, and trophic group) from Barnett et al. (2007) and unpublished updates from Beisner et al. (in prep), using the *FD* package (Laliberté and Shipley 2011). We selected these traits because they affect feeding and biomass either directly (body length, feeding type, trophic group) or indirectly (habitat preference – reflective of which parts of the ponds zooplankton can graze phytoplankton and produce biomass). Habitat preference consisted of three categories: littoral, intermediate, and pelagic. Trophic group consisted of four categories: herbivore, omniherbivore, omnivore, omnicarnivore. The trait for feeding type consisted of raptorial feeding, C-filter feeding (scraping and filtering), D-filter feeding (stationary feeding with filtering apparatus on 3rd and 4th legs), and S-filter feeding (stationary feeding with filtering apparatus on legs 1-5) which we expect to determine the type of food particles caught (described in Barnett et al. 2007). Because we considered multiple filter feeding types we added a fifth trait, raptorial vs. filter feeding, to differentiate filter feeding from raptorial feeding. When calculating our measures of functional diversity, the new feeding type trait and the original feeding type trait both received half the weighting that we gave to each of the other traits. This allowed us to maintain equal weighting of the four initial traits. Including this additional trait to differentiate filter and raptorial feeding resulted in more logical functional associations between species (Fig. A–2a) but did not significantly change our results (results excluding additional trait not shown). Only the trait for body size was numeric so the traits were not standardized. Traits were matched based on our highest level of taxonomic resolution (generally species).

FEve and FDiv were calculated as both presence-absence ($_{pa}$) and abundance weighted ($_{ab}$) measures. We also created a functional dendrogram based on Ward’s clustering method of the five traits (Fig. A–2a)(Petchey and Gaston 2006). This dendrogram was used as a visual representation of the groupings of functional diversity but was not analysed directly as a measure of functional diversity (sensu Petchey and Gaston 2006). We also compared the predictive efficacy of single traits with our multi-trait indices. For this, we calculated the functional richness of each individual trait for comparison with the functional diversity measures based on multiple traits. Functional divergence and evenness cannot be calculated for single traits.

We chose to use two phylogenetic diversity measures: Faith's Phylogenetic Diversity (PD)(Faith 1992), and standard effect size mean pairwise distance (sesMPD)(Webb et al. 2002). PD provides a simple measure of the phylogenetic relatedness of a community based on the summed branch lengths of its phylogenetic tree. We expected this measure to capture functional complementarity well if more distantly related species are more functionally unique. However, PD is highly dependent upon species richness, so we also chose to use sesMPD, which provides a measure of phylogenetic diversity that is independent of species richness. sesMPD is equal to -1 times the net related index (NRI) (Webb et al. 2002) and was used instead of NRI because it increases with community phylogenetic diversity. PD and sesMPD were calculated using the *Picante* package (Kembel et al. 2010), using the phylogenetic tree published in Helmus et al. (2010)(Fig. A2–b). Taxa were matched to the tree based on our finest level of taxonomic resolution (generally species). Harpacticoid copepods were not included on this tree and so were added, halfway between the calanoid and cyclopoid copepods, as was done by Helmus et al. (2010) when sequence data was not available, and according to the taxonomic tree provided by Huys and Boxshall (1991). sesMPD was calculated as both presence absence ($_{pa}$) and abundance weighted ($_{ab}$).

Statistical Analysis

We used linear regression to test for relationships between ecosystem function and our explanatory variables. Type II linear regression, with the ranged major axis method to account for error in both the independent and dependent variables using the *lmodel2* package (Legendre 2013), was used to determine the slope of relationships, unless a polynomial term was included, in which case a Type I regression was used. Response variables were ln transformed to improve normality. The diversity measure of each type (taxonomic, functional, and phylogenetic) that best explained ecosystem function was selected based on the Akaike Information Criterion (AIC). Overlap in variance explained by the best performing diversity measures of each type was evaluated using variation partitioning in *vegan* (Oksanen et al. 2011). The correlation between traits and phylogeny was calculated using collectively using a Mantel test (Pavoine et al. 2013) in *vegan*. Phylogenetic signal for each individual trait was tested using Blomberg's K statistic of phylogenetic signal in *Picante* (Kembel et al. 2010) for continuous traits (body size), using the phylogenetic D statistic (Fritz and Purvis 2010) in the *caper* package (Orme et al. 2013) for binary traits (raptorial vs. filter feeding), and using Pagel's λ (Pagel 1999) in the *GEIGER* package (Harmon et al. 2008) for multistate traits (habitat, feeding type, and trophic group).

Last, we explored effects of environment on community diversity and ecosystem function together using structural equation modelling (SEM) (Grace 2006). This allowed us to determine if our diversity-ecosystem function relationships were a product of both co-varying with environment, or if there was an independent and direct effect of diversity on the ecosystem functions as hypothesized. We started with a model involving all plausible pathways between environment, our best diversity measures (identified through linear regression), and the two ecosystem functions (Fig. A–3). We then compared this model to simplified models where pathways had been removed and used model selection based on AIC to determine the best fit model of the two ecosystem functions. If the pathway between diversity and the ecosystem function remains significant when environment is allowed to affect both diversity and the ecosystem function, we can conclude that there is an independent effect of diversity on the ecosystem function. We compared models including three combinations of our environmental variables: 1) total phosphorous (only for predicting chlorophyll *a*); 2) subsets of environmental variables determined as important predictors of each function based on multiple regression and model selection based on comparing all variable combinations using the *leaps* package (Lumley and Miller 2009); 3) the first two axes from a PCA of all standardized environmental variables (Fig. A–4) calculated using the *vegan* package (Oksanen et al. 2011). The first two axes of the PCA contained 57.1% of the variation in the environmental variables. All analyses were performed in *R,* version 3.0.2 (R Development Core Team 2014).

RESULTS

Zooplankton Community Characteristics

Average pond species richness was 4.42, ranging from 2 to 7, with a regional richness of 10. Across all ponds, zooplankton community biomass was 249.57 μg L^{-1} on average, ranging from 0.25 to 938.04 μg L^{-1}. Species richness was positively, albeit weakly, related to the number of zooplankton present in our samples ($R^2 = 0.29$; $p = 0.006$). However, the rarefaction curves saturated in the majority of samples (87%), suggesting that our estimates of richness were not greatly biased by differences in the abundance of zooplankton amongst the ponds (Fig. A–5).

Daphnia pulex comprised 51.3% of the zooplankton biomass over all ponds and was present in 14 of the 23 ponds. The next most abundant genus, *Microcyclops rubellus,* comprised 15.8% of the zooplankton biomass in all ponds and was present in 18 of the 23 ponds. *Acanthocyclops vernalis* comprised 12.1% of the zooplankton biomass in all ponds and was present in 15 of the 23 ponds. This species is carnivorous as an adult but was retained in our analysis because it consumes phytoplankton in its juvenile stages (Brandl 1998). There were seven rarer taxa, *Alonella sp., Ceriodaphnia dubia, Chydorus sphaericus,* Harpacticoida, *Sida crystallina, Simocephalus sp.,* and *Tropocyclops prasinus mexicanus*, that each made up less than 5% of the average biomass, and all but Harpacticoida were negatively correlated with *D. pulex* abundance. Phytoplankton abundance was 6.56 μg chl *a* L^{-1} on average, ranging from undetectable to 33 μg L^{-1}. Zooplankton species richness was not related to either chlorophyll *a* ($R^2 = 0.07$; $p = 0.211$) or total phosphorous ($R^2 = 0.10$; $p = 0.134$).

The combined zooplankton traits were closely correlated with their phylogeny (Fig. A–2; Mantel test, $r = 0.852$, $p = 0.001$, 999 permutations). Feeding type and our raptorial vs. filter feeding traits showed significant phylogenetic signal (feeding type – $\chi^2(1) = 7.54$, $p = 0.006$;; raptorial vs. filter feeding – $D = -3.73$, $p < 0.001$), indicating phylogenetic conservatism for these traits. The body length, habitat preference, and trophic group traits did not show significant phylogenetic signal (body length – $K = 0.84$, $p = 0.172$; habitat preference – $\chi^2(1) = 0.004$, $p = 0.950$, trophic group – $\chi^2(1) = 2.52$, $p = 0.112$), indicating little or no phylogenetic conservatism for these traits.

Zooplankton Community Biomass

Five out of the 11 diversity measures tested explained a significant proportion of variance in zooplankton community biomass, and in all cases, there was a positive influence of diversity on biomass (Table 2–1). These significant models included taxonomic, functional, and phylogenetic measures. Abundance weighted functional divergence ($FDiv_{ab}$), explained the most variance of

Table 2–1. Results of the linear models for predicting zooplankton community biomass (ln), ranked in increasing order of AIC. The highest ranked model of each diversity type is bolded. *P* values that are less than 0.05 are bolded.

	variable	type	d.f.	AIC	ΔAIC	R^2	R^2 Adj	slope	*p*
1	FDiv$_{ab}$ + Env*	other	6	70.6	0	0.585	0.493	-	**0.002**
2	**FDiv$_{ab}$**	**functional**	3	73.5	2.9	0.388	0.359	9.875	**0.001**
3	Trophic group	1 function	3	74.9	4.3	0.351	0.321	1.258	**0.003**
4	Raptorial vs. filter	1 function	3	75.5	4.9	0.334	0.303	1.688	**0.004**
5	Env.*	other	5	75.6	5.0	0.446	0.359	-	**0.009**
6	**SR^{2}**	**taxonomic**	4	75.8	5.2	0.383	0.321	4.2190*x-0.4007*x^2	**0.008**
7	Body size	1 function	3	75.9	5.3	0.324	0.291	3.974	**0.005**
8	**sesMPD$_{ab}$**	**phylogenetic**	3	78.7	8.1	0.234	0.198	0.677	**0.019**
9	PD	phylogenetic	3	79.0	8.4	0.212	0.186	0.002	**0.023**
10	FRic	functional	3	79.9	9.3	0.192	0.153	6.076	**0.037**
11	FDiv$_{pa}$	functional	3	80.7	10.1	0.165	0.125	11.488	0.055
12	Feeding type	1 function	3	80.9	10.3	0.159	0.119	0.745	0.060
13	FEve$_{pa}$	functional	3	81.3	10.7	0.142	0.101	7.150	0.076
14	SR	taxonomic	3	81.3	10.7	0.142	0.010	0.613	0.077
15	Env. PCA**	other	4	81.8	11.2	0.197	0.116	-	0.116
16	sesMPD$_{pa}$	phylogenetic	3	82.8	12.2	0.084	0.040	0.839	0.180
17	Chl *a*	other	3	83.2	12.6	0.070	0.026	-0.673	0.221
18	Simpson	taxonomic	3	84.0	13.0	0.012	-0.035	-1.401	0.624
19	Shannon	taxonomic	3	84.7	14.1	0.006	-0.041	-0.660	0.723
20	FEve$_{ab}$	functional	3	84.8	14.2	0.002	-0.045	0.337	0.833
21	Habitat type	1 function	3	84.8	14.21	0.002	-0.046	0.170	0.847

* Environmental variable model includes elevation, DIC, and ln TP

** Environmental PCA includes first 2 axes of PCA on all standardized environmental variables any diversity measure (Fig. 2–2b; $R^2 = 0.39$; $p = 0.001$). Species richness (SR), explained the second most variance, although it exhibited a unimodal relationship with zooplankton community biomass, where the highest biomass was found in ponds with intermediate species richness (Fig. 2–2a; $R^2 = 0.38$; $p = 0.008$). This unimodal relationship between species richness and community zooplankton biomass outperformed a model that assumed a linear relationship ($R^2 = 0.14$, $p = 0.077$). Abundance weighted standard effect size mean pairwise distance ($sesMPD_{ab}$) explained the third highest proportion of variance of the single diversity measure models (Fig. 2–2c; $R^2 = 0.23$; $p = 0.019$).

Based on variation partitioning, SR, $FDiv_{ab}$, and $sesMPD_{ab}$ together explained 66% of the variation in zooplankton community biomass, and overlapped in explaining 6% of the variation (Fig. 2–2d). SR and $FDiv_{ab}$ overlapped to explain 9% of the variation. SR and $sesMPD_{ab}$ overlapped to explain 7% of the variation. $FDiv_{ab}$ and $sesMPD_{ab}$ overlapped to explain 4% of the variation. SR, $FDiv_{ab}$, and $sesMPD_{ab}$ uniquely explained 10%, 17%, and 3% of the variation respectively.

Three of the five traits (trophic group, raptorial vs. filter feeding, and body length) individually explained a significant amount of variance in zooplankton biomass but none outperformed the best functional diversity measure ($FDiv_{ab}$) although ΔAIC was small (Table 2–1). These three single traits outperformed the best phylogenetic diversity measure ($sesMPD_{ab}$).

The best performing model of environmental variables for predicting zooplankton community biomass consisted of elevation, DIC, and ln TP, and explained a significant amount of variation ($R^2 = 0.45$; $p = 0.009$). However, when $FDiv_{ab}$ was included in the model, none of these environmental variables remained as significant predictors, although the model outperformed that of $FDiv_{ab}$ alone (Table 2–1). Chlorophyll *a* did not explain a significant amount of variance in zooplankton community biomass ($R^2 = 0.07$; $p = 0.221$).

The pathway between $FDiv_{ab}$ and zooplankton community biomass, was always significant, regardless of how we specified the effect of environment in our SEM (Fig. A-6). The most

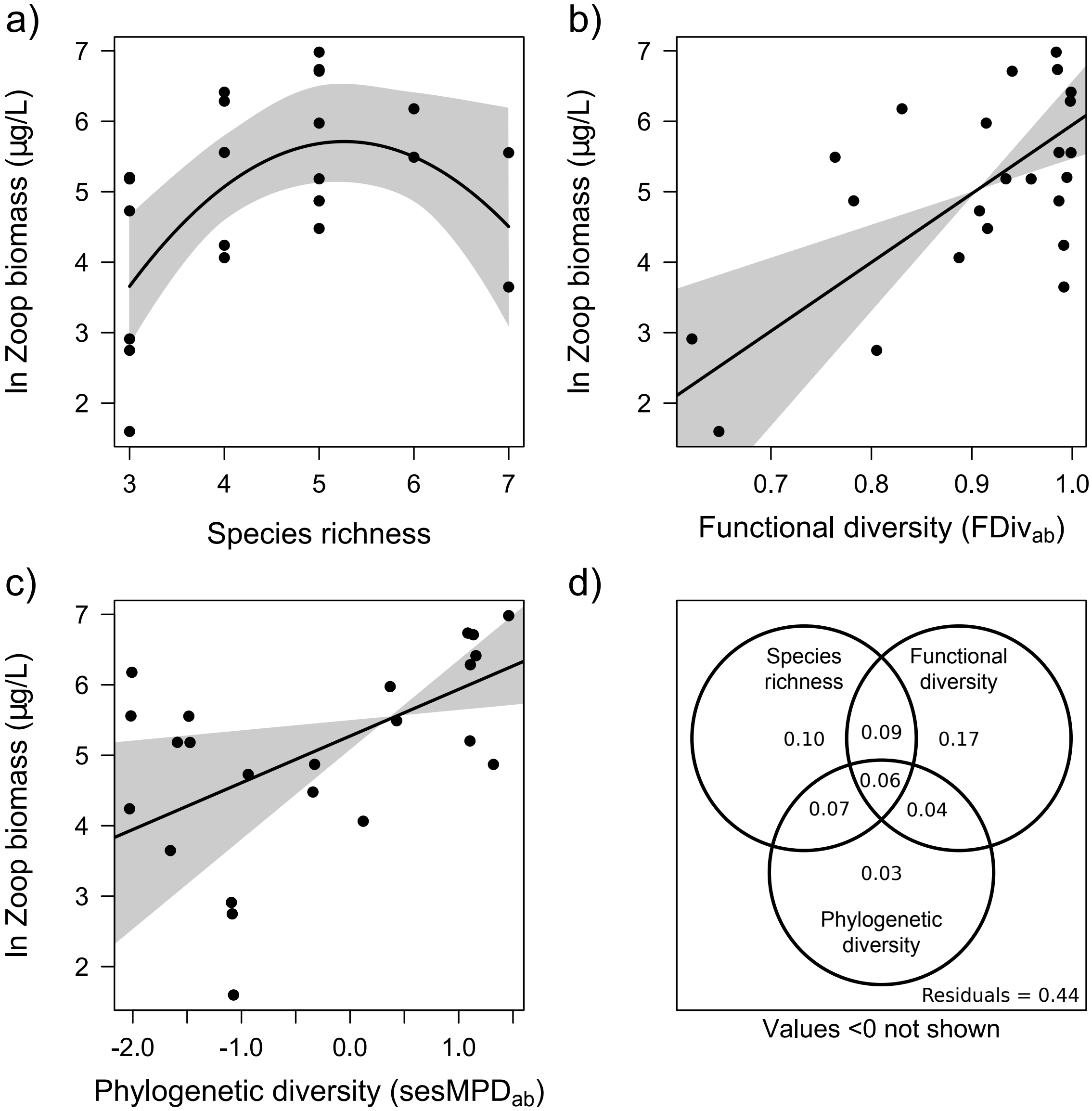

Figure 2-2. Zooplankton community biomass in the 23 ponds as predicted by the best diversity indices in each category: taxonomic diversity - species richness (a), functional diversity - abundance weighted functional divergence (b), phylogenetic diversity - abundance weighted standard effect size mean pairwise distance (c), and the variation partitioning for these three models with their adjusted R^2 (d). Significant model trends are shown as black lines. The grey bands indicate the 95% confidence intervals for the predicted values (a) and the slope of the regression lines (b,c).

parsimonious model, based on AIC, only included the direct pathway from $FDiv_{ab}$ (Table A-1). This suggests that our linear models adequately capture the relationship between diversity and zooplankton biomass.

Phytoplankton Abundance

Three out of the 11 zooplankton diversity measures explained a significant proportion of variance in chlorophyll *a*, and in all but one case, there was a negative influence of diversity on chlorophyll *a* (Table 2–2). These significant models included functional and phylogenetic, but not taxonomic diversity measures. The best single diversity measure for predicting chlorophyll *a* was the phylogenetic diversity measure $sesMPD_{pa}$ (Fig. 2–3c; $R^2 = 0.38$; $p = 0.002$). There was one outlier in this relationship, which was found to have significant influence (Cook's distance > 0.5) on the analysis (Fig. 2–3c - unfilled point). Chlorophyll *a* was not detectable in this pond, although the predicted concentration should have been relatively high based on the measured zooplankton phylogenetic diversity. We cannot be sure if this chlorophyll *a* concentration is a measurement error, so we compared model fit with and without including it. Removing this outlier from our analysis did not have a large effect on the slope of the relationship but greatly improved the model fit (Fig. 2–3c, dashed line; $R^2 = 0.59$, $p < 0.001$).

The functional diversity measure with the lowest AIC was abundance weighted functional evenness ($FEve_{ab}$; $R_2 = 0.26$, $p = 0.013$), which in contrast to all other diversity measures, had a positive relationship with chlorophyll *a*. Again, excluding the outlying pond did not change the slope of the relationship but improved the model fit ($R^2 = 0.33$, $p = 0.005$). The next best performing functional diversity measure was FRic (Fig. 2–3b; $R^2 = 0.24$; $p = 0.017$). Again, excluding the outlying pond did not change the slope of the relationship but improved the model fit (Fig. 2–3b, dashed line; $R^2 = 0.44$, $p < 0.001$). The best measure of taxonomic diversity was species richness (SR; Fig. 2–3a; $R^2 = 0.07$; $p = 0.211$), but no taxonomic diversity measure was able to explain a significant portion of variance in chlorophyll *a*. Again, excluding the outlying pond did not change the slope of the relationship but improved the model fit (Fig. 2–3a, dashed line; $R^2 = 0.17$, $p = 0.069$).

Table 2–2. Results of the linear models for predicting chlorophyll *a* (ln), ranked in increasing order of AIC. The highest ranked model of each diversity type is bolded. *P* values that are less than 0.05 are bolded.

	variable	type	d.f.	AIC	ΔAIC	R^2	R^2 Adj.	slope	*p*
1	**$\text{sesMPD}_{\text{pa}}$**	**phylogenetic**	3	58.4	0	0.376	0.345	-1.164	**0.002**
2	sesMPDpa + Env*	other	9	59.8	1.4	0.663	0.382	-	0.080
3	Raptorial vs. filter	1 function	3	60.9	2.5	0.301	0.267	-1.138	**0.007**
4	FEve_{ab}	functional	3	62.3	3.9	0.258	0.222	5.557	**0.013**
5	**FRic**	**functional**	3	62.8	4.4	0.241	0.204	-6.032	**0.017**
6	Feeding type	1 function	3	63.1	4.7	0.233	0.196	-0.642	**0.020**
7	PD	phylogenetic	3	65.6	7.2	0.143	0.102	-0.002	0.075
8	FDiv_{ab}	functional	3	65.8	7.4	0.136	0.094	-3.200	0.084
9	Env.*	other	8	66.1	7.7	0.432	0.219	-	0.121
10	Body length	1 function	3	66.3	7.9	0.118	0.076	-1.705	0.109
11	FEve_{pa}	functional	3	66.3	7.9	0.115	0.073	-8.791	0.113
12	FDiv_{pa}	functional	3	67.1	8.7	0.085	0.041	-10.069	0.177
13	**SR**	**taxonomic**	3	67.4	9.0	0.074	0.029	-0.581	0.211
14	Trophic group	1 function	3	67.4	9.0	0.073	0.029	-0.408	0.212
15	Zoop. Biomass	other	3	67.5	9.1	0.070	0.026	-0.875	0.221
16	Simpson	taxonomic	3	67.9	9.5	0.051	0.006	4.446	0.298
17	Shannon	taxonomic	3	68.2	9.8	0.041	-0.005	3.125	0.354
18	$\text{sesMPD}_{\text{ab}}$	phylogenetic	3	68.3	9.9	0.034	-0.010	-0.323	0.388
19	Habitat type	1 function	3	68.5	10.1	0.027	-0.019	-0.469	0.451
20	TP	other	3	69.1	10.7	0.004	-0.044	-0.075	0.781
21	Env. PCA**	other	4	70.6	12.2	0.023	-0.075	-	0.796

* Environmental variable model includes % tree cover, DIC, ln area, ln depth, pH, and ln DOC

** Environmental PCA includes first 2 axes of PCA on all standardized environmental variables

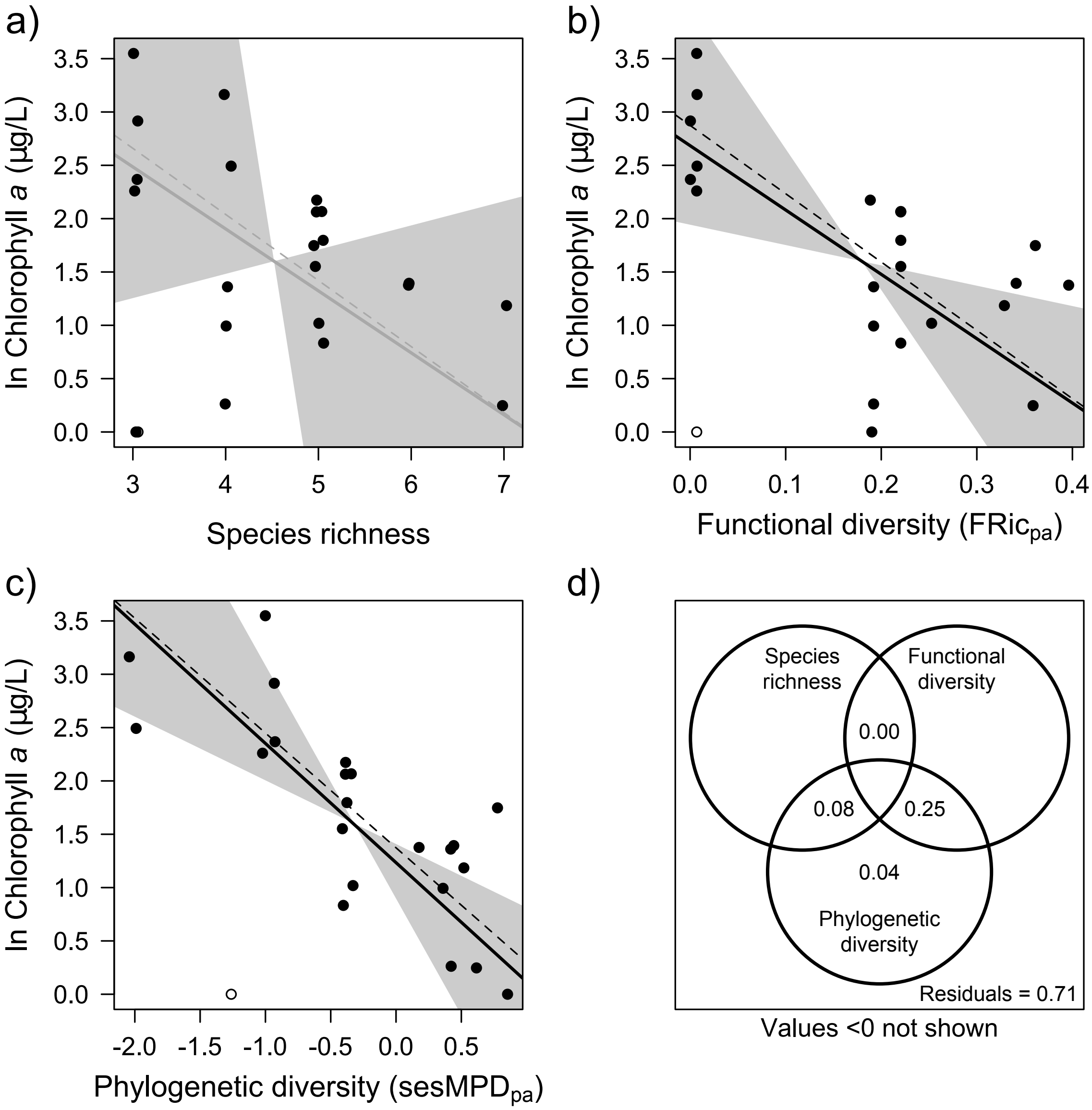

Figure 2–3. Chlorophyll *a* in the 23 ponds as predicted by the best diversity indices in each category: taxonomic diversity - species richness (a), functional diversity – functional richness (b), phylogenetic diversity – presence absence standard effect size mean pairwise distance (c), and the variation partitioning for these three models with their adjusted R^2 (d). Significant model trends are shown as black lines. Insignificant model trends are shown as grey lines. The empty circles indicate the pond that is an outlier to the predicted trend. The dashed lines indicate the model trend when this outlier is removed. The grey bands indicate 95% confidence intervals for the slope of the regression lines.

Based on variation partitioning, SR, FRic, and sesMPD_{pa} together explained 29% of the variation in chlorophyll *a* (Fig. 2–3d). However, all variation explained was captured by sesMPD_{pa}, either alone (4%) or with SR (8%) or FRic (25%). SR and FDiv each uniquely did not contribute to explaining variation in chlorophyll *a*, nor did the overlap between all three indices, and this resulted in less variation explained by the three indices together than that explained by sesMPD_{pa} on its own, because adjusted R^2 penalizes for the additional degrees of freedom used in the combined model.

Two of the five traits (raptorial vs. filter feeding, and feeding type) individually explained a significant amount of variance in chlorophyll *a* and the raptorial vs. feeding type trait outperformed the best functional diversity measure (FRic)(Table 2–2). No single trait performed as well as the best phylogenetic diversity measure (sesMPD_{pa}).

The best performing model for chlorophyll *a* containing only environmental variables consisted of % tree cover, DIC, ln pond area, ln depth, pH, and ln DOC but was not significant ($p = 0.121$). The model combining these environmental variables plus sesMPD_{pa} did not perform as well as the model with sesMPD_{pa} alone (Table 2–2). Neither zooplankton community biomass nor *D. pulex* biomass explained a significant amount of variation in chlorophyll *a* (Community Biomass $R^2 = 0.07$; $p = 0.221$; *D. pulex* – $R^2 = 0.07$; $p = 0.221$).

The pathway between sesMPD_{pa} and chlorophyll *a*, was always significant, regardless of how we specified the effect of environment in our SEM (Fig. A–7). Matching to the SEM with zooplankton community biomass, the most parsimonious model explaining variation in chlorophyll *a* did not include environment, but it included the direct pathway from sesMPD_{pa} (Table A–2). This again suggests that our linear models adequately capture the relationship between diversity and chlorophyll *a*.

DISCUSSION

Previous tests of the effect of functional and phylogenetic diversity on ecosystem functioning have been largely based on experimental plant communities (Flynn et al. 2011, Clark et al. 2012, Cadotte 2013). Here, we evaluated these relationships across trophic levels in natural pond communities. Our linear models revealed strong and highly significant correlations between the functioning and the diversity of pond zooplankton communities, and our structural equation models demonstrated that these relationships were not simply driven by variation in environmental conditions. Both zooplankton functions considered here—the production of zooplankton biomass and top-down control of phytoplankton abundance—increased with diversity. This is consistent with previous experimental evidence and theory (Duffy et al. 2007, Griffin et al. 2013), but we found a clear relationship in complex and ephemeral natural communities, despite large variation in abiotic environments between ponds (e.g. phosphorous spans the natural gradient from oligotrophic 4.4 $\mu g\ L^{-1}$ to hypereutrophic 315 $\mu g\ L^{-1}$ (Carlson 1977)).

As predicted, we found that positive diversity ecosystem function relationships emerged most clearly when measures of functional and phylogenetic diversity were used, and that these measures explained variation in ecosystem function beyond that explained by taxonomic diversity measures, such as species richness. Previous studies relating the diversity of animals to ecosystem function have relied on taxonomic diversity measures (Petchey et al. 1999, Gamfeldt et al. 2005), knowledge of the functional complementarity of species (Burkepile and Hay 2008, Schmitz 2009), single traits (Ye et al. 2013) or on taxonomic differences (Griffin et al. 2013) (but see Best et al. 2012). Although we found a subset of single traits (e.g. trophic group, raptorial vs. filter feeding, and body length) performed almost as well in predicting zooplankton biomass, they never explained as much variation as the best diversity measures ($FDiv_{ab}$). In addition, species richness and phylogenetic diversity ($sesMPD_{ab}$) each explained additional unique variation. In contrast, phylogenetic diversity ($sesMPD_{pa}$) was the best predictor of phytoplankton consumption, and no additional variation was uniquely explained by species richness and functional diversity (FRic). These findings suggest that metrics that quantitatively integrate trait or phylogenetic information have the potential to improve our understanding of variation in the functioning of complex multi-trophic ecosystems.

While species richness was a good predictor of zooplankton community biomass, the relationship was unimodal, and not a saturating function, as observed in most biodiversity-function research (Duffy et al. 2007, Cardinale et al. 2011). A thorough sampling of these ponds may have revealed additional rare species, although our rarefaction curves indicate that we sampled adequately to capture species richness in the majority of ponds. Nevertheless, our findings should be robust to this variability, as levels of both ecosystem functions were greatest with high functional and phylogenetic diversity, but not species richness. The unimodal relationship between species richness and zooplankton biomass is reminiscent of the commonly observed relationship between productivity and species richness at small spatial scales (Mittelbach et al. 2001). However, we find no evidence that productivity underlies the relationship described here, as zooplankton species richness was unrelated to either phytoplankton abundance or total phosphorous. The linear relationship between ecosystem function and both functional and phylogenetic diversity suggests that these measures better capture the diet complementarity between zooplankton species. It is not clear why functioning decreases at higher richness, but perhaps reflects an increasing representation of rare species that contribute little to ecosystem function, as we discuss further below.

The exception to the positive diversity ecosystem function relationship was the negative correlation between functional evenness and top-down control of phytoplankton. In this instance, functional evenness poorly reflects the complementarity of the zooplankton grazing function. Evenness is unaffected by the number of traits present within a community, rather, it is highest when the tips on the functional dendrogram of the community are evenly spaced (Villeger et al. 2008). For example, our community with the highest functional evenness was comprised entirely of copepods, which all are evenly spaced across the branch containing the raptorial feeders. However, no filter feeders were present within the community and so grazing complementarity was low. This highlights the need for careful consideration when choosing between indices. In contrast, functional richness provided a much more realistic estimation of grazing complementarity, and exhibited the predicted diversity function relationship.

Neither functional nor phylogenetic diversity were consistently the best predictor of ecosystem function, and the degree to which they explained unique variation differed depending on the measured function. While functional diversity ($FDiv_{ab}$) explained the most variation in zooplankton biomass, both species richness and phylogenetic diversity ($sesMPD_{ab}$) explained some overlapping and unique variation. In contrast, phylogenetic diversity ($sesMPD_{pa}$) explained the most variation in phytoplankton abundance and although both species richness and functional diversity (FRic) explained overlapping variation, these were subsets of that explained by phylogenetic diversity. These findings suggest that the three types of diversity indices capture some of the same functional differences in community composition. This is perhaps unsurprising because functional traits and niche differences are often phylogenetically conserved (Freckleton et al. 2002, Srivastava et al. 2012), as reflected by the high overall correlation between the traits and phylogeny. However, the diversity measures did not overlap completely in the variance in ecosystem function that they explained, and each function was best predicted by a different diversity measure. For example, body length showed little phylogenetic signal, but was predictive of zooplankton community biomass, and this correlation may explain why functional diversity explained more variation than phylogenetic diversity for this ecosystem function. In contrast, the fact that phylogenetic diversity explained additional variation in phytoplankton abundance to that explained by functional traits is suggestive of other important, but unmeasured, functional differences that covary with phylogeny. Each class of metric thus captured some unique aspect of the way that the communities use resources (Loreau and Hector 2001), highlighting the value of combining different diversity metrics in models explaining ecosystem function.

The two aspects of zooplankton function we measured appear to be dependent on different aspects of community diversity. We intentionally chose diversity metrics that captured different aspects of community composition to provide insight into the mechanisms behind the diversity-ecosystem function relationships (Villeger et al. 2008). Thus we would not expect all of our diversity measures to correlate significantly with a given function, and it is this variation in predictive ability that provides insights into the different ways in which these communities exploit resources. This is highlighted by the fact that the two functions were best predicted by different subsets of our diversity indices; zooplankton community biomass was best predicted by abundance weighted measures of diversity, while the ability of this community to suppress phytoplankton through grazing was best predicted by diversity measures that only account for presence/absence. Furthermore, we found that there was no significant relationship between the two types of functions. This is surprising because we might have expected that the communities with the greatest biomass would be the most effective at grazing phytoplankton (Jeppesen et al. 1997). However, experimental evidence suggests that different functions are often produced by different subsets of the community (Zavaleta et al. 2010), and our results support this interpretation.

The greatest zooplankton community biomass occurred in communities where abundance was spread between taxa that are functionally and phylogenetically distant. This was likely driven by the two most abundant taxa, *Daphnia pulex* and *Microcyclops rubellus*, which combined made up over two thirds of the average biomass in the ponds, but have very different functional traits, and are phylogenetically distant. The traits for trophic group, raptorial vs. filter feeding, and body length, were all predictive of total zooplankton biomass, and these taxa differ in all three of these traits. In contrast, both species share habitat preferences (pelagic habitats), and habitat preference diversity was not predictive of zooplankton community biomass. The disproportionate abundance of these two taxa resulted in a trade-off between species richness and functional or phylogenetic diversity so that the communities with the highest biomass generally had intermediate species richness. This decline in biomass with increasing species richness is due to the high number of rare taxa that contribute relatively little biomass to the community, which tend to be present when *D. pulex* is not abundant. We suspect that this negative correlation with *D. pulex* may be the result of competition, but it could also be due to factors such as differences in environmental preference. However, the relationship between community biomass and functional and phylogenetic diversity remained linear because the highest abundance-weighted diversity did not correspond to the highest species richness; the addition of rare taxa resulted in a small increase in abundance weighted diversity but this was more than compensated for by the corresponding reduction in *D. pulex* abundance.

Contrasting with the determinants of zooplankton community biomass, the ability for the zooplankton community to graze phytoplankton was dependent upon the presence of phylogenetically and functionally diverse taxa, regardless of abundances. We suggest that this is due to complementary grazing, whereby taxa specialize on different habitats and types of phytoplankton, and so communities with higher diversity were better able to suppress the abundance of all phytoplankton types. These functional differences appear to be well captured by our traits describing feeding type. For example, different cladoceran subgroups each employ a different type of filter feeding, while these copepod taxa are raptorial feeders. Similarly, Ye et al. (2013) found that that the strength of top down control increases with the size diversity of marine zooplankton. Rare species have been found to contribute disproportionately to ecosystem functioning in communities of alpine plants, tropical trees, and coral fishes (Mouillot et al. 2013). Given that abundances were not important for predicting top-down control in our ponds suggests this may also be the case for phytoplankton grazing by zooplankton.

Functional and phylogenetic diversity have been found to be informative of ecosystem functioning across trophic levels in a few other studies. Dinnage et al. (2012) found a bottom-up effect of the phylogenetic diversity of plants on the diversity and abundance of arthropod herbivores and predators. In contrast, functional diversity, but not phylogenetic diversity, was informative of the grazing pressure of marine amphipods (Best et al. 2012), highlighting the fact that the traits of interest may not always correlate with phylogeny. In our case, grazing appears to have been well captured by phylogenetic diversity, providing evidence of the value of these diversity measures for understanding ecosystem function across trophic levels.

Our diversity measures performed better than any combination of the local environmental variables in predicting both ecosystem functions. This includes total phosphorous, the limiting nutrient for phytoplankton growth in the vast majority of freshwater systems (Schindler 1977), but which was not retained as a significant predictor of phytoplankton abundance in our model.

However, nitrogen and nitrogen-phosphorous co-limitation can also limit phytoplankton growth (Elser et al. 1990). As we did not measure nitrogen concentrations, we cannot rule out that nutrient limitation may still play a role in these ponds. Nonetheless, our findings suggest that compositional differences in these zooplankton communities, which are captured in functional and phylogenetic diversity measures, have a larger impact on ecosystem function than do the local environmental conditions. This is supported by the results of our structural equation models, where our diversity measures were always the most significant predictors of ecosystem function, even when including environmental predictors. Furthermore, our most parsimonious model for predicting both ecosystem functions included only the relationship with zooplankton diversity.

CONCLUSIONS

Our study provides evidence that the functional and phylogenetic diversity of natural zooplankton communities determines their ability to produce biomass, as well as suppress phytoplankton through top-down grazing. There is a good theoretical basis for the expectation that trait based functional and phylogenetic diversity measures should outperform simple taxonomic measures in explaining ecosystem function. However, previous use of these indices has been largely confined to experimental plant communities. Our study suggests that these indices can also increase our understanding of the functioning of ecosystems in natural environments. We suggest that the congruence of our results with clear a priori predictions based on a well-established body of theory and experimental evidence (Srivastava et al. 2012, Griffin et al. 2013) provides support for our conclusions.

Furthermore, the two functions we explored here, biomass production and top-down control of phytoplankton, were each explained by different, but related, biodiversity metrics. These metrics provide insight into the underlying ecological processes responsible for each function. Zooplankton biomass production is best explained by functional diversity, whereas suppression of phytoplankton production was best explained by phylogenetic diversity. Therefore, we suggest combining functional and phylogenetic diversity measures to provide a richer understanding of the effects of biodiversity on ecosystem function.

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CONNECTING STATEMENT

In Chapter 2, I presented a survey of the pond zooplankton communities of Mont St. Hilaire, demonstrating how the functioning of these communities was determined by their phylogenetic and functional diversity. This survey also allowed me to determine how the local zooplankton communities were structured by environmental factors and their spatial arrangement on the mountain (Appendix B). This analysis indicated that the zooplankton communities clustered into three groups, depending on whether they were dominated by *Daphnia* species, cyclopoid copepod species, or ostracods (Fig B-1). Pond compositional differences appear to be determined by pond depth, and the concentration of dissolved organic carbon (DOC) (Fig B-2), both of which are strongly affected by precipitation patterns and rates of evaporation that are expected to change with climate change (Magnuson et al. 1997, Porcal et al. 2009). In contrast, the spatial arrangement of the ponds on the mountain was not informative of their community composition (Table B-1). This suggests that this metacommunity may exhibit species sorting dynamics, where dispersal rates are high enough to allow communities to be structured by the local environmental conditions, but not so high that mass effects homogenize ponds that are in close proximity (Cottenie 2005). If this is the case, then current rates of dispersal may provide spatial insurance if the local environmental conditions in the ponds were to change.

In Chapter 3, I follow up on this idea by using these pond communities to empirically test the spatial insurance hypothesis in the context of realistic environmental change. I used the field survey from Chapter 2 to identify ponds that differed in their composition and environmental conditions, and used these to set up heterogeneous metacommunities in experimental mesocosms. I had hoped to follow up on the results of Chapter 2 and ask whether dispersal could preserve functional and phylogenetic diversity, and thus ecosystem function, in changing environments. Unfortunately, the functioning of the communities in the mesocosms was largely determined by the single dominant genus, *Ceriodaphnia*, and so the link between functional and phylogenetic diversity and ecosystem function did not hold. Instead, I chose to focus Chapter 3 as a more general test of the potential for spatial insurance in an empirical metacommunity experiencing directional warming.

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3. WARMING INDUCES SYNCHRONY AND DESTABILIZES EXPERIMENTAL POND ZOOPLANKTON METACOMMUNITIES

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ABSTRACT

The spatial insurance hypothesis predicts that intermediate rates of dispersal between patches in a metacommunity allows species to track favourable conditions, preserving diversity and stabilizing biomass at local and regional scales. However, theory is unclear as to whether dispersal will provide spatial insurance when environmental conditions are changing directionally. In particular, increased temperatures as a result of climate change are expected to cause synchronous growth or decline across species and communities, and this has the potential to erode the stabilizing compensatory dynamics facilitated by dispersal. Here we report on an experimental test of how dispersal affects the diversity and stability of metacommunities under warming using replicate two-patch pond zooplankton metacommunities. Initial differences in local community composition and abiotic conditions were established by seeding each patch in the metacommunities with plankton and sediment from one of two natural ponds that differed in water chemistry and species composition. We exposed metacommunities to a 2°C increase in average ambient temperature, crossed with three rates of dispersal (none, intermediate, high). In ambient conditions, intermediate dispersal rates preserved diversity and stabilized metacommunities by promoting spatially asynchronous fluctuations in biomass, especially between local populations of the dominant genus, *Ceriodaphnia*. However, warming synchronized their populations so that these effects of dispersal were lost. Furthermore, because the stabilizing effect of dispersal was primarily due to asynchronous fluctuations between populations of a single genus, metacommunity biomass was stabilized, but dispersal did not stabilize local community biomass. Our results show that dispersal can preserve diversity and

provide stability to metacommunities, but also show that this benefit can be eroded when warming is directional and synchronous across patches of a metacommunity, as is expected with climate warming.

INTRODUCTION

Climate change is altering biodiversity at local, regional, and global scales (Sala et al. 2000, Bellard et al. 2012). We are currently witnessing shifts in the phenology and distribution of many species, as they respond to warming conditions (Chen et al. 2011, Ovaskainen et al. 2013). Early indicators suggest that warming is changing which species are favoured locally, inducing changes in population dynamics, and widespread changes in the composition of many ecological communities (Walther et al. 2002, Sommer and Lengfellner 2008). Therefore, an open question is how climate-driven temperature changes will affect the stability and composition of natural communities.

The temporal variation in total biomass is one important indicator of community stability (Ives and Carpenter 2007). Variability in community-level biomass can be reduced by temporal asynchrony between species fluctuations, known as "compensatory dynamics" (Gonzalez and Loreau 2009). Whether climate warming affects the synchrony of species fluctuations will depend on differences in species' demographic responses to increased temperatures. Typically, population growth rates increase with warming until optimal temperatures are reached, after which conditions become stressful and increased mortality causes populations to decline (Savage et al. 2004). Therefore, warming may cause synchronous population growth and decline, or compensatory growth and decline, depending on whether species differ in their thermal optima, and whether temperatures exceed these optima. Moreover, at sub-lethal temperatures at which increased population growth rates occur, populations tend to oscillate to a greater degree (Beisner et al. 1996). However, if sustained warming becomes too stressful, diversity may decrease through declines in relative abundances or because of local extinctions (Thompson and Shurin 2012). Such diversity loss may result in increased overall community biomass variability because of the breakdown of statistical averaging (the portfolio effect hypothesis – Doak et al.

1998), or because of reduced response diversity (the insurance hypothesis – Yachi and Loreau 1999). Understanding how patterns of community synchrony are altered by climate warming is required if we are to manage the stability and resilience of future ecological communities.

The spatial insurance hypothesis suggests that dispersal is a key processes mediating community stability and diversity in changing environments (Loreau et al. 2003, Gonzalez et al. 2009). When environmental changes are of short duration and differ between local habitats, dispersal can maintain diversity, facilitate asynchronous population dynamics in both space and time, and sustain these conditions for community stability (Loreau et al. 2003, Howeth and Leibold 2010, Steiner et al. 2011, Wang and Loreau 2014). Dispersal allows species to move between local habitat patches to find favourable conditions, and thus is expected to play an important role in preserving diversity and stabilizing communities in fluctuating environments. This effect of dispersal is expected to be strongest when rates are low to intermediate; dispersal rates must be high enough to allow species to track favourable conditions across space and through time, but not so high that mass effects synchronize the metacommunity (Loreau et al. 2003, Gonzalez et al. 2009).

The spatial insurance hypothesis predicts a unimodal relationship between biomass variability and the rate of dispersal, with intermediate rates resulting in the lowest variability (Loreau et al. 2003). However, the model predictions also suggest that metacommunity variability should remain low with high dispersal rates. This occurs because, in the model, high dispersal stabilizes local environmental fluctuations through spatial averaging, but there is no temporal variation in the mean metacommunity environment. Therefore, we expect that metacommunity variability should also increase with high dispersal rates in natural metacommunities, which are subject to regional fluctuations in environmental conditions. The spatial insurance hypothesis also predicts a unimodal relationship between species richness and dispersal, with intermediate rates resulting in the highest richness (Loreau et al. 2003). However, the model predictions suggest that high regional species richness can be maintained with low dispersal, if each local community contains a different subset of the regional species pool; predictions which have been supported by experimental zooplankton communities (Vogt and Beisner 2011).

When environmental changes are directional, long term, and widespread, such as with climate warming, theory is less clear about how dispersal should affect stability (Abbott 2011). On the one hand, dispersal can allow species tolerant of warmer conditions to colonize new habitats, where they can compensate for losses in functionally similar but heat-sensitive species, maintaining community biomass (Thompson and Shurin 2012). However, the spread of heat-tolerant species could also reduce composition differences between local communities, which are necessary for spatial insurance (de Boer et al. 2014). When metacommunities are homogeneous in composition, even low rates of dispersal are expected to be destabilizing because they can synchronize population fluctuations in space (Liebhold et al. 2004, Gouhier et al. 2010). In addition, because climate warming is expected to raise temperatures across entire regions, spatially synchronous responses may be expected by resident populations through the Moran effect (Moran 1953, Ranta et al. 1997, Gouhier et al. 2010). Such a synchronous response is expected to reduce the stabilizing effect of spatial insurance, especially if the synchronizing effect of warming is strong enough to overwhelm local environmental heterogeneity. Research is needed to quantify the degree to which climate warming will disrupt the spatial insurance effects of connectivity and diversity.

Here we report the results of an experiment designed to test the hypothesis that climate warming will reduce spatial insurance by synchronizing metacommunity dynamics. We used replicate two-patch zooplankton metacommunities in mesocosms with each patch initially seeded with plankton and sediments from different natural source ponds. We applied a warming treatment (ambient outdoor summer conditions vs. ~2°C above ambient) crossed with a dispersal treatment consisting of three dispersal rates: none (0%), intermediate (1% every 5 days), and high (10% every 5 days). The temperature treatment was applied to both patches of the metacommunity, but local conditions differed based on the species pool and water chemistry in each local community. These differences were maintained over the course of the experiment by the presence of sediment containing resting eggs from the two different source ponds.

We predicted that warming would alter interspecific synchrony, likely by promoting synchronous population responses, either through growth or decline. We also predicted that warming would increase the spatial synchrony of populations by favouring similar species in both patches. Therefore, we expected a decline in species richness and that the total biomass at both local and metacommunity scales would become more variable under the warming treatment. Following the spatial insurance hypothesis (Loreau et al. 2003), we predicted that the highest metacommunity species richness would be retained when dispersal is absent or present at an intermediate rate (1%), and the greatest local species richness would be retained with intermediate dispersal. Furthermore, we predicted that intermediate dispersal rates would also stabilize biomass at both local and metacommunity scales by allowing species to move between the patches to find conditions to which they are most suited, and so promote both interspecific and spatial compensatory dynamics. However, we expected that these benefits of intermediate dispersal would be reduced in the warmed treatment, because the correlated growth response across the metacommunity would increase interspecific and spatial synchrony.

METHODS

Experimental Setup

Twenty-four, 2-patch metacommunities were set up using 114L Rubbermaid containers outdoors at the central McGill campus, Montreal Canada. Each mesocosm was filled with tap water on May 3rd 2012 and left to sit for two weeks to dechlorinate. The tanks were then seeded with sediment and zooplankton from the natural pond metacommunity in the Gault Nature Reserve, Mont Saint Hilaire, Quebec (45° 32’ 10” N, 73° 09’ 10”, W). We selected source ponds so that each patch of each metacommunity would contain different initial species composition based on a field survey of the ponds conducted the previous year (Thompson et al. 2015). Each experimental metacommunity consisted of two patches: patch A, which was seeded from three copepod-dominated ponds; and patch B, which was seeded from two *Daphnia*-dominated ponds. All source ponds were shallow (< 1 m deep), similar to that of the mesocosms. The sediment and plankton were collected on May 14-16, 2012 and added to the tanks on May 17th, 2012. Each tank received 4L of amalgamated sediment collected with a 500μm mesh kick net and plankton sieved

(63μm) from 10L of pond water. The communities were left to establish for two weeks prior to the start of the experiment. The sediment provided a bank of resting eggs for plankton to hatch from throughout the experiment. The tanks were shaded with high-density polyethylene (HDPE) agricultural shade cloth (Tek Knit, Canada) that provided 60% shade (manufacturer's rating) from June 11 until the end of the experiment. Water levels in the mesocosms fluctuated due to evaporation and rainfall, but remained at least two thirds full for the entire experiment.

Two additional mesocosm tanks were set up, but were not seeded with sediment or plankton, to test levels of ambient dispersal. These mesocosms were fertilized with 10 μg/L phosphorus as KH_2PO_4 and 200 μg/L nitrogen as $NaNO_3$ on June 26 to stimulate primary productivity.

Treatments

Treatments were initiated on June 2, 2012 after sampling the initial zooplankton community composition. Treatments consisted of a 2x3 factorial design with warming (control vs. warmed) and dispersal (none, intermediate, and high dispersal between patches). The warmed tanks were maintained at an average of 1.85°C (temporal s.d. of mean difference = 0.51°C; s.d. of mean temperatures across warmed tanks = 0.20°C) above the ambient tanks using 25W aquarium heaters (Hagen, Canada) following Thompson and Shurin (2012). This warming treatment allowed the tanks to follow natural fluctuations in temperature (Fig. C-1).This increase in temperature falls in the range of IPCC warming scenarios for 2100, but is modest compared to the 4.8°C worst-case scenario (IPCC 2013). Temperatures were monitored using Hobo Pendant temperature/light data loggers (Onset Computer Corporation, USA), suspended in the centre of each mesocosm, 10 cm above the bottom.

Dispersal treatments were imposed every five days, with the exception of June 7th, by transferring water between mesocosms in each metacommunity. We chose rates that corresponded to low (0%), intermediate (1%), and high (10%) dispersal from the spatial insurance model (Loreau et al. 2003). For this, twelve liters of water from each mesocosm was collected in separate buckets using a 2L Van Dorn sampler. Two liters of this water was removed and used for the zooplankton samples, described below. The remaining volume was used for the dispersal treatments: 10L

(~10% of mesocosm volume) for the high dispersal treatment, and 1L (~1% of mesocosm volume) for the intermediate dispersal treatment, transferred reciprocally between mesocosms in each metacommunity. All remaining water from the buckets was transferred back to the original mesocosms so that all dispersal treatments were subjected to the same effects of removing and adding water.

Sampling

The crustacean zooplankton community composition was sampled every 10 days by sieving 2 L of water through a 63μm mesh. Mean sample size was 147 individuals L^{-1}, with a median of 102 L^{-1}. Samples were preserved in 95% ethanol (final concentration ~70%). All adult individuals were identified to the highest possible taxonomic resolution, which was generally species for cladocerans and genus for copepods, according to Haney et al. (2010). Samples were enumerated using a stereo microscope (Leica Microsystems, Germany) at 60x magnification. All zooplankton are reported at the genus level to maintain consistency and because all identified species were from unique genera. Biomass was estimated using average measured body lengths and length-weight regressions (McCauley 1984), multiplied by the number of adult individuals.

Water chemistry (total phosphorus – TP, total nitrogen – TN, dissolved organic carbon - DOC, and dissolved inorganic carbon - DIC) was measured midway through the experiment (TP and TN – June 28 ; DOC and DIC – July 19) and on the final day of the experiment (Aug 31) and samples were analyzed by the GRIL-UQAM Aquatic Analytical Laboratory (UQAM, Montreal). Samples were refrigerated (4°C) until analysis. TP was measured spectrophotometrically using the molybdenum blue method, following digestion with persulfate (Griesbach and Peters 1991). TN content was determined with alkaline persulfate digestion using an air segmented continuous flow analyzer (Alpkem RFA-300) (Patton and Kryskalla 2003). DOC and DIC were analyzed after filtration (1.2μm) and samples were processed with sulfuric acid and oxidized via persulfate on a 1010 TOC analyzer (OI Analytical, College Station, Texas, USA). Unfortunately, 25 of our August 31 TP/TN samples were contaminated in the analysis and so were excluded from consideration. The samples were lost randomly with regard to the treatments and so statistical analyses were still possible, but with reduced sample size.

Statistical analysis

All analyses were conducted using *R* v.3.0.2 (R Development Core Team 2014). Treatment effects were calculated on data collected after the total biomass of the metacommunities began to diverge according to the treatments so as to exclude initial transient growth in response to mesocosm conditions. This point in time was defined as the one at which total biomass differed by at least one standard error between at least two treatment combinations.

Community and metacommunity composition were averaged over the sampling dates, and treatment differences were tested using permutational MANOVA with Bray-Curtis distances using the *vegan* package (Oksanen et al. 2011). Local communities were grouped by metacommunity in the local community analysis. Community composition differences were displayed using an NMDS ordination. Water chemistry differences were tested using a MANOVA with metacommunity as a random factor.

Species richness was calculated as the average number of species in each local community or metacommunity averaged over the sampling dates. Local community biomass was calculated as the summed biomass, per liter, across all zooplankton species in each mesocosm. Metacommunity biomass was calculated as the sum of the biomass in both patches of each metacommunity. Local and metacommunity variability were calculated as the coefficient of variation (CV) of the local and metacommunity biomass respectively.

The overall effects of the treatments on species richness and biomass variability were tested using ANOVA. Shapiro-Wilk's (vegan package Oksanen et al. 2011) and Levene's tests (car package Fox and Weisberg 2011) were used to ensure that all variables met the assumptions of normality and homoscedasticity. Metacommunity was included as a random factor, using the *nlme* package (Pinheiro *et al.* 2013), when testing for treatment effects on local scale variables. Planned polynomial orthogonal contrasts were used to test for the quadratic and linear effects of dispersal. The quadratic contrast tests the hypothesis that 1% dispersal resulted in species richness or variability that was different from either the 0 or 10% dispersal treatments, as predicted by the spatial insurance hypothesis (Loreau et al. 2003). The linear contrast tests the hypothesis that species richness or variability were altered by dispersal.

We estimated aspects of community temporal synchrony using the index of community-wide synchrony (Loreau and de Mazancourt 2008) which scales from 0 (perfect asynchrony) to 1 (perfect synchrony). For metacommunity level synchrony, we estimated: spatial synchrony of local community biomass (spatial synchrony), interspecific synchrony at the metacommunity scale (interspecific synchrony), and the population synchrony for each species (population synchrony). Spatial synchrony quantifies the synchrony between the total biomass of the two local communities in each metacommunity. Interspecific synchrony quantifies the synchrony between taxa after summing their biomass in both local communities of each metacommunity. Population synchrony quantifies the synchrony between populations for each species in the two patches of the metacommunity. For local community synchrony, we quantified the interspecific synchrony between taxa within each patch.

Multiple regression was used to determine which measures of metacommunity synchrony best determined metacommunity variability, and variable selection was done by comparing all variable combinations using the *leaps* package (Lumley and Miller 2009). All variance inflation factors were less than 2.2, indicating that variance was not greatly inflated by multicollinearity. Type II linear regression, with the ranged major axis method to account for error in both the independent and dependent variables (Legendre 2013), was used to estimate the slope of the relationship between metacommunity variability and each measure of community synchrony. Variation partitioning using the *vegan* package (Oksanen et al. 2011) was used to estimate the amount of overlap in variation in metacommunity variability explained by the metacommunity synchrony measures selected in the multiple regression. The relationship between local community variability and local community synchrony was determined using a mixed effect linear regression with metacommunity as a random effect using the *nlme* package (Pinheiro *et al.* 2013) and the *MuMIn* package (Bartoń 2014) was used to estimate the marginal R^2. The overall effects of the treatments on estimates of synchrony were tested using ANOVA with planned orthogonal contrasts.

RESULTS

Treatment effects on community biomass began to emerge, at both local and metacommunity scales, one month after the treatments were applied (Fig. C-2; on July 12). Therefore, all reported comparisons between treatment combinations are based on the community, beginning on July 12.

Community composition and species richness

The zooplankton metacommunity was composed of eight genera of crustacean zooplankton. *Ceriodaphnia* and *Daphnia* were the two dominant genera, averaging 68.4% and 20.3% of community biomass respectively.

There were no significant overall effects of warming or dispersal on metacommunity species richness (Warm – $F_{1,18} = 0.92$, $p = 0.350$; Disp. – $F_{2,18} = 2.42$ $p = 0.117$; Warm x Disp. – $F_{2,18} = 1.67$, $p = 0.217$). However, under ambient conditions, metacommunity species richness tended to be highest with 1% dispersal, and this pattern was not observed with warming (Fig. 3-1a). This was consistent with our predictions, but the pattern was not statistically significant (Quad. Dispersal x Warming – $t_{2,18} = 1.82$, $p = 0.085$).

Species richness was greater in local community A than community B (Fig. 3-1b,c; Com A = 6.2 ± 0.17 SE vs. Com B = 5.6 ± 0.17 SE; $F_{1,18} = 12.45$, $p = 0.002$), and there was a tendency for higher richness with warming (Warm – $F_{1,18} = 3.89$, $p = 0.064$), but there were no significant overall effects of dispersal. (Disp. – $F_{2,18} = 0.87$, $p = 0.435$; Warm x Disp. $F_{2,18} = 1.57$, $p = 0.235$). However, in ambient conditions, both communities tended to have the highest species richness with 1% dispersal, a pattern not present with warming. This was consistent with our predictions, although not statistically significant (Quad. Dispersal x Warming – $t_{2,18} = 1.28$, $p = 0.218$).

Warming and dispersal interactively affected metacommunity composition (Fig. C-3; $F_{2,18} = 2.44$, $p = 0.047$). Species-specific responses to the treatments are shown in Table C-1. Local

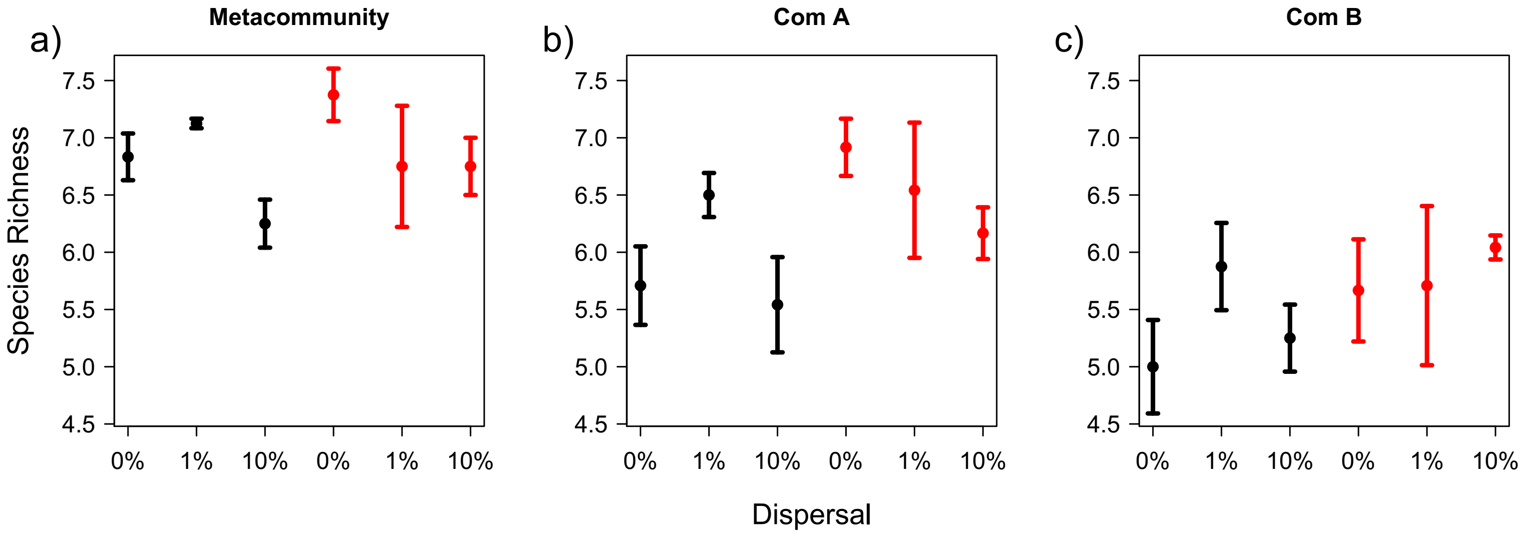

Figure 3-1. Species richness at metacommunity (a) and local scales (b, c) in ambient (black) and warmed (red) treatments crossed with the three dispersal treatments (0%, 1%, and 10%). Error bars represent 1 standard error around the mean (n=4).

zooplankton community composition, averaged through time (July 12 – Aug 31), differed based on initial community type (Fig. C-4; $F_{1,36} = 18.52$, $p < 0.001$), despite the homogenizing effect of dispersal ($F_{2,36} = 2.63$, $p < 0.001$). Warming also significant altered local community composition, both directly ($F_{1,36} = 3.66$, $p < 0.001$), and by altering the effect of dispersal ($F_{2,36} = 1.98$, $p < 0.001$). A single taxon, *Ceriodaphnia* was found in one of the two tanks that were not seeded with zooplankton, indicating that levels of ambient dispersal were far below those of our dispersal treatments.

Water Chemistry

Local water chemistry also differed between the two initial community types (mid experiment – $F_{1,35} = 8.24$, $p < 0.001$; end of experiment – $F_{1,9} = 11.28$, $p < 0.006$), and was not significantly affected by dispersal (mid experiment – Com. x Disp.; $F_{2,35} = 1.68$, $p = 0.400$; end of experiment – $F_{2,9} = 1.36$, $p = 0.292$). Community A had lower concentrations of TP and TN, but higher concentrations of DIC and DOC at mid experiment, but by the end of the experiment, all concentrations were higher in community A (Table C-2). Warming altered the final water chemistry of the mesocosms ($F_{1,9} = 7.32$, $p = 0.017$), decreasing concentrations of TP while increasing concentrations of TN, DOC, and DIC (Table C-2), but these effects were not significant midway through the experiment ($F_{1,35} = 1.06$, $p = 0.421$).

Metacommunity Biomass Variability

There were no significant overall effects of warming and dispersal on metacommunity biomass variability (Warm – $F_{1,18} = 0.23$, $p = 0.640$; Disp. – $F_{2,18} = 2.50$ $p = 0.111$; Warm x Disp. – $F_{2,18} = 2.98$, $p = 0.077$). However, the planned contrast for the quadratic effect of dispersal was significant ($t_{1,18} = 2.75$, $p = 0.013$), indicating that metacommunity biomass variability was substantially lower with 1% dispersal in ambient conditions (Fig. 3-2a). There was also a significant interaction between the planned contrast for the quadratic effect of dispersal and warming ($t_{1,18} = -2.23$, $p = 0.039$) arising because the stabilizing effect of 1% dispersal was lost in warmed conditions (Fig. 3-2a).

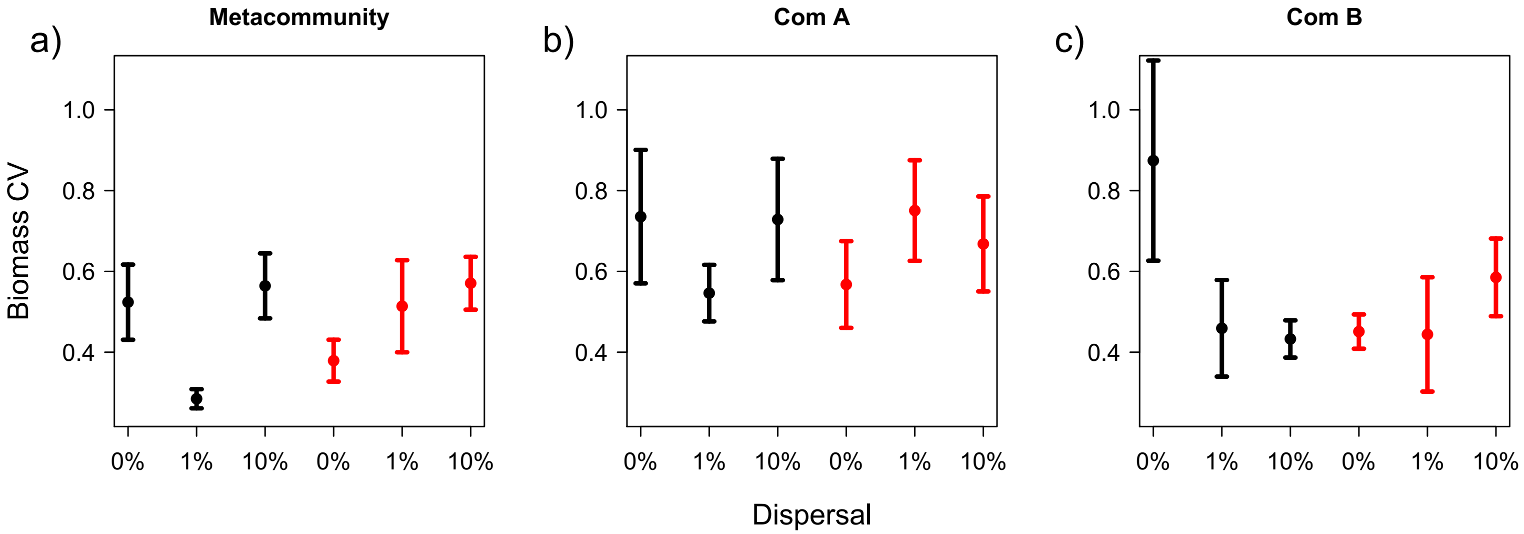

Figure 3-2. Biomass coefficient of variation at metacommunity (a) and local scales (b,c) in ambient (black) and warmed (red) treatments crossed with the three dispersal treatments (0%, 1%, and 10%). Error bars represent 1 standard error around the mean (n=4).

The measures of synchrony that were selected as the best predictors of metacommunity biomass variability were metacommunity interspecific synchrony (Fig. 3-3a; R^2_{adj} – 0.51, $F_{1,22}$- 24.70, $p <$ 0.001) and *Ceriodaphnia* population synchrony (Fig. 3-3c; R^2_{adj} – 0.40, $F_{1,22}$- 16.34, $p < 0.001$). The next best model also included metacommunity spatial synchrony (Fig. 3-3b; R^2_{adj} – 0.36, $F_{1,22}$- 13.81, $p = 0.001$) and thus we included this in our variation partitioning (Fig. 3-3d). All three measures of synchrony were positively related to metacommunity biomass variability. Of the other species, only *Microcyclops* population synchrony was significantly related to metacommunity biomass variability (R^2_{adj} – 0.21, $F_{1,22}$- 7.00, $p = 0.015$; see Table C–3 for species specific relationships). Metacommunity interspecific synchrony and spatial *Ceriodaphnia* synchrony overlapped in explaining 35.8% of the variation in metacommunity biomass CV, with unique contributions of 22.5% and 10.5 % respectively (Fig. 3-3d). Spatial *Ceriodaphnia* synchrony accounted for all variation in metacommunity biomass CV that was explained by spatial community synchrony.

Spatial *Ceriodaphnia* synchrony decreased with 1% dispersal in ambient conditions (Fig. C-5a; Quad. Disp.; $t_{1,18} = 3.22$, $p = 0.005$) but not in warmed conditions, as indicated by the significant interaction between warming and dispersal (Warm x Quad. Disp.; $t_{1,18} = -2.53$, $p = 0.021$). This was reflected in the time series of *Ceriodaphnia* abundances, wherein metacommunities with 1% dispersal showed obvious spatial compensatory dynamics in ambient, but not with warmed temperatures (Fig. 3-4). There was also a positive significant linear effect of dispersal on spatial *Ceriodaphnia* synchrony (Linear Disp.; $t_{1,18} = 2.65$, $p = 0.016$). Metacommunity interspecific synchrony increased linearly with dispersal (Fig. C-5b; Linear Disp.; $t_{1,18} = 2.41$, $p = 0.027$) but was unaffected by warming ($t_{1,18} = 0.361$, $p = 0.722$).

Local Biomass Variability

Local biomass variability was not significantly affected by dispersal (Fig. 3-2b,c; $F_{2,18} = 0.73$, $p =$ 0.496) and warming ($F_{1,18} = 0.20$, $p = 0.664$) or their interaction ($F_{2,18} = 1.51$, $p = 0.248$) but values were 1.23 times greater in community A than in community B ($F_{1,18} = 4.36$, $p = 0.051$).

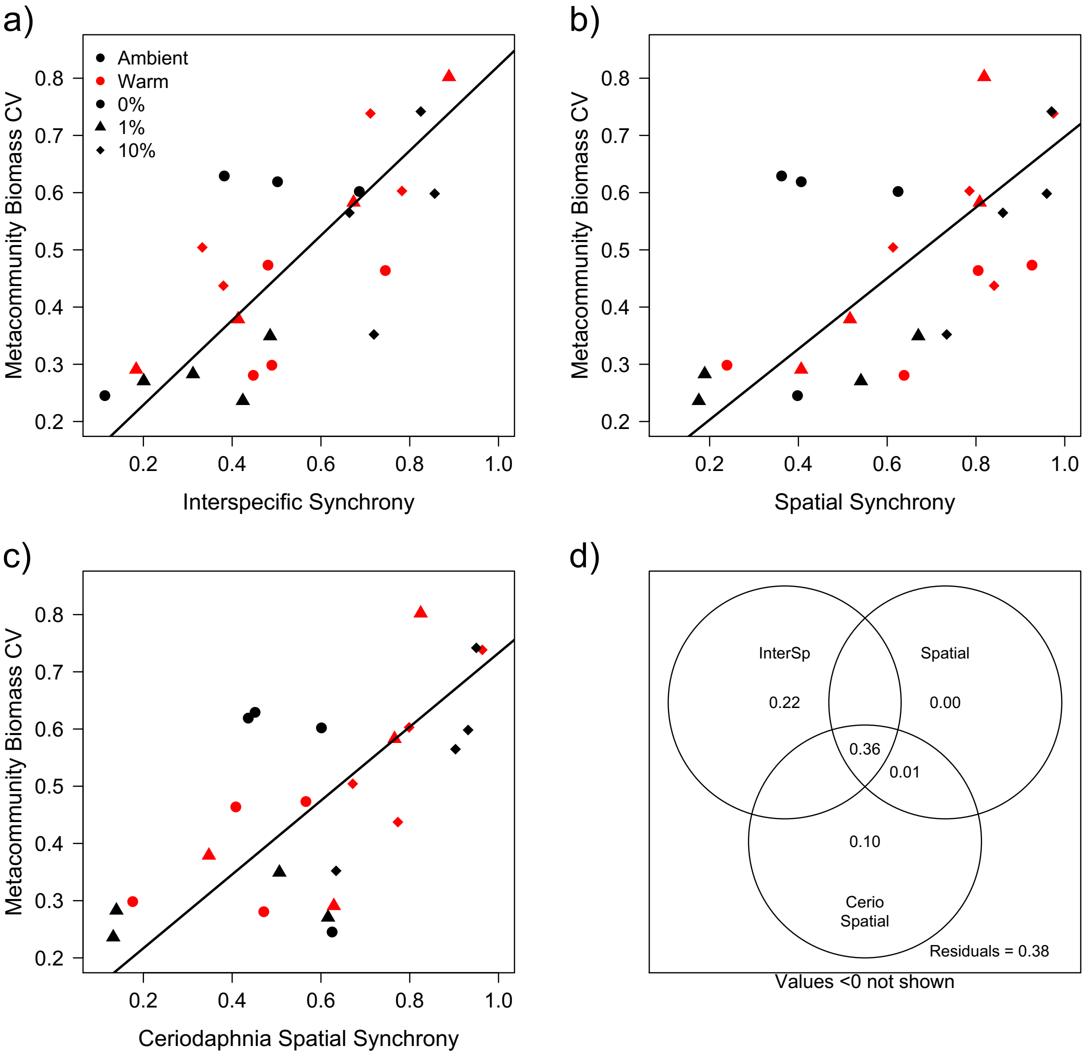

Figure 3-3. Metacommunity biomass coefficient of variation compared to interspecific metacommunity synchrony (a), spatial synchrony (b), and *Ceriodaphnia* spatial synchrony (c). Panel d shows the variation explained by each measure of synchrony, and their overlap.

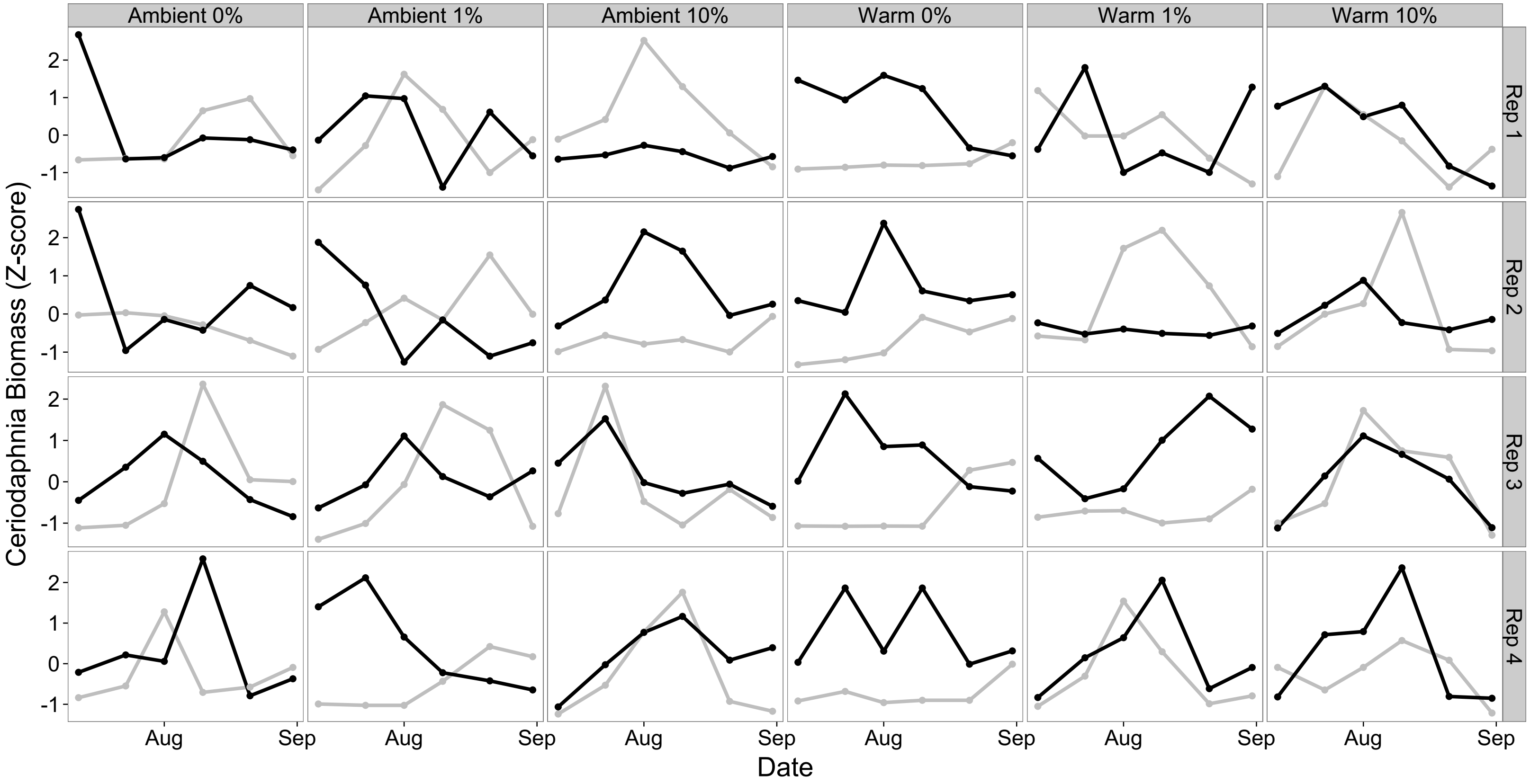

Figure 3-4. *Ceriodaphnia* biomass (standardized) time series in each paired metacommunity replicate (community A = grey, community B = black). Treatment combinations are ordered by column.

Local biomass variability was positively related to local community synchrony (Local CS; $R^2_{marginal} = 0.38$, $t_{1,23} = 5.38$, $p < 0.001$) and local *Ceriodaphnia* variability ($R^2_{marginal} = 0.49$, $t_{1,23} = 6.69$, $p < 0.001$). Both local CS and local *Ceriodaphnia* variability were retained as significant predictors of local community variability in a combined model ($R^2_{marginal} = 0.82$). There was no significant effect of warming, dispersal, or source community on local community synchrony. *Ceriodaphnia* variability was greater in community A than community B ($F_{1,18} = 41.58$, $p < 0.001$) and decreased with dispersal ($F_{2,18} = 5.30$, $p = 0.016$). Local biomass variability was not significantly related to local species richness ($R^2_{marginal} = 0.06$, $t_{1,23} = -1.77$, $p = 0.091$).

DISCUSSION

Our results show that warming can reduce spatial insurance by increasing synchrony across metacommunities. As predicted, intermediate dispersal rates stabilized metacommunity biomass and tended to increase species richness. However, this stability was not due to spatial insurance involving interspecific compensatory dynamics (Loreau et al. 2003). Rather, stability was conferred under ambient conditions because intermediate dispersal promoted spatially asynchronous dynamics of the most abundant zooplankton genus, *Ceriodaphnia*. However, warming synchronized *Ceriodaphnia* dynamics, so that the stabilizing effect of dispersal was lost. Furthermore, because dispersal did not promote interspecific compensatory dynamics, its effect did not translate to greater stability at the local community scale.

As predicted by the spatial insurance hypothesis (Loreau et al. 2003), the greatest levels of species richness were retained with no or an intermediate level of dispersal at the metacommunity scale, and intermediate dispersal at local scales, but only under ambient conditions. Although this pattern was not statistically significant, the trends clearly follow our predictions, and are consistent with the patterns found for biomass variability. As in the spatial insurance hypothesis (Loreau et al. 2003), it appears that intermediate dispersal promoted species richness by allowing for colonization of each local community by non-resident species. Yet, local differences in composition were maintained so that homogenization of the metacommunity did not result in loss of diversity, as it did with high dispersal. The loss of this pattern in warmed conditions arose because warming reduced compositional differences in the communities: community B became more compositionally similar to community A (Fig. C-4 – the warmed community B tanks tended to be closer to those from community A than the un-warmed tanks), although the reduced species richness in community B indicates that it was a subset of community A species. Therefore, while dispersal could promote diversity in ambient conditions, warming appears to have favoured similar species in both local patches and thus this benefit of spatial insurance was lost.

At the regional scale, and under ambient temperatures, metacommunities connected by intermediate dispersal rates were the most stable, as predicted by the spatial insurance hypothesis (Loreau et al. 2003, Gonzalez et al. 2009). However, this occurred because intermediate dispersal reduced the spatial synchrony of biomass between the local communities, rather than because of changes in the synchrony amongst species; both interspecific and spatial synchrony were found to stabilize metacommunity biomass, but only spatial synchrony was affected by dispersal. That interspecific synchrony was not affected by dispersal was surprising, given its effects on diversity. However, in this case, spatial synchrony was responsible for the patterns of metacommunity stability. Specifically, the synchrony of the dominant *Ceriodaphnia* was lowest at intermediate dispersal. Without dispersal, the local *Ceriodaphnia* populations appeared to fluctuate independently of each other, but intermediate dispersal sustained clear spatial compensatory dynamics, which stabilized metacommunity biomass (Fig. 3-3). Low rates of dispersal coupled the local populations of *Ceriodaphnia* enough to allow populations to track local conditions favourable to growth. Our data do not provide insight into the mechanism responsible for these asynchronous fluctuations in populations but it is likely that they were driven by differences in resource availability or interspecific interactions (Liebhold et al. 2004). Finally, as predicted by theory (Loreau et al. 2003, Gonzalez et al. 2009), high dispersal caused the local populations to become almost completely synchronized, and this resulted in high variability in metacommunity biomass.

The stabilizing effect of dispersal was lost when the metacommunities were warmed because warming increased the synchrony between *Ceriodaphnia* populations connected by intermediate dispersal. This interaction between warming and dispersal was consistent with our prediction that warming would increase spatial synchrony by causing similar species to be favoured in both patches. Warming reduced differences between the patches that, under ambient conditions, resulted in compensatory dynamics between *Ceriodaphnia* populations (Fig. 3-4). However, this was not accompanied by the predicted changes in interspecific synchrony despite the altered metacommunity composition that resulted from warming in combination with dispersal. Regional fluctuations in weather have long been known to synchronize populations through the Moran effect (Moran 1953), and recent evidence suggests that climate change may play a similar role (Post and Forchhammer 2002, Jones et al. 2003).These findings are consistent with the broad conclusion that anthropogenic change has the potential to synchronize metacommunities.

At local scales, the spatial insurance predicted by Loreau et al. (2003) did not occur because local diversity, and the prevalence of interspecific compensatory dynamics, did not increase with intermediate dispersal. Again, this was surprising since intermediate dispersal promoted local species richness in ambient conditions. However, the dominance of *Ceriodaphnia* in both communities reduced the contribution of other species, precluding strong compensatory fluctuations. When communities are dominated by a single taxon, the potential for insurance effects is known to be limited (Ives and Hughes 2002, Gonzalez and Descamps-Julien 2004). Furthermore, for spatial insurance to stabilize local communities, the taxa that best tolerate the prevailing conditions must track those conditions in time and space (Loreau et al. 2003, Gonzalez et al. 2009). While compensatory dynamics did occur in some notable cases (Fig. C-6, S7), these were rare relative to the frequency with which *Ceriodaphnia* dominated communities and with no relationship to dispersal treatments. Therefore, at the local scale, community stability was determined by the variability of the dominant genus, *Ceriodaphnia*, and the degree to which it exhibited compensatory dynamics with other taxa.

Local stability was also unaffected by warming, despite our expectation that community biomass would become more variable owing to correlated growth or decline under warmer conditions. The 2°C increase in temperature did result in compositional changes in the local communities, but these changes did not translate into changes in community biomass stability. Similar warming has resulted in changes in stability in other experimental plankton communities, where biomass was more equally distributed across the community (Kratina et al. 2012) (but see McKee et al. 2002). It is likely that other factors such as the local sediment bank, water chemistry, or species interactions were more important determinants of community composition than warming in our experiment. Furthermore, these zooplankton species are likely well adapted to large fluctuations in temperatures because the ponds from which they were collected are small and shallow, and thus are exposed to large fluctuations in water temperature.

In this experiment, stability occurred because dispersal facilitated spatial compensation by a single genus, *Ceriodaphnia*, rather than because of compensatory dynamics between multiple taxa. Despite the fact that intermediate dispersal rates appear to have increased species richness, there was no evidence that this increase in diversity contributed to metacommunity or local stability. This type of spatial compensation by a single taxon can stabilize variability of regional, or metacommunity biomass, but cannot confer stability to local communities. This highlights the scale-dependence of the different mechanisms responsible for spatial insurance. In addition to spatial scale, local stability may also depend on temporal scale. In our 90-day experiment, *Ceriodaphnia* was locally dominant in both patches, which was surprising given the different water chemistry and sediment egg banks in the mesocosms. A longer experiment may have allowed other species to emerge and become dominant, making interspecific compensatory dynamics possible in the long term. Predictions from theoretical models are often derived from dynamics that play out over ten to hundreds of generations. Time series from lake observational studies may allow tests of long-term compensatory dynamics (Keitt 2008, Vasseur et al. 2014b).

Interspecific synchrony was a significant predictor of metacommunity variability in our experiment, and it is likely that emergence of zooplankton from the sediments may have facilitated these interspecific compensatory dynamics through a form of internal dispersal. The sediments appear to have maintained local differences in community composition and they may have provided a stabilizing effect on local biomass by allowing different species to emerge as conditions changed (Hairston et al. 2005). However, the fact that there were no significant effects on interspecific synchrony suggests that if emergence of zooplankton did play a role in stabilizing the communities, it was unaffected by warming or dispersal.

Our study provides clear empirical evidence of the stabilizing potential of dispersal for metacommunities experiencing environmental change. Dispersal can stabilize the biomass dynamics of metacommunities, where local abiotic and biotic conditions vary, but for which weather, seasonal and long term climate changes are likely to be common across patches. The prevalence of spatial insurance in the face of climate warming will depend on the dispersal rates and thermal tolerances of the focal organisms. Freshwater zooplankton have been estimated to disperse readily between waterbodies, but rates are limiting enough so that communities are structured by both spatial and environmental factors (Beisner et al. 2006, Shurin et al. 2009, Gray and Arnott 2011). While it is hard to compare the rates used in our experiment to those in natural communities, our range of dispersal rates likely spans the natural rates for most communities because our high dispersal rates homogenized local dynamics and was therefore not limiting. Together, theory and field data support the conclusions that dispersal plays an important role in stabilizing zooplankton metacommunities in nature.

Our results also suggest that future climate warming may erode the stabilizing mechanisms arising from dispersal. This occurred in our experiment with a modest 2°C of warming, which is below the predicted warming by 2100 of all but the most optimistic climate change scenario of the IPCC, and well below the 4.8°C worst-case scenario (IPCC 2013). Our findings should also extend to any other environmental stressor that increases synchrony within metacommunities. Increases in spatial synchrony in response to climate change and other anthropogenic stressors have been witnessed in caribou (Post and Forchhammer 2004), salmon (Moore et al. 2010), freshwater invertebrates (Angeler and Johnson 2012), and cholera epidemics (Constantin de Magny et al. 2007). Taken together, evidence suggests that ongoing environmental change has the potential to greatly affect the synchrony and stability of ecological communities.

The spatial insurance hypothesis (Loreau et al. 2003) provides a framework for considering the role of dispersal for the stability of metacommunities in fluctuating environments. However, the theory currently does not address directional change, such as climate warming. More theory is needed to extend the spatial insurance hypothesis to consider directional change, and clarify under which conditions dispersal can be expected to provide stability. Future experiments that build on our findings could address other recent theoretical developments by increasing the number and spatial topology of patches in the metacommunities (Gonzalez et al. 2011), testing multiple levels of warming, increasing temperature variability (Vasseur et al. 2014a), altering ecosystem phenology (Winder and Schindler 2004), contrasting different food web configurations (Gouhier et al. 2010, Rooney and McCann 2012), and including interactions between different environmental stressors (Vinebrooke et al. 2004).

SUMMARY

Our study provides experimental evidence that warming can reduce the role of dispersal for maintaining diversity and stability in metacommunities. Dispersal maintained diversity and provided stability for metacommunity biomass under ambient conditions by facilitating compensatory dynamics in local community biomass. However, warming increased the synchrony of local communities, eroding the metacommunity scale compensation that occurred under ambient conditions. Furthermore, the stabilizing contribution of dispersal did not involve interspecific compensatory dynamics, but rather relied upon biomass asynchrony of the most abundant taxon. These results suggest that by influencing interspecific and spatial synchrony, climate change has the potential to alter the mechanisms that currently maintain diversity and provide stability in ecosystems. Furthermore, our findings highlight how close ties between theory and experiments can improve our understanding of the factors that contribute to ecological stability in a changing world.

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CONNECTING STATEMENT

In Chapter 3, I experimentally tested whether dispersal could provide spatial insurance to metacommunities under warming. As predicted by the spatial insurance hypothesis, intermediated rates of dispersal preserved zooplankton diversity and stabilized zooplankton biomass at the metacommunity scale. However, warming synchronized the metacommunity so these benefits of dispersal were lost. These results suggest that the spatial insurance effects of biodiversity may be lost in regions experiencing strong directional environmental change.

In Chapter 4, I continue the theme of spatial insurance from Chapter 3, now using theoretical simulations to ask how dispersal affects the ability of regional metacommunities to produce multiple ecosystem functions in changing environments. This idea that species and ecological communities can produce multiple ecosystem functions connects back to Chapter 2, where I demonstrated how two types of zooplankton functioning were each linked to different aspects of the phylogenetic and functional diversity present within the pond communities of Mont St. Hilaire. Despite the knowledge that ecosystems sustain multiple functions, so far, the spatial insurance hypothesis has focused only on a single function, the production of biomass. Chapter 4, addresses this key gap in our knowledge, providing a framework for understanding how dispersal and environmental heterogeneity affect the multifunctionality of communities from local to regional scales.

4. SPATIAL INSURANCE EXTENDS TO MULTIPLE ECOSYSTEM FUNCTIONS ACROSS METACOMMUNITIES

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ABSTRACT

Ecosystem multifunctionality – the number of ecosystem functions that are simultaneously produced – depends on community diversity and the spatial scale at which it is measured. Metacommunity processes determine the strength of the relationship between biodiversity and ecosystem function at local and regional scales, but we do not understand how they affect multifunctionality. Here we use metacommunity theory to show how dispersal mediates the shape of the diversity – multifunctionality relationship. The number and identity of functions produced both locally and regionally varies strongly with the dispersal rate. Intermediate dispersal rates maximize the number of functions produced by ensuring that species can move between patches to track favourable environmental conditions, while still maintaining the differences in local community composition that contribute to regional multifunctionality. This spatial insurance stabilizes multifunctionality at regional scales, but increases local variability. Considering dispersal will improve how we manage landscapes for ecosystem multifunctionality.

INTRODUCTION

Human wellbeing depends upon the supply of many ecosystem services produced by the diversity of organisms in the landscapes in which we live (Millennium Ecosystem Assessment 2005, Cardinale et al. 2012). Ecosystem services are sustained by multiple ecosystem functions, such as biomass production, nutrient cycling, and pollination (Costanza *et al.* 1997). These ecosystem functions are, in turn, mediated by the diversity and composition of communities distributed across the landscape (Bennett et al. 2009, Mace et al. 2012). Therefore, managing landscapes for multifunctionality, the simultaneous production of multiple ecosystem functions

(Hector and Bagchi 2007), is desirable, and theory is needed to understand how this can be done. Connectivity and rates of dispersal between local communities are known to be important for species diversity (Mouquet and Loreau 2003, Venail et al. 2008, Thompson et al. 2014) and are predicted to be important for ecosystem service production (Mitchell et al. 2013, 2014). Yet, how connectivity mediates the production of multiple ecosystem functions is currently unknown (Mitchell *et al.* 2013). Here we develop a metacommunity framework to formalize how environmental heterogeneity and species dispersal mediate the supply and stability of multiple ecosystem functions from the local to regional scales.

The production of multiple ecosystem functions within a single community generally requires greater diversity than is required for single functions (Hector and Bagchi 2007, Zavaleta et al. 2010, Maestre et al. 2012). Individual species generally contribute to the production of multiple ecosystem functions, but the amount of overlap in the functions they contribute to varies considerably across taxonomic groups and communities (Hector and Bagchi 2007, Gamfeldt et al. 2008). Moreover, species that do contribute to the same functions differ in the amount of each function that they produce, and the conditions under which they are productive (Isbell *et al.* 2012). Because of this, maintaining high rates of production of multiple functions generally requires more diversity than is required to maintain a single ecosystem function (Gamfeldt *et al.* 2008).

Multifunctionality also depends upon the spatial scale at which it is measured. Most multifunction studies have measured ecosystem functioning in small plots. While local communities rarely contain the diversity required to sustain the high production of all functions through time, this may be possible at the metacommunity scale where multiple functions are produced by a set of compositionally diverse local communities (Zavaleta et al. 2010, Pasari et al. 2013). At one extreme, each local community may only produce high rates of a single function, but if each community produces a different function, regional multifunction will be high. Alternatively, each local community could produce multiple functions at low or intermediate rates. To date, theory on how multifunctionality is realized at local scales and across patches at regional scales has been outpaced by experimental findings (Pasari et al. 2013). Metacommunity theory suggests that dispersal is a key process linking biodiversity to ecosystem function across scales, and offers a framework to formalize this relationship for multiple ecosystem functions.

Metacommunity theory was used to define the spatial insurance hypothesis (Loreau et al. 2003, Gonzalez et al. 2009), the idea that dispersal is a key parameter that jointly determines the composition and diversity of species and the productivity, and stability, of a single ecosystem function across a metacommunity. When local conditions fluctuate, diversity and ecosystem function can be maintained if species are able to disperse to patches where conditions are favourable, thus tracking environmental change in both space and time. For example, by tracking conditions favourable for growth, species are able to compensate for environmental variability and maintain high and stable rates of biomass production across the metacommunity. To date, analysis of the spatial insurance hypothesis has assumed that all species contribute equally to a single ecosystem function (Loreau et al. 2003, Gonzalez et al. 2009), but here we extend this framework to multiple ecosystem functions.

We hypothesize that, in fluctuating environments, dispersal can allow metacommunities to sustain high and stable rates of multiple ecosystem functions at local and regional scales. Because altering the rate of dispersal changes the diversity and composition of communities, it should also affect the diversity of functions produced by these communities. We examined 1) how dispersal rates mediate diversity and the supply of multiple functions when species vary in the degree to which they overlap in their contribution to different functions, and 2) how the production and stability of multiple functions changes across local and regional scales; 3) whether there is a trade-off in the rates of dispersal that maximize the production of multiple functions and the stability of these functions through time.

MATERIALS AND METHODS

We incorporated multiple ecosystem functions into the metacommunity resource competition model previously used to define the spatial insurance hypothesis (Loreau et al. 2003, Gonzalez et al. 2009). In this model, the metacommunity consists of a set of patches where the local environment fluctuates through time (e.g. rainfall). These fluctuations are sinusoidal and are out of phase, so that all patches experience the same fluctuations in environment, but at any one time the local conditions differ. The species in the metacommunity differ in the environmental conditions that they are best adapted to and this determines their ability to compete for a single common resource in each patch. We assume that all species convert this resource to new biomass with the same efficiency, and that they all die at the same rate. Dispersal is global, and equal between all patches, and all species disperse at the same rate, although the model is robust to relaxing this assumption (Fig. D-1, Fig. D-2). Without dispersal, only a single species is able to persist in each patch, but dispersal allows species to track their optimal environmental conditions, and allows for coexistence through the spatial storage effect (Chesson 2000a).

We add to the model the assumption that species are able to contribute to multiple ecosystem functions. The species have traits that define their contribution to each function and determine what proportion of their production contributes to each function. We assume that total ecosystem function production is equal to the rate at which resources are converted to new biomass. Therefore, although the species differ in their production of each function, they all produce equal total function.

Resource Competition Metacommunity Model

The equations determining the dynamics of the metacommunity read:

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

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

where $N_{ij}(t)$ is the biomass of species i and $R_j(t)$ is the amount of resource in patch j at time t. The metacommunity consists of M patches and S species. The resource is constantly renewed at a rate I and lost at a rate l in each patch j. Species i consumes the resource in patch j at a rate of $c_{ij}(t)$, converts it to biomass and productivity with an efficiency of e, and dies at a rate m. All species disperse at rate a. Dispersal is global and even across all k patches, excluding the source patch j.

We assume that the environment E_j in each patch j fluctuates between 0 and 1 and follows a sinusoid with a period T such that:

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

where the initial conditions $Einit_j$ are equally spaced across the environmental range. We further assume that the consumption rate $c_{ij}(t)$ of species i is determined by the match between its environmental optima H_i and the local environment E_j(t) in patch j at time t such that:

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

The environmental optima H_i of the S species are equally spaced across the environmental range so that the species differ in which patches they are competitively superior at any given time.

Modelling Multiple Ecosystem Functions

We assume that the productivity ϕ_{ij}(t) of species i is equal to the rate at which it converts resources to new biomass in patch j at time t:

5) $$\phi_{ij}(t) = ec_{ij}(t)R_j(t)N_{ij}(t).$$

We assume that species can simultaneously contribute to multiple ecosystem functions. Species productivity is apportioned to D ecosystem functions, where F_{dj} represents the production of function d in patch j at time t:

6) $$F_{dj}(t) = \sum_i^S \left(A_{id}\phi_{ij}(t)\right).$$

A_{id} represents the trait that determines portion of the productivity ϕ_{ij}(t) of species i that contributes to function d. Whether or not species i receives a trait A_{id} value is determined by a random draw from a binomial distribution $B(1, p)$, where p is the probability of success, which determines whether or not there is high functional overlap between species (high p) or if species are functional specialists (low p). If successful, the trait A_{id} is randomly drawn from a uniform distribution, and standardized so that the sum of all traits for each species i is equal to one:

7) $$A_{id} = \frac{unif(0,1)B(1,p)}{\sum_d^D A_{id}}.$$

Simulations Details

We show results from metacommunities consisting of 30 patches and nine species capable of contributing to seven ecosystem functions, but our results are robust to variations in all of these parameters (Fig. D-3 – D-5). The following parameters were used in all of our simulations: e = 0.2, m = 0.2, I = 150, l = 10, $N_{ij}(t = 1) = 10$, and $R_j(t = 1) = 9$. We used an extinction threshold of $N_{ij} = 0.1$, below which, local populations were assumed to be extinct and were set to zero.

We contrasted communities spanning ten levels of functional overlap by varying p between 0.1 (each species produces one function) and 1 (all species produce all functions). The production of functions was measured in each community, with a given set of functional traits, over a range of 11 dispersal rates a. Results were averaged over 100 replicate draws of traits at each level of functional overlap p. Simulations lasted 140 000 time steps (Euler approximation with $\Delta t = 0.08$) with a period T chosen to be large enough (T = 40 000) so that there was rapid competitive exclusion in the absence of dispersal amongst communities.

Response Variables

We calculated multifunction as the number of functions that simultaneously exceed a given threshold of production in a single patch (Byrnes *et al.* 2014):

8) $$MF_j(t) = \sum_{d=1}^{D}\big(F_{dj}(t) > Threshold\big).$$

The threshold is based on the maximum production of a single function across all dispersal rates and time steps when all species contribute equally to all functions. We use this reference for maximum production because it represents the highest rate that all functions can simultaneously be produced. This differs from the proposed reference of the absolute maximum production of each function (Byrnes *et al.* 2014) because it is possible to produce individual functions at thresholds greater than 1 when species are not complete generalists. Therefore, we used 8 thresholds of maximum production spanning the gradient from 0.25 to 2. Regional multifunction is calculated in the same way but after summing functions across the metacommunity.

The temporal mean species richness, effective species diversity (Jost 2006), the average individual function production, the temporal variability (CV) of individual functions, multifunction, and the temporal variability of multifunction (SD) were calculated at local and regional scales over the final 40 000 time steps (to exclude initial transient dynamics). We calculated multifunction variability as one standard deviation of multifunction rather than using the coefficient of variation (CV) because we do not expect multifunction variability to scale with its mean. All simulations and data analysis was performed in R version 3.1.1 (R Development Core Team 2014).

Results

Species Diversity and Individual Functions

Low to intermediate dispersal rates ($a = 0.005 – 0.05$) allow for the persistence of all species at both local and regional scales (Fig. 4-1a); very low or high dispersal rates result in the persistence of fewer species. At the extremes, only a single species is retained in each patch. When dispersal is very high ($a \geq 0.5$), the same single species is retained in all patches. When dispersal is low, multiple species are able to persist regionally, each in different patches. Local effective species diversity peaks with the highest dispersal rates that allow for the persistence of all species ($a = 0.05$) and regional effective diversity peaks at the lowest range of dispersal rates that allow for persistence of all species ($a = 0.005 – 0.01$).

Dispersal rates on the lower end of those that maximize species richness result in the highest average production of the individual functions (Fig. 4-1b). Lower dispersal rates result in a large drop in production, while high dispersal rates allow moderate rates of production to be sustained. This pattern is identical at local and regional scales, only differing in the magnitude of production. Because we assume that all species have the same rate of overall productivity, the average production of each species, as well as local and metacommunity productivity follow this

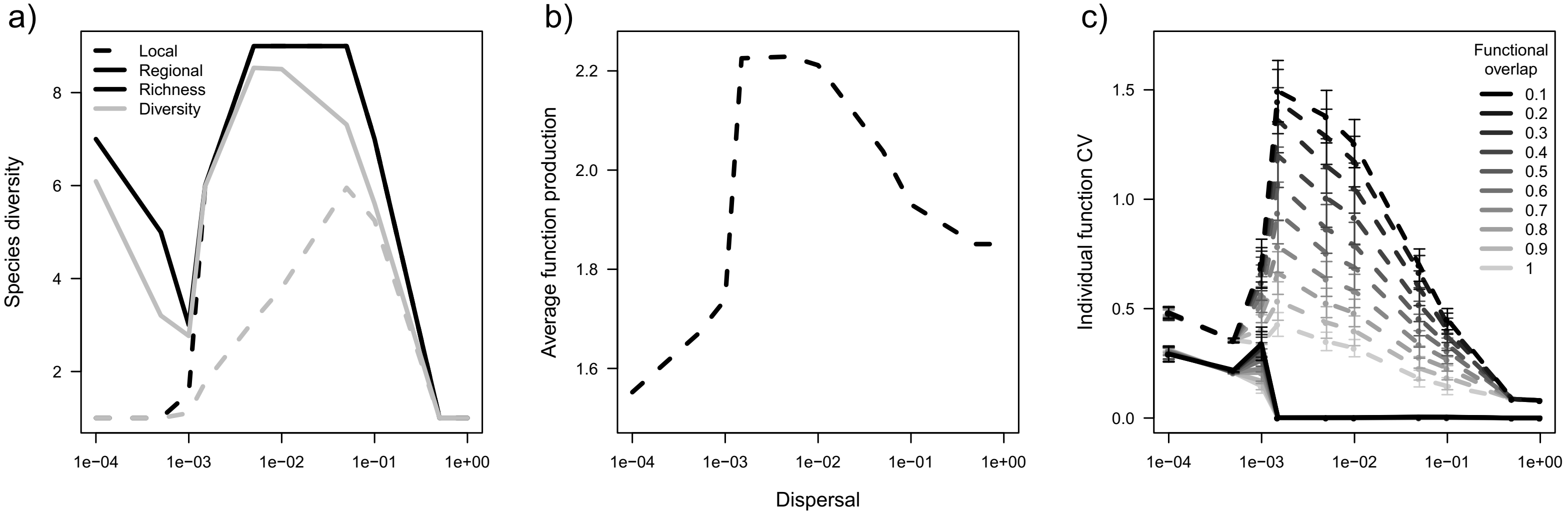

Figure 4-1. The relationship between the dispersal rate and species diversity (a), the average production of each function (b), and the average temporal variability (CV) of the individual functions (c) at local (dashed lines) and regional (solid lines) scales. Only the local scale pattern for the average production of each function is shown. The regional pattern is the same, but is 30 times higher. Species richness and average individual function production do not vary across replicates. One standard deviation around the mean value from 100 replicates are shown for the temporal variability of the individual functions.

same pattern, but differ in magnitude. Function production tends to increase with species richness, but this relationship is greatly mediated by the rate of dispersal (Fig. 4-2a).

The local production of individual functions is relatively stable at low and high dispersal rates, but is highly temporally variable at intermediate dispersal rates ($a = 0.001 – 0.05$; Fig. 4-1c). This variability peaks at low ($a = 0.001$) dispersal rates. At the regional scale, the production of each function is stable when dispersal rates are greater than 0.001 (Fig. 4-1c). There is some regional variability for each function at low dispersal rates but this is always less than the variability at the local scale.

Multifunction Production

At the local scale, multifunction generally increases with dispersal rate and peaks at intermediate rates, but the shape of this relationship depends on the threshold for production, the spatial scale, and the functional overlap of the species (Fig. 4-3). The effect of dispersal decreases as we increase the threshold for production. Regional multifunction generally exceeds local multifunction (Fig. 4-3, Fig. D-6) especially at low dispersal rates ($a < 0.001$). Local multifunction is always equal to regional multifunction when dispersal rate is high ($a > 0.1$). Communities with high functional overlap can produce more functions at lower thresholds, but they produce fewer functions in excess of high thresholds (Fig. 4-3, Fig. D-6). The relationship between multifunction and species richness is strongly mediated by the dispersal rate (Fig. 4-2b, Fig. D-7).

Changing the rate at which species disperse alters which functions are produced in a given patch and across the metacommunity, even when all other parameters are kept constant (Fig. 4-4).

Multifunction Stability

Local multifunction variability is greatest at intermediate dispersal rates (with the exception of high species overlap), and regional multifunction variability is greatest at low dispersal rates (Fig. 4-5). Multifunction variability increases at lower thresholds for production. Regional

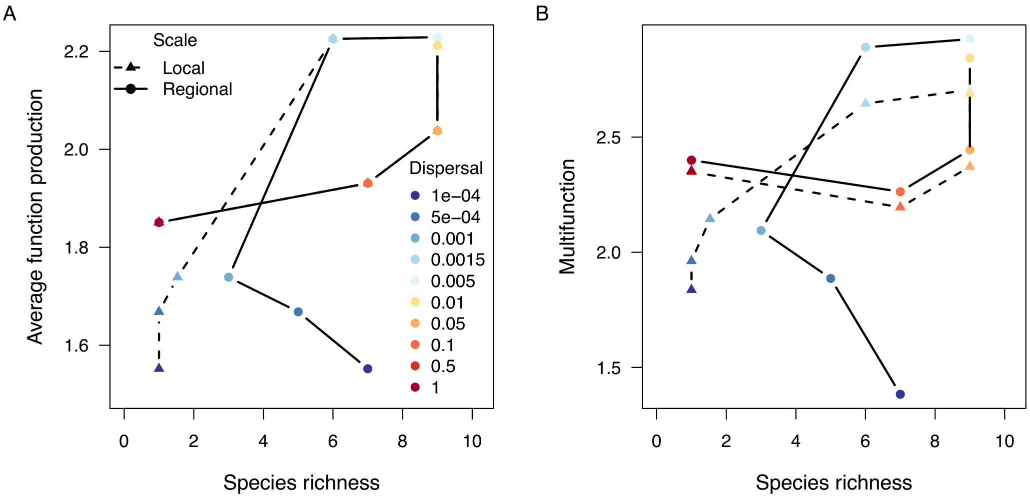

Figure 4-2. Illustration of how the relationship between species richness and the average production of each function (a) or multifunction (b) depends on the dispersal rate. Dispersal rates are indicated by the colour of the points (blue – low, red – high) and the lines connect the points in order of dispersal. Local values are indicated as triangles and regional values are indicated with circles. Here we only show the pattern for multifunction with a functional overlap of 0.5 and a threshold for production of 1. The relationship for all values of functional overlap and thresholds are shown in Figure D-7.

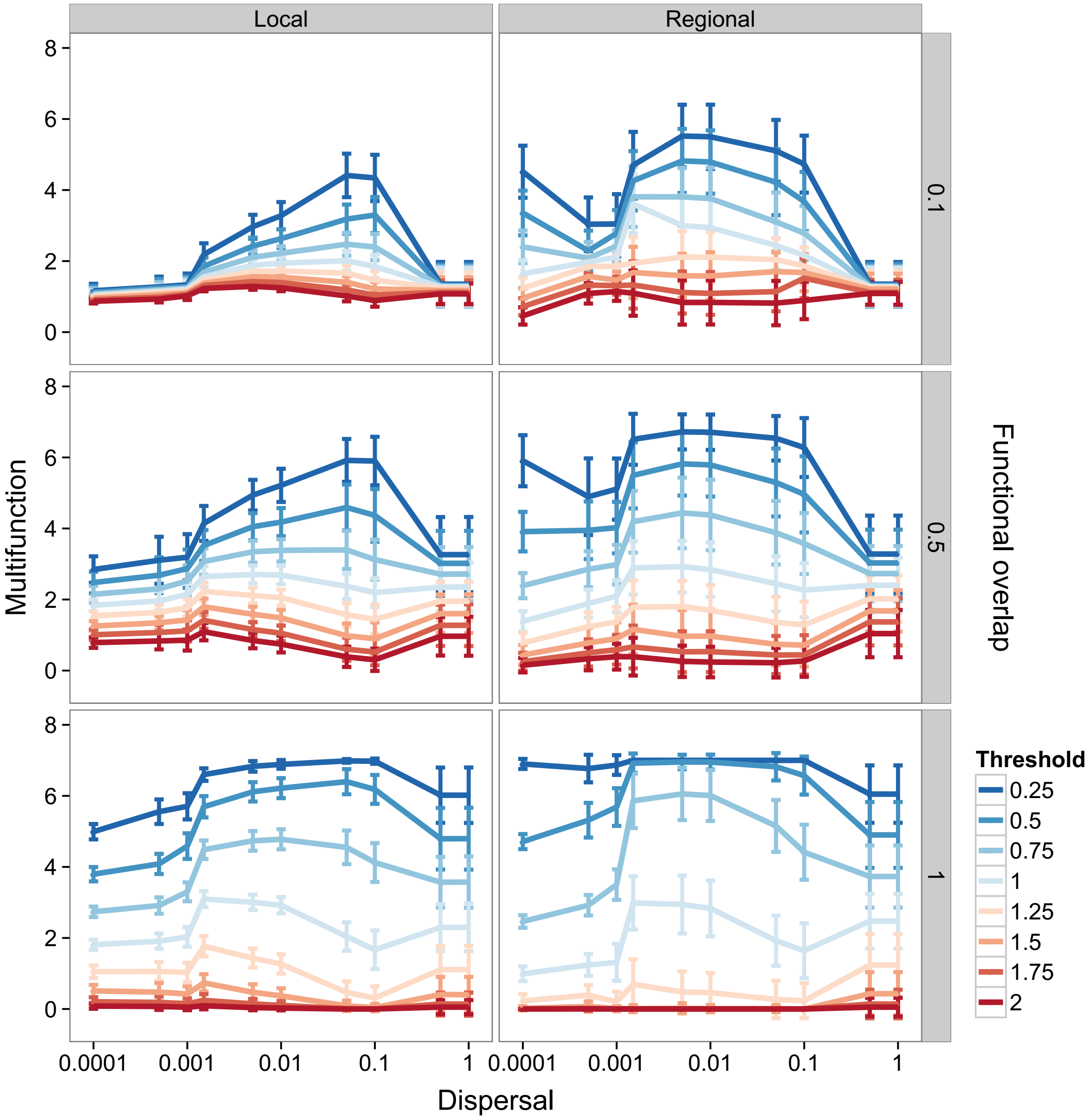

Figure 4-3. The relationship between multifunction and the rate of dispersal, at local and regional scales. The three rows of panels show three representative levels of functional overlap (0.1, 0.5, 1). One standard deviation around the mean value from 100 replicates is shown for our calculations of multifunction.

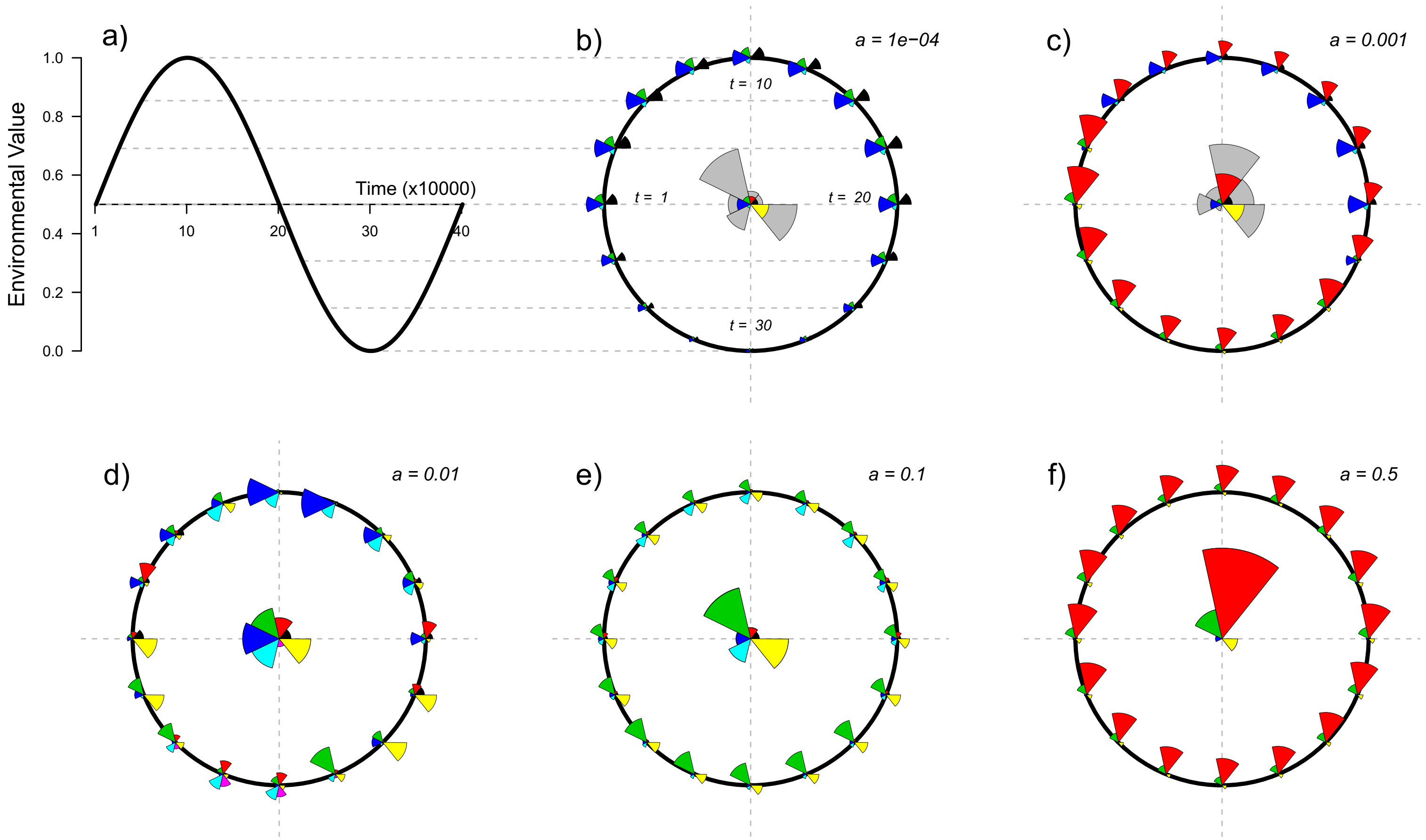

Figure 4-4. Functions produced in one example metacommunity at 5 dispersal rates (b-f). The functional overlap between species is 0.5. Each function is shown as one coloured petal, with the amount corresponding to the size of the petal. The outer ring (b-f) depicts the temporal change (in a clockwise direction corresponding to the environmental change – panel a) in the functions produced in one local patch. The regional function is depicted by the petals in the centre of the ring, with the coloured and grey section of each petal indicating the temporal minimum and maximum, respectively, of each function produced.

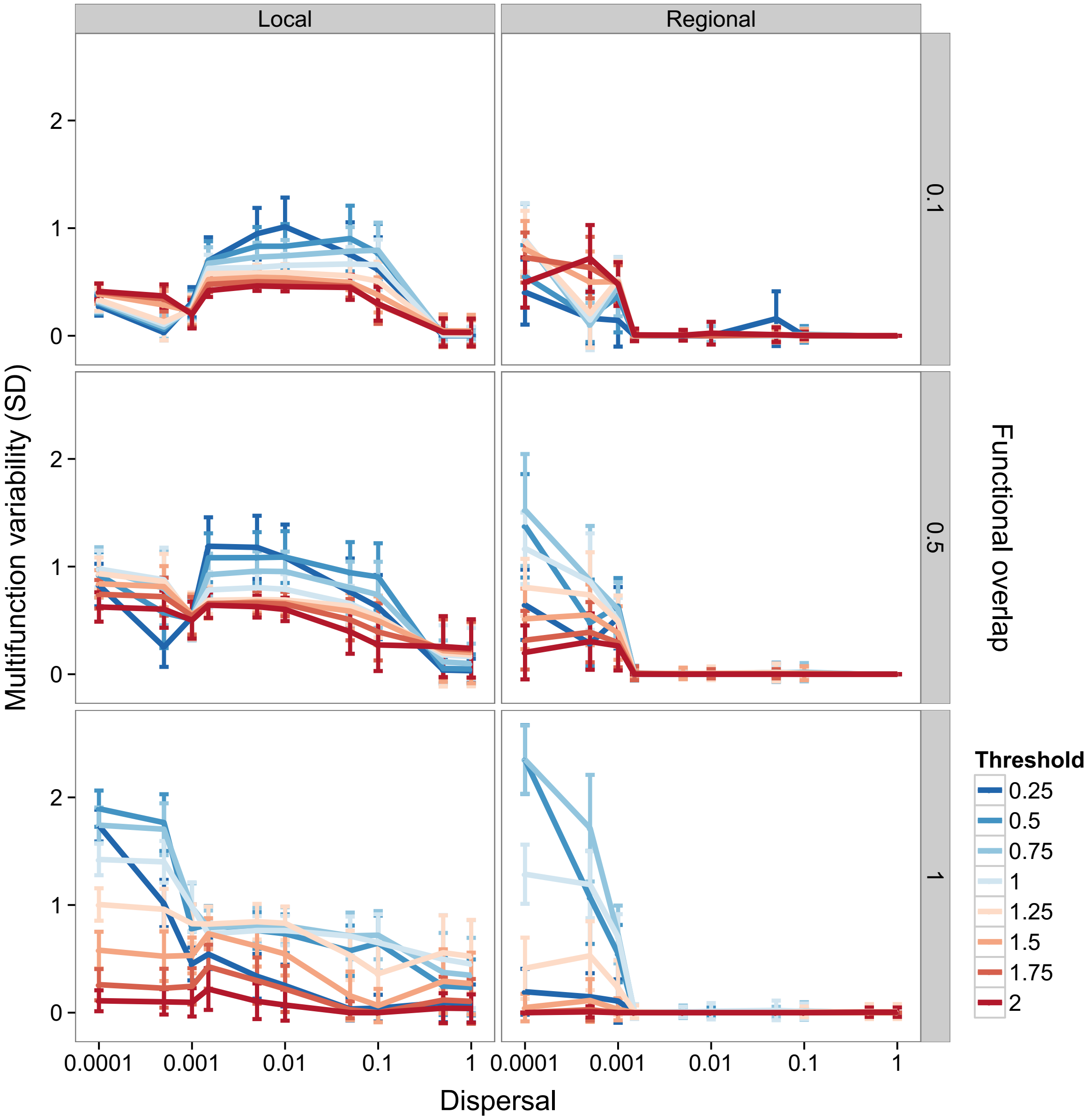

Figure 4-5. The relationship between multifunction temporal variability (SD) and the rate of dispersal, at local and regional scales. The three rows of panels show three representative levels of functional overlap (0.1, 0.5, 1). One standard deviation around the mean value from 100 replicates is shown for our calculations of multifunction variability. Values of multifunction variability are not shown when multifunction is zero.

multifunction varies when dispersal rates are below 0.001. Regional multifunction is less variable than local multifunction, except when dispersal rates are very low (a < 0.001; Fig. D-8). Multifunction variability at low dispersal rates (a<0.001) tends to increase with functional overlap across species.

DISCUSSION

We find that the rate of dispersal between local communities mediates the production and stability of multiple ecosystem functions in a metacommunity. Previous studies have shown that the production of multiple ecosystem functions is so strongly dependent on biodiversity that the production of a full suite of functions can only be achieved at regional scales (Hector and Bagchi 2007, Zavaleta et al. 2010, Maestre et al. 2012, Pasari et al. 2013). This is because local communities rarely contain the species diversity required to consistently produce all functions, especially when local environmental conditions fluctuate (Isbell et al. 2012). We predict that dispersal rate is a key process mediating this biodiversity-multifunction relationship.

Our findings extend the spatial insurance hypothesis by demonstrating how intermediate dispersal rates also maximize the production of multiple functions across spatial scales. Intermediate dispersal rates provide spatial insurance by allowing species to track fluctuations in environmental conditions, thus ensuring that biodiversity is maintained and that species are located in patches where they are most productive (Loreau et al. 2003, Gonzalez et al. 2009). The simultaneous production of multiple functions is highest when species are best able to track fluctuations in the local environments. This occurs when dispersal rates are intermediate; dispersal rates must be high enough to allow species to track changes in environment, but not so high that mass effects homogenize the metacommunity, reducing it effectively to a single patch (Mouquet and Loreau 2003). Intermediate dispersal rates promote multifunctioning because they ensure that biodiversity is preserved at both spatial scales. However, having high biodiversity alone is not sufficient for the production of multiple functions. Conditions must also be favourable for these species to be productive (Isbell et al. 2012). This is the reason that multifunction is not simply a function of the diversity of the community (Fig. 4-2b). Dispersal mediates the shape of this diversity multifunction relationship because it determines whether or not species are found in environmental conditions where they are most productive across the metacommunity.

We find that in general a greater number of functions can be sustained at the regional scale than at the local scale (Fig. 4-3), which is consistent with findings from empirical systems (Zavaleta et al. 2010, Pasari et al. 2013). However, the same dispersal rates optimize multifunction locally and regionally, suggesting that it is possible to manage for multiple ecosystem functions across from the local to the metacommunity scale. There are differences in the specific dispersal rates that optimize multifunction at each scale, and these depend on the threshold for production and the functional overlap amongst species in the community, but when multifunction is high locally, it tends to be high regionally as well. The exception to this is when dispersal rates are low enough that each local community only contains a single species, and especially when species are functional specialists. In this case, the number of functions produced in each patch is low, but because the functions produced differ between patches, a greater number of functions are produced at the regional scale. However, the number of functions produced in this case is never as high as when dispersal rates are intermediate, and multifunction is maximized at both scales. Intermediate dispersal rates are required to track fluctuating environmental conditions across the metacommunity. This suggests that regional multifunctionality is best produced in regions where patches contain a diversity of species and are connected by dispersal, rather than where each patch is maintained as a different monoculture.

Dispersal mediates an important trade-off; dispersal rates that allow for the high production of a few functions tend to be lower than the rates that allow for the production of many functions (Fig. 4-1b vs. Fig. 4-3). This is because the production of an individual function is maximized when dispersal rates are high enough to allow species persistence in all patches, but not so high so that they are present in high abundances when conditions are not favourable (a strong source-sink effect). In general, only the few functions produced by the species that is currently favoured by prevailing environmental conditions will exceed high thresholds for production. Higher, but still intermediate, dispersal rates result in more even local community abundances (Fig. 4-1a), which produce more functions at the expense of the functions produced by the dominant species. Maestre *et al.* (2011) found that community evenness decreased multifunctioning, where multifunction was calculated as the average proportion of the maximum function across all functions. In our case, this calculation corresponds to the average production of each function, and we see that higher multifunction is achieved over the lower range of the intermediate dispersal rates when the community is less even. This highlights the value of the multiple threshold approach for calculating multifunctioning, because it shows how dispersal affects different aspects of multifunctioning (Byrnes et al. 2014).

The full set of functions is only produced at our lowest thresholds of production, when species overlap greatly in the functions they contribute to, and dispersal rates are intermediate (Fig. D-6, Fig. 4-3). Although all functions can be produced simultaneously when thresholds are equal or less than one, this cannot be sustained through time. Communities with high overlap between species are able to produce more functions than communities comprised of function specialists, but this comes at the cost of producing each function in high amounts (Fig. 4-3). This result arises because we assume that all species have equal total production across all functions. Because of this, generalist species will necessarily produce less of a function than species specialized on producing only that function. In nature, the degree of overlap amongst species in how they contribute to distinct functions varies greatly between communities and between taxonomic groups (Hector and Bagchi 2007, Gamfeldt et al. 2008). Our results suggest that more research is needed to understand how this might affect the production of multiple ecosystem functions.

Because dispersal plays a strong role in determining community composition (Loreau et al. 2003, Gonzalez et al. 2009), changing the dispersal rate also results in a shift in which functions are produced in a given location (Fig. 4-4). This emphasizes how regional processes shape ecosystem multifunctioning, even at local scales, and suggests that landscape fragmentation and other processes that affect the connectivity of metacommunities will have consequences for number and identity of ecosystem functions produced in local habitat patches. This extends the idea of extinction debts to function debts whereby loss of connectivity result in the long-term loss of multiple ecosystem functions (Gonzalez and Chaneton 2002, Gonzalez 2013, Isbell et al. 2015).

The spatial insurance hypothesis predicts that community productivity is stabilized by intermediate dispersal rates (Loreau et al. 2003, Gonzalez et al. 2009), here we show that locally this is not the case for individual functions (Fig. 4-1c), or the number of functions produced (Fig. 4-5). The stabilizing effect of dispersal on overall productivity is the result of turnover in community composition as the local environmental conditions change. But, when species differ in the identity and the amount of each function they contribute to, the result is high local variability in the production of each function. This variability is reduced as the degree of functional overlap between species increases (Fig. 4-1c) because each function can be produced under a greater range of environmental conditions. Local compositional turnover also results in temporal variation in the number of functions that are simultaneously produced because species differ in how they allocate their overall production to each individual function. Consequently, we see the greatest variability in the number of local functions at intermediate dispersal rates (Fig. 4-5), except for at low thresholds when functional overlap is high. In this case, we see the greatest variability at low dispersal rates when each community contains a single species and the number of functions that exceed low thresholds varies greatly as the productivity of these generalist species fluctuates in response to changes in the environment. Overall, at the local scale, dispersal mediates a trade-off between producing high rates of multiple functions, and producing stable and reliable rates of multiple functions at the local scale.

However, this production-stability trade-off does not extend to the regional scale (Fig. 4-5). Once dispersal rates are high enough that the number of immigrants is sufficient to form a viable population (i.e. exceeding the extinction threshold), the regional production of each function and the number of functions produced becomes increasingly stable with increasing dispersal rate. By tracking changes in the local environment, each species is able to maintain a constant production of functions at the regional scale. Our model assumes that the regional environment does not fluctuate and so we see no variation in regional production of functions. These results are consistent with the suggestion that the stable production of individual functions is more easily obtained at regional scales, because rates of local production are sensitive to environmental fluctuations (Zavaleta et al. 2010, Isbell et al. 2012). This is especially true in metacommunities when dispersal rates allow species to track local fluctuations in environment. Our results highlight a trade-off in local vs. regional multifunction stability that is relevant for management of multiple ecosystem functions.

Our model has allowed us to isolate the role of dispersal in maintaining multifunctionality in changing environments. Coexistence in this model relies on dispersal (Chesson 2000a, Loreau et al. 2003, Gonzalez et al. 2009), but other coexistence mechanisms such as specialization on different resources (Tilman 1990), non-linear responses to environmental change (Armstrong and McGehee 1976, Levins 1979), or temporal storage effects (Chesson 2000b) might also allow for ecosystem multifunctionality. Future work on these other mechanisms would be valuable. The asynchrony of the local environmental fluctuations ensures strong spatial insurance in our model. However, spatial insurance will occur whenever there is dispersal, species differ in their response to differences in environment, and environmental conditions are not perfectly synchronous in space (Gonzalez et al. 2009). We have also shown that spatial insurance is very robust to variation in the number of species, patches, and functions modelled (Appendix D; Fig. D-1 – D-5). Our model does not explicitly specify the covariance between the functional traits, nor do we specify covariance between the functional traits and the traits for the species environmental optima. Further research is needed to understand how trait covariance might affect ecosystem multifunctionality, given that functionally unique species contribute disproportionately to the production of multiple functions (Mouillot et al. 2011).

Our results illustrate how the regional connectivity, and the movement of organisms between local communities can affect the production of multiple ecosystem functions. Recent experimental results from the lab and the field strengthen this conclusion (Tewksbury et al. 2002, Brudvig et al. 2009, Staddon et al. 2010, Chisholm et al. 2010, Thompson and Shurin 2012). This has important implications for the management of landscapes for multiple ecosystem functions and services. Regardless of whether the focus is local or regional, connectivity and the diversity of patches in the landscape should be valued, as this allows multifunctioning to be maintained when local conditions change. The loss of habitat worldwide is increasing landscape fragmentation (Millennium Ecosystem Assessment 2005, Fischer and Lindenmayer 2007, Haddad et al. 2015) making movement and dispersal more difficult (Collingham and Huntley 2000). Our results suggest that conservation strategies that preserve landscape connectivity (Bunn et al. 2000, Estrada and Bodin 2008, Rayfield et al. 2011) and designing landscapes as connected networks of ecosystems (Opdam *et al.* 2006) will maintain multiple ecosystem functions at local and regional scales (Gonzalez *et al.* 2011). This is especially important as local environmental conditions are becoming increasingly variable as a result of climate change (IPCC 2013). Connectivity is expected to mediate the provisioning of ecosystem services but relatively little data is available to ground theory at this time (Mitchell et al. 2013, 2015). The strong effects of dispersal in the production and stability of multiple ecosystem functions we find suggests that landscape connectivity is a critical feature for landscape management.

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CONNECTING STATEMENT

In Chapters 3 and 4, I focused on the ability for dispersal to provide spatial insurance in regional scale metacommunities. At this scale, habitat patches are in close enough proximity so that they do not span large climatic gradients. In Chapter 4, all habitats fluctuated around the same mean environmental value, while in Chapter 3, all patches in a single metacommunity experienced the same temperatures. At this scale, I found that directional warming synchronized the metacommunity, and the stabilizing effect of dispersal was lost.

In Chapter 5, I consider the role of dispersal in larger landscapes experiencing warming. At this scale, habitats are spread out over climatic gradients, with cooler patches at higher elevations and latitudes and warmer patches at lower elevations and latitudes. Because of this, species will differ in their response to warming depending on where on the landscape they are present, and dispersal can allow them to track directional change by shifting their ranges on the landscape. Yet, biotic interactions can restrict the ability for species to successfully colonize new habitats even if the climate is suitable, and this leads to uncertainty in our predictions of the composition of ecological communities under future climates. In Chapter 5, I consider how biotic interactions and the rate at which species disperse interactively affect the predictability of multispecies range shifts under climate warming at landscape scales.

5. CONNECTIVITY MAKES FUTURE COMMUNITIES MORE PREDICTABLE UNDER CLIMATE CHANGE

This chapter is in preparation for submission to an academic journal: Patrick L. Thompson & Andrew Gonzalez. *Nature Climate Change*.

The future distribution of biodiversity under climate change will depend on whether species can disperse fast enough to track changes in their climate niches and on the network of species with which they interact (Gilman et al. 2010, Boulangeat et al. 2012). Landscape fragmentation from human land use is restricting dispersal (Collingham and Huntley 2000, Haddad et al. 2015), and shifts in the complex spatial networks of biotic interactions are hard to predict (Gonzalez et al. 2011). This dual source of uncertainty hinders easy prediction of future biodiversity (Davis et al. 1998, Araújo and Luoto 2007, Urban et al. 2013, Svenning et al. 2014). We expect that the degree of uncertainty caused by biotic interactions will depend on the rate at which species disperse across changing landscapes. Here, we show that biotic interactions, both positive and negative, cause species to differ in the speed at which they track climate change, resulting in altered extinction sequences and the assembly of novel communities. However, our uncertainty is minimized when dispersal rates are great enough that resident populations cannot easily repel colonizing species better suited to the current climate. These results suggest that managing landscapes for connectivity will allow communities to respond predictably to climate change by shifting in elevation and latitude.

To keep pace with climate change in the 21st century, species will have to disperse an average of 0.42 km per year (Loarie et al. 2009). Already we are witnessing shifts in species distributions to higher altitudes and latitudes (Parmesan and Yohe 2003), but estimates suggest that climate change will result in the extinction of many species, especially those with limited dispersal ability (Thomas et al. 2004). Species must disperse to new habitats to keep pace with climate change, but because of human land use change, they are doing so in landscapes that are increasingly fragmented (Haddad et al. 2015). Habitat fragmentation restricts the movement of organisms and makes species more vulnerable to climate change (Collingham and Huntley 2000, Opdam and Wascher 2004).

Bioclimatic envelope models are used to make predictions about the distribution of species and the composition of communities under future climates by correlating current distributions with climatic variables to define a climate niche that is then used to map future distributions under projected climate scenarios (Elith and Leathwick 2009, Araújo and Peterson 2012). However, the accuracy of these models has been questioned because they rarely take into account realistic dispersal scenarios or complex networks of biotic interactions (Davis et al. 1998, Heikkinen et al. 2006, Brooker et al. 2007, Araújo and Luoto 2007, Urban et al. 2013).

Biotic interactions such as competition, mutualism, parasitism, and predation affect patterns of extinction and colonization and so create uncertainty in bioclimatic envelope predictions (Davis et al. 1998, Brooker et al. 2007, Van der Putten et al. 2010, Urban et al. 2013). Competition can slow climate tracking by preventing colonization of new patches, even if conditions would otherwise be favourable to growth (Urban et al. 2012). Positive interactions such as mutualism can facilitate colonization (Spasojevic et al. 2014) but can also hinder colonization if the facilitating species is not present in the new habitat (Gilman et al. 2010). In food webs, trophic interactions can become decoupled if predators and prey do not shift their ranges at the same rate (Van der Putten et al. 2010). Furthermore, biotic interactions can act as multipliers, increasing the risk of extinction from climate change (Norberg et al. 2012), especially in food webs (Zarnetske et al. 2012). Together, biotic interactions are expected to disrupt current associations between species and climatic variables, resulting in ‘no-analogue’ communities, that is, combinations of species that do not currently occur (Gilman et al. 2010, Urban et al. 2012).

We have a limited understanding of how habitat fragmentation, which alters dispersal, interacts with biotic interactions to affect range shifts (Gonzalez et al. 2011). Although the degree to which biotic interactions mediate the composition of no-analogue communities has been shown to depend on dispersal (Urban et al. 2012), we do not know how dispersal and biotic interactions combine to affect the predictability of range shifts across entire communities with networks of mixed trophic interactions. There is a considerable need to improve our ability to predict the diversity and composition of communities in the future, in part because changes in diversity and composition will have consequences for the supply of ecosystem services that are vital to human wellbeing (Cardinale et al. 2012).

Here, we evaluate the interactive effect of dispersal and biotic interactions on the predictability of multi-species range shifts in response to climate warming. We simulate a landscape of 200 habitat patches, spanning a temperature gradient and occupied by 80 species. The abundance and distribution of these species is governed by their species-specific temperature optima, their intrinsic rate of growth, their interactions with other species, and their dispersal between patches in the landscape (see methods). We compare four community interaction scenarios: 1) no interspecific interactions; 2) only competitive interactions; 3) mixed interactions – competition, mutualism, and parasitism; and 4) a food web with three trophic levels.

We simulated these communities over a range of dispersal rates, which define the proportion of biomass of each species that disperses in each time step. Dispersal was assumed to decrease exponentially with the distance between patches. After allowing the communities to reach equilibrium, we simulated a gradual increase in temperatures across the landscape. We predicted that the composition and abundance of the community in a warmed patch would match that of the patch with the same temperature prior to warming (Fig. 5-1). The 50 warmest and coolest patches were excluded from our predictions because their abundances are affected by edge effects that arise from the way that we model dispersal. We measured prediction accuracy as the average Bray-Curtis similarity between the predicted and realized communities, but our results hold for other measures of accuracy (Appendix E; Fig. E-1). Bray-Curtis similarity quantifies the multivariate similarity of the predicted and realized communities, ranging between 0 (no accuracy) and 1 (perfect accuracy)(Fitzpatrick et al. 2011).

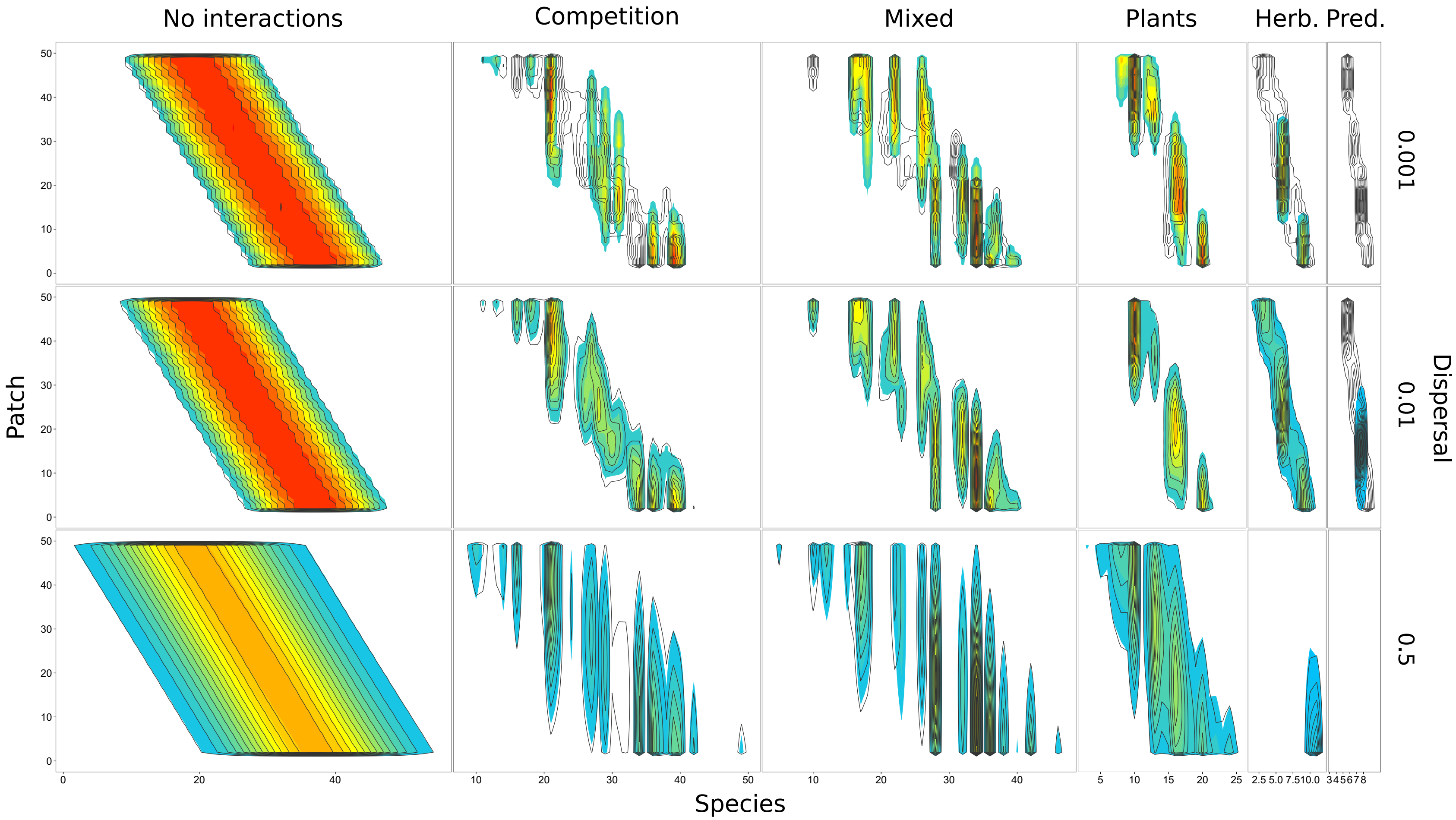

Figure 5-1. The predicted (black contours) vs. realized (coloured contours) distributions of species in the 4 community interaction scenarios (columns), over three representative dispersal rates (rows). The number of contours (predicted) and the temperature of the colour (realized) indicate the abundance of each species in each patch. One replicate draw of species interaction values is shown.

Biotic interactions and the rate of species dispersal interactively determine the abundance and distribution of species prior to, during, and following warming (Fig. 5-1). Without interspecific interactions, distributions follow a predictable pattern that is determined by temperature tolerances. Interspecific interactions greatly alter these distributions. Negative interactions (e.g. competition, top down effects of predation or parasitism) restrict ranges and can even prevent persistence (e.g. Fig. 5-1 – species 23, competitive interactions), while positive interactions (mutualism, commensalism, bottom up affects of predation or parasitism) can potentially extend ranges (e.g. Fig. 5-1 – species 28, mixed interactions). Dispersal also extends ranges through source-sink effects, allowing persistence in patches where populations would otherwise not survive. Biotic interactions and dispersal affect species' distributions because they interact to affect abundances. Therefore, changing the dispersal rate can result in different species persisting, even though the interactions are unchanged (e.g. Fig. 5-1 – sp. 20, mixed interactions). Because of this, dispersal and biotic interactions also mediate the way in which species shift their ranges in response to climate warming.

We find that dispersal and biotic interactions interact to determine how well climate envelope predictions match realized distributions and community compositions. Without interspecific interactions, the realized distributions closely match our predicted distributions (Fig. 5-1), and our predictions are accurate except when dispersal rates are so low that species are unable to track the warming temperatures (Fig. 5-2a,b). However, when species interact with one another, the realized distributions deviate from our predictions, and the degree to which they do so depends on the dispersal rate. Prediction accuracy, for communities with all interaction types, has a unimodal relationship with dispersal, peaking when dispersal rates are intermediate (Fig. 5-2a.b).

Biotic interactions result in differences in how easily species colonize new habitats to track changes in climate, and this unimodal relationship occurs because the dispersal rate affects how large these differences are (Fig. 5-2c,d). Differences in colonization ability cause extinctions and

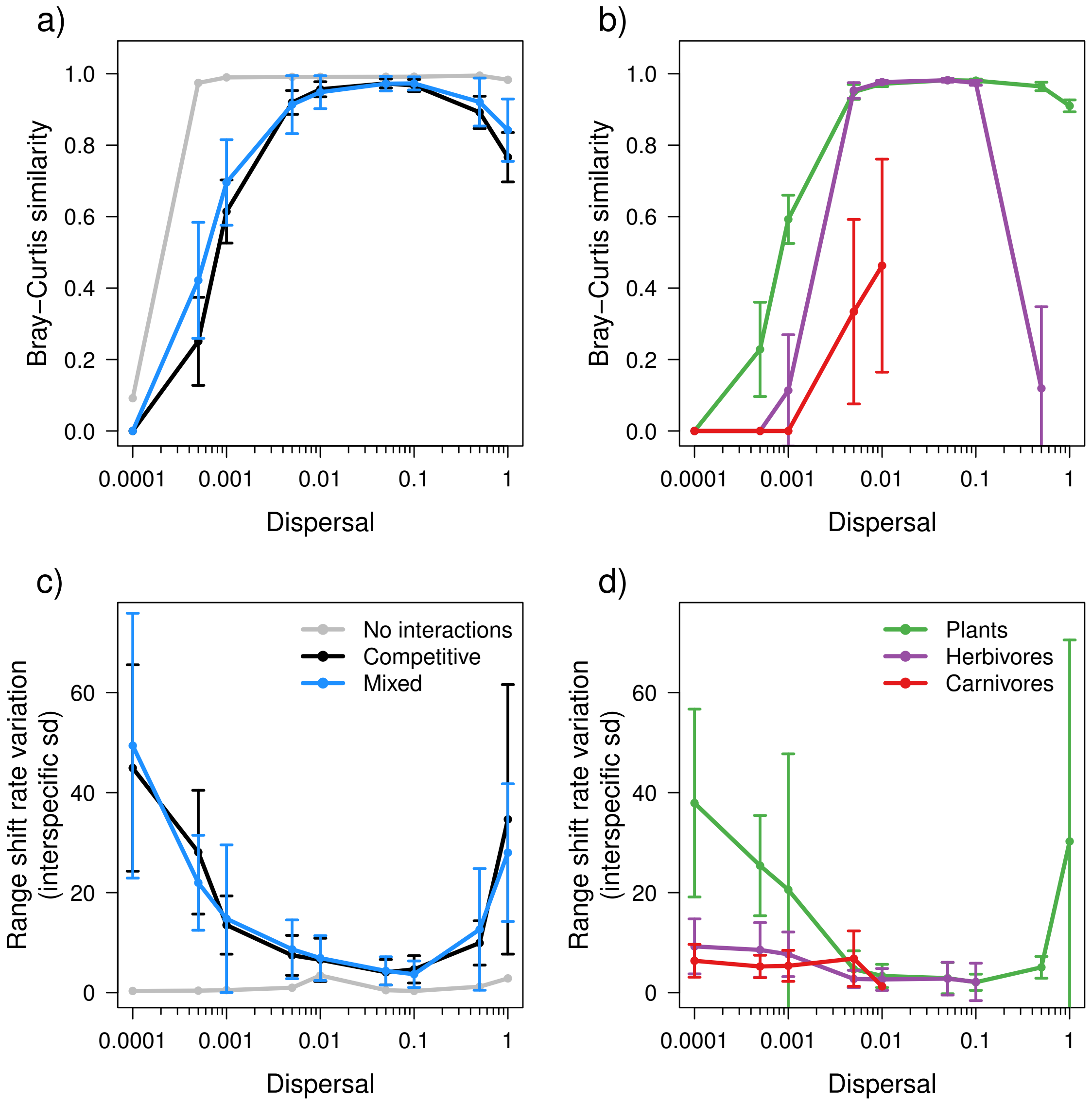

Figure 5-2. The relationship between the rate of dispersal and prediction accuracy (Bray-Curtis similarity; a, b) and interspecific variation (standard deviation) in range shift rates (c, d). Panels a and c show this relationship in communities with no interactions (grey), competitive interactions (black), and mixed interactions (blue). Panels b and d show this relationship across three trophic levels. One standard deviation around the mean, based on 50 replicates is shown.

turnover in the species that co-occur, both of which lead to 'no-analogue' communities. We can visualize this turnover by comparing how local networks of biotic interactions are altered as they track the changing climate (Fig. 5-3, Fig. 5-4). When dispersal rates are intermediate, these local networks of biotic interactions remain largely intact, but at lower and higher dispersal rates there is great turnover in the species that are interacting.

Differences in colonization ability are high when dispersal is low because only a small number of individuals arrive as potential colonists (Fig. 5-2c,d). The larger populations of resident species can easily repel these individuals, even if the colonists are better suited to the current environment. Therefore, at low dispersal rates the ability to colonize a new habitat is greatly determined by how each individual species interacts with the resident species. At higher dispersal rates, colonists arrive in greater abundance and so are less easily repelled. Therefore, the current environmental conditions have a greater influence on which species are able to persist. This minimizes the interspecific differences in the ability for species to colonize new habitats, allowing communities of co-occurring species to track the changing climate together. However, when dispersal rates are very high, emigration reduces local populations and spreads them out across the landscape. Colonists on the leading edge of the shifting range are further away from their environmental optima, as are many of the resident species. Here, again, biotic interactions become a larger determinant of the species that are successful, and this leads to differences between species in their ability to track climate change, which causes greater turnover in species co-occurrence.

All types of biotic interactions reduce the accuracy with which we predicted range shifts, but this was most pronounced for food web interactions at higher trophic levels (Fig. 5-2b). Higher trophic levels are only able to track climate change when their prey are in sufficient abundance in the habitats that they are colonizing. Climate change reduces population sizes when dispersal rates limit range shifts, and so higher trophic levels cannot survive range shifts when dispersal rates are lower. Likewise, when dispersal rates are too high, source-sink effects reduce population sizes and higher trophic levels cannot persist, even in stable climates. Therefore, the range of dispersal rates that allow species to persist becomes narrower as trophic level increases. Top

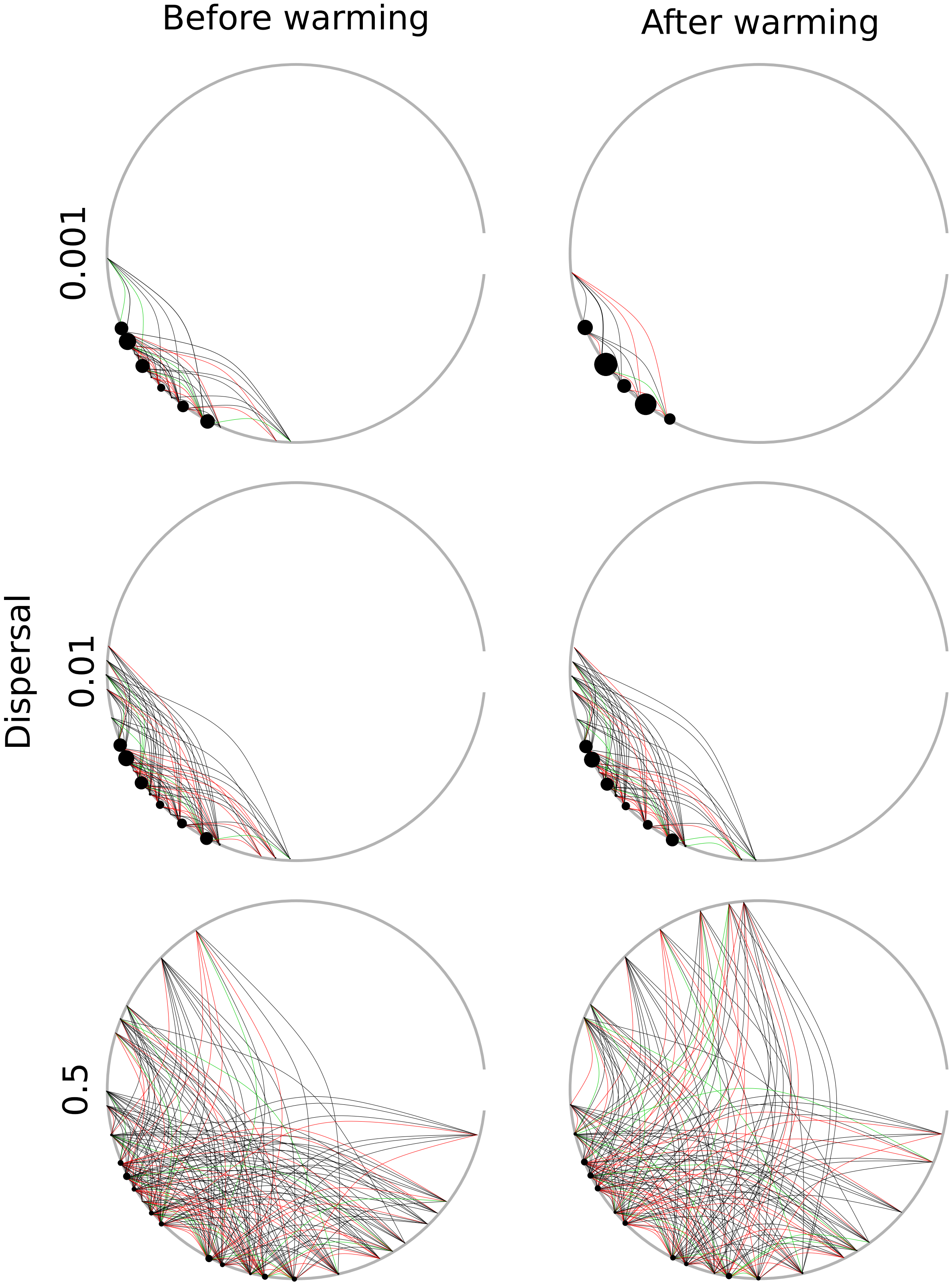
Before warming
After warming
Dispersal
0.001
0.01
0.5

Figure 5-3. A comparison of a local network of biotic interactions (mixed) before and after warming (columns), over three representative dispersal rates (rows). The local network from patch 100, prior to warming, and patch 150, which has the corresponding climate after warming are shown here. Species are shown as the nodes around the ring (ordered clockwise by temperature optima starting from the right hand break in the ring), and their interactions are represented as the color of the connecting lines (black = competition, green = mutualism, red = parasitism). Species abundances are represented by the size of the nodes.

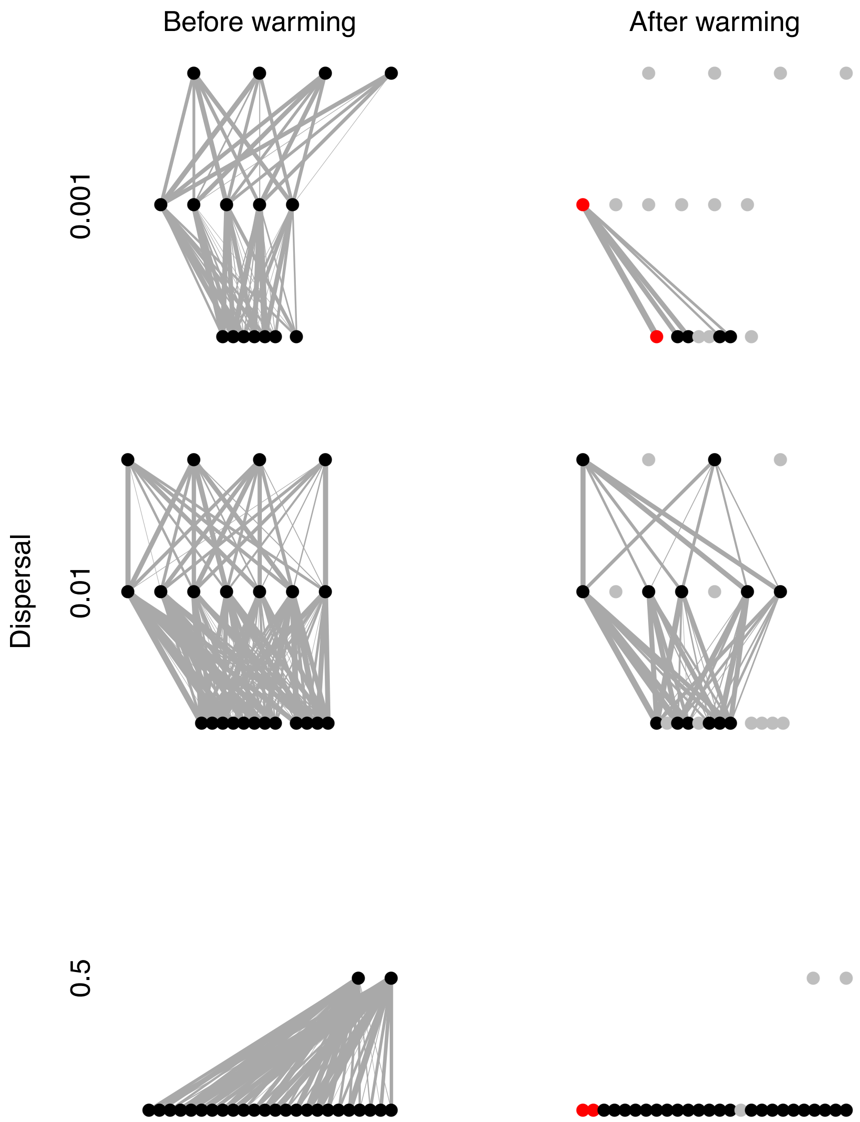

Figure 5-4. A comparison of a local network of biotic interactions (foodweb) before and after warming (columns), over three representative dispersal rates (rows). The local network from patch 100, prior to warming, and patch 150, which has the corresponding climate after warming are shown here. Species are shown as the nodes in the food web with trophic links represented by the grey links. In the food webs after warming, black nodes represent species that were present in the corresponding community prior to warming, grey nodes represent species that were lost, and red nodes represent species that were not present in the pre-warmed community.

predators are known to be especially vulnerable to climate change (Voigt et al. 2003, Zarnetske et al. 2012). Our results suggest that their future distributions are also the most difficult to predict.

The rate of dispersal affects the type of inaccuracy in our predictions. The realized communities can deviate from our predictions in two ways: 1) species are predicted to be present but are not – false discovery rate, and 2) species are present in patches where they were not predicted – false negative rate. The false discovery rate indicates the degree to which species ranges are shrinking as they shift with climate change. False discoveries show an inverted unimodal hump with dispersal (Fig. E-2a,b) and are responsible for the unimodal relationship between prediction accuracy and dispersal (Fig. 5-2a,b). The false negative rate indicates when range shifts cause species to be present in conditions where they were not initially present. This occurs when range shifts alter the composition of the community associated with a given climate, allowing for the establishment of a new species. False negatives are most common when dispersal rates are limiting (Fig. E-2c,d) because these rates result in large interspecific differences in colonization ability (Fig. 5-2c,d), and species are only present in a portion of the patches in which they can potentially persist (i.e. without biotic interactions; Fig. 5-1).

Biotic interactions are known to make the order in which species go extinct as a result of a stressor unpredictable (Ives and Cardinale 2004), but we find the degree of this unpredictability depends on the rate of dispersal. Without interspecific interactions, extinctions occur in a predictable order, based on the temperature tolerances (Fig. 5-5a). Biotic interactions disrupt this order, and this is most pronounced when dispersal rates are lowest (Fig. 5-5b). Extinction orders are most disrupted by food web interactions, where predation greatly affects the response of prey species to warming (Fig. 5-5c). Food web interactions disrupt extinction orders most for lower trophic levels. This is consistent with the cascading disruption of lower trophic levels that often occurs when a top predator is lost (Zarnetske et al. 2012).

Our model of metacommunity dynamics provides insight into how biotic interactions and dispersal interact to affect the predictability of range shifts. These findings are robust to changing the overall strength of biotic interactions (Appendix E; Fig. E-3). They are also robust to

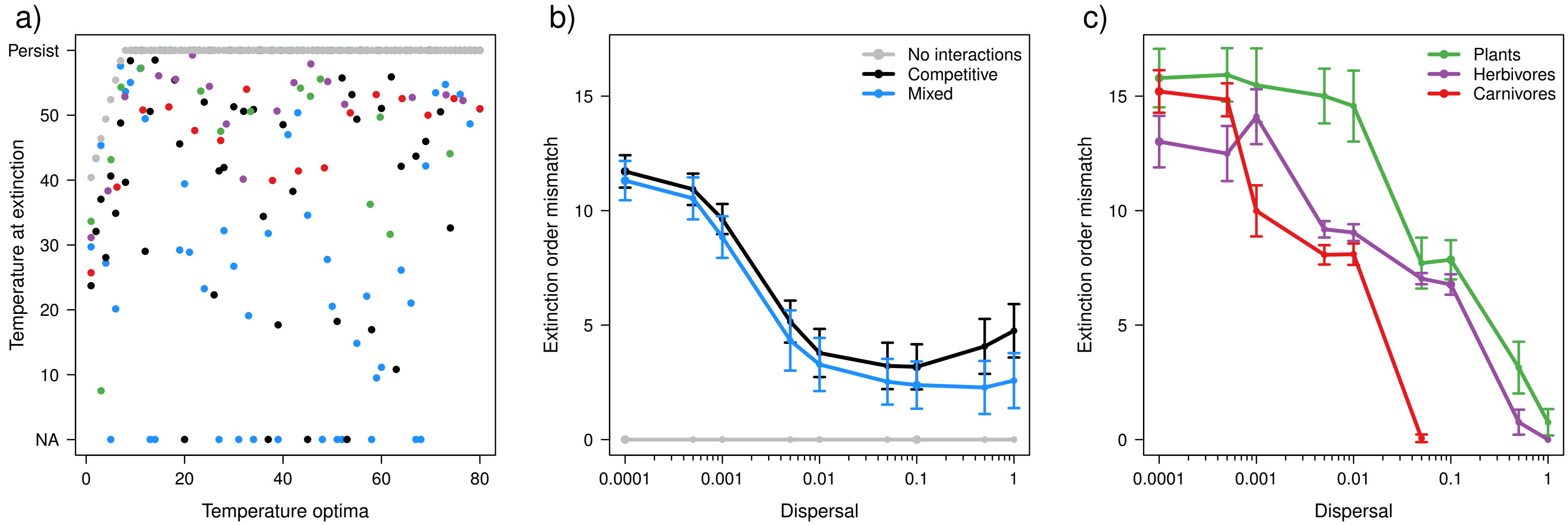

Figure 5-5. The temperature optima of each species vs. the temperature at which that species went extinct (a) in communities with no interspecific interactions (grey), competitive interactions (black), arbitrary interactions (blue), and food web interactions (green, purple, red) in a single replicate with a dispersal rate of 0.001. Species that went extinct before warming occurs are plotted as NA for temperature at extinction. Species that survived warming are plotted at persist on the x-axis. The summed mismatch order of this relationship across all species is shown over the range of dispersal rates for communities with the four interaction types (b) and across three trophic levels (c). One standard deviation around the mean, based on 50 replicates is shown.

incorporating more realistic community processes, such as interspecific variation in dispersal rate and climate niche breadth (Appendix E; Fig. E-4). However, our findings suggest that any process that results in variation in the ability of co-occurring species to colonize new habitats should decrease the accuracy of bioclimatic envelope predictions. Our model does not consider the effects of evolution (Norberg et al. 2012, Henry et al. 2013), mortality during dispersal (Eklof et al. 2012), variation in interspecific dispersal (Urban et al. 2012), or the direct effects of climate change on biotic interactions (Blois et al. 2013), but all of these processes are likely to affect the predictability of future communities.

Climate change and biotic interactions combine to make the future of ecological communities unpredictable, but our findings suggest that this unpredictability is minimized when dispersal is unimpeded. Globally, fragmentation is high and worsening in regions of the world expected to experience the greatest climate change impacts (Haddad et al. 2015). Habitat fragmentation will restrict dispersal, making it harder for species to track changes in climate (Collingham and Huntley 2000). We find that fragmentation will facilitate the formation of 'no-analogue' communities, making future communities unpredictable. Bioclimatic envelope models now have the potential to incorporate realistic dispersal scenarios and biotic interactions (Boulangeat et al. 2012, Thuiller et al. 2013), and we expect this will improve predictions. However, the conservation implications of our findings are clear: managing landscapes to preserve connectivity will greatly improve our ability to predict the structure of future ecological communities and help maintain the full diversity of interactions and species under future climates.

METHODS

Lotka-Volterra metacommunity model

Community dynamics and response to a changing environment were simulated using modified Lotka-Volterra equations (Ives and Cardinale 2004):

$$1)\quad X_{ij}(t+1) = X_{ij}(t)exp\left[C_i + \sum_{k=1}^{S} B_{ik}X_{kj}(t) + A_{ij}(t)\right] + I_{ij}(t) - X_{ij}(t)a$$

where $X_{ij}(t)$ is the abundance of species i in patch j at time t, C_i is its intrinsic rate of increase, B_{ik} is the per capita effect of species k on species i, $A_{ij}(t)$ is the effect of the environment in patch j on species i at time t, $I_{ij}(t)$ is the abundance of immigrating biomass of species i to patch j at time t, and a is the proportion of biomass that disperse in each time step. The metacommunity consists of M patches and S species.

We assume that the patches are equally spaced across a linear environmental gradient and that the species environmental optima H_i within each trophic level are equally distributed across the initial conditions $E_j(t = 1)$ in the metacommunity. The effect of environment in patch k at time t on species i follows a Gaussian function such that:

$$2)\quad A_{ij}(t) = h - \left[h\, exp\left(-\frac{\left(E_j(t)-H_i\right)^2}{2\sigma^2}\right)\right]$$

where h is a scaling parameter, $E_j(t)$ is the environment in patch j at time t, and σ is the standard deviation of the Gaussian function.

We assume that the abundance of immigrants to patch j from all other patches is governed by:

$$3)\quad I_{ij}(t) = \sum_{l \neq j}^{M} aX_{il}(t) exp\left(-Ld_{jl}\right)$$

where d_{jk} is the geographic distance between patches j and l and L is the strength of the exponential decrease in dispersal with distance. Individuals that disperse off the either edge of the metacommunity are reflected back so that all patches have the same potential to receive immigrants.

Range shift simulations

We simulated metacommunities consisting of $M = 200$ patches and $S = 80$ species with the following parameters: $X_{ij}(t = 1) = 10$, $C_i = 0.05$, $h = 300$, $\sigma = 50$, and $d_{1,200} = 200$. Species interaction parameter values were modified from Ives and Cardinale (2004). We fixed intraspecific interaction values across species to isolate the effects of interspecific interactions. In the competitive communities, all values of intraspecific competition were set to -0.2 and values of interspecific competition were drawn from a uniform distribution [-0.15, 0]. In the arbitrary communities, all values of intraspecific competition were set to -0.2, 65% of the interactions were competitive (-/-), 25% were predator prey or parasitic (+/-), and 10% were mutualistic (+/+), following Ives and Cardinale (2004). Negative and positive interactions were drawn from uniform distributions [-0.15, 0] [0,0.075] respectively. In the tri-trophic communities, intraspecific interactions were set to -0.2 for plants and herbivores, and -0.15 for predators. Interspecific interactions were drawn from uniform distributions between 0 and -0.1 (competition between plants), -0.3 (the effect of herbivores on plants), 0.1 (the effect of plants on herbivores), -0.1 (the effect of predators on herbivores), and 0.08 (the effect of herbivores on predators). In the no-interactions community, intraspecific interactions were set to -0.2 and all interspecific interactions were set to 0. All values of B were scaled to the number of species in the simulations by dividing by ($0.33*S$). The rate of exponential decay in dispersal distance L was 0.3 except in the tri-trophic communities where it was set to 0.3 for plants, 0.2 for herbivores, and 0.1 for predators, so that dispersal distances increased with trophic level(Urban et al. 2013).

Simulations ran for a total of 7,000 time steps. The initial environment was a linear gradient from $E_1(t = 1) = 1$ to $E_{200}(t = 1) = 80$. The environment remained constant for the first 2000 time steps to allow the communities to reach equilibrium based on local conditions and competition. The environmental values in all communities were then steadily increased by 20 over the next 3000 time steps to simulate warming. The environment was held constant for the final 2000 time steps to allow the communities to reach to equilibrium in the warmer conditions.

We contrasted 9 dispersal rates, a, from 0.0001 to 1 that specify the proportion of the population moves in each time step. This was replicated 50 times for each community type, each time with a new randomly generated interaction matrix.

Response variables and analysis

All response variables were calculated using only the 100 central patches to avoid metacommunity edge effects. We used the initial species distributions and abundances, prior to environmental change (*t* = 2000), to predict abundances and distributions after change has occurred (*t* = 7,000). Our null hypothesis was that the community composition and abundances of the final communities would match the initial communities with the corresponding environments. We made predictions about the 50 coolest patches, where the final environments match conditions that were initially present in the 50 warmest patches.

We measured the accuracy of our predictions as the average Bray-Curtis similarity between the predicted and realized communities(Fitzpatrick et al. 2011) (see Appendix E for other measures of accuracy). Range shift variation was calculated as the interspecific standard deviation of the mean number of time steps between successful colonisations of new patches at the leading edge of the range shift.

The temperature at extinction was estimated for each species as the temperature in the coolest patch when it is lost from the metacommunity. We calculated the extinction order mismatch as the average absolute difference between the expected order of extinction, based on temperature optima and the realized order of extinction:

$$4)\quad Extinction\ order\ missmatch = \frac{\sum_{i=1}^{S}|H_i - D_i|}{S}$$

where D_i is the order in which species *i* went extinct from the metacommunity. Species that went extinct prior to the onset of warming were not included in this calculation because warming did not contribute to their extinction.

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6. SYNTHESIS, CONCLUSIONS, AND FUTURE DIRECTIONS

CONCLUSIONS AND CONTRIBUTION TO KNOWLEDGE

Landscape fragmentation restricts the ability for species to shift their distributions in response to climate change, and, together, these anthropogenic stressors are expected to greatly disrupt future ecosystems. Managing landscapes to maintain habitat connectivity is therefore the most commonly recommended strategy for preserving biodiversity under climate change (Heller and Zavaleta 2009). Yet, this strategy is largely based on the basic understanding that landscape connectivity will allow species to persist by tracking their climate niches. Effective management of landscapes requires a more detailed understanding of how altering connectivity affects the resilience of ecosystems to climate change. In particular, how does the rate at which species disperse between habitats affect the composition, stability, functioning, and predictability of ecological communities in changing environments? The spatial insurance hypothesis began to address this gap in our knowledge, demonstrating that the rate at which species disperse between habitats affects the ability of metacommunities to maintain biodiversity and produce new biomass at high and stable rates in changing environments (Loreau et al. 2003, Gonzalez et al. 2009).

Chapters 2 and 3 of this thesis build upon this work by demonstrating the potential for, and limitations of, spatial insurance in real metacommunities. In Chapter 2, I introduced the pond zooplankton metacommunity of Mont St. Hilaire, illustrating how the functioning of this metacommunity was determined by the composition, and not just the diversity, of species in each local pond. I showed how measures of functional and phylogenetic diversity, which are indicative of the functional differences between species (Díaz and Cabido 2001, Srivastava et al. 2012), explained more of the variation in ecosystem functioning than simple taxonomic measures of biodiversity. Similar patterns have been found in experimental plant communities (Cadotte et al. 2009, Flynn et al. 2011); however, this was one of the first studies to show that these measures of diversity were predictive of the functioning of complex multi-trophic communities in nature. I also demonstrated that different types of zooplankton diversity were responsible for different types of zooplankton functioning, that is, biomass production and top down grazing of phytoplankton. These results demonstrate how these measures of functional and phylogenetic diversity can help us to understand the consequences of biodiversity loss and compositional turnover on the functioning of natural multi-trophic ecosystems.

In Chapter 3, I conducted a mesocosm experiment using the pond zooplankton from Mont. St. Hilaire to experimentally test the spatial insurance hypothesis under realistic environmental change. Previous tests forced the local environments to vary asynchronously, thereby creating the ideal conditions for spatial insurance (Howeth and Leibold 2010, Steiner et al. 2011, 2013). However, regional metacommunities often experience environmental fluctuations that are synchronous across all patches (e.g. weather), but local communities differ because of variation in other types of environmental variables. In particular, it was unknown how directional change, such as climate warming, might affect the potential for dispersal to stabilize regional metacommunities. In this experiment, I showed how intermediate rates of dispersal between patches that differed in water chemistry and community composition resulted in spatial compensatory dynamics, which stabilized overall metacommunity biomass. However, warming synchronized these fluctuations in biomass, so that the stabilizing effect of dispersal was lost. This study empirically demonstrates how dispersal can stabilize metacommunities where the local environmental conditions are not forced to be asynchronous. It also demonstrates how directional environmental change, such as climate warming, has the potential to erode these stabilizing benefits by synchronizing dynamics across metacommunities. Together, these findings suggest that climate warming is likely to erode the potential for dispersal to provide stability to ecosystems against localized environmental variability.

A limitation of the spatial insurance hypothesis was that it assumed that all species within a metacommunity contributed equally to a single function (Loreau et al. 2003, Gonzalez et al. 2009). As we found in Chapter 2, communities produce multiple ecosystem functions, and species differ in the amount they produce. In Chapter 4, I extended the spatial insurance hypothesis to consider how dispersal mediates the production of multiple ecosystem functions in environmentally heterogeneous metacommunities. Previous studies had identified the strong positive relationship between community diversity and ecosystem multifunctionality (Hector and Bagchi 2007, Gamfeldt et al. 2008, Maestre et al. 2012). Here, I demonstrated that, in fluctuating environments, the shape of this diversity-multifunctionality relationship is clearly mediated by the rate at which species disperse between habitats. Changing this dispersal rate not only alters the number of ecosystem functions but also changes the functions that are produced in each local habitat and in the overall metacommunity. I showed that metacommunities connected by intermediate rates of dispersal tend to produce the most ecosystem functions, across spatial scales. Yet, while these dispersal rates ensure the stable supply of each function in the overall region, they result in high temporal and spatial variability of each function in the local habitats. This chapter provides a framework for understanding how dispersal and environmental heterogeneity mediate the multifunctionality of metacommunities, across spatial scales. These findings begin to addresses a key gap in our understanding of how landscape connectivity affects the multifunctioning of ecosystems, and the provisioning of multiple ecosystem services (Mitchell et al. 2013).

In Chapter 5, I demonstrated how biotic interactions and the rate at which species disperse interactively affect our ability to accurately predict the composition of communities in warming landscapes. It is widely acknowledged that biotic interactions and poor estimates of species dispersal create uncertainty in bioclimatic models that are used for predicting future species distributions (Davis et al. 1998, Araújo and Luoto 2007, Urban et al. 2013). However, how these two sources of uncertainty interact to produce no-analogue communities has rarely been studied (but see Urban et al. 2012, Norberg et al. 2012), and how this interaction affects the accuracy of our predictions was previously unknown. In this chapter, I showed how biotic interactions cause differences in the ability of species to colonize new habitats, resulting in no-analogue communities, which cannot be accurately predicted. However, when dispersal rates are high enough, resident populations cannot easily repel colonizing species that are well suited to the current environmental conditions. Therefore, when dispersal between habitats is unimpeded, current community assemblages are better maintained because species are able to track changes in climate at similar rates. These findings suggest that bioclimatic envelope models will provide the most accurate predictions when landscape fragmentation is limited. More importantly, from a conservation perspective, managing landscapes to limit fragmentation should minimize the disruption caused by climate change, allowing communities to shift to cooler climates as intact units. These results provide much a needed appreciation of how different levels of landscape fragmentation might affect response of ecosystems to climate change, moving us beyond the basic notion that more biodiversity will be preserved in connected landscapes (Heller and Zavaleta 2009, Baron et al. 2009).

FUTURE DIRECTIONS

Incorporating functional and phylogenetic diversity into the spatial insurance hypothesis

The patterns identified in the multifunction spatial insurance model in Chapter 4 depend on the degree to which species' functions overlap and whether individual functions are produced by species that differ in their environmental preferences. A logical next step would be to extend this model using functional traits or phylogenetic relationships between species. Functional traits and phylogenies are now widely available for many taxonomic groups and, as I demonstrated in Chapter 2, are informative of how species perform multiple ecosystem functions.

In my Chapter 4 model, I compared a range of levels of functional overlap and attributed functional traits randomly, with no relationship to the environmental optima of the species. Using functional traits from natural communities, or informing relationships between species using phylogenies, would give us more realistic estimates of how dispersal and environmental heterogeneity affect the multifunctioning of metacommunities. For example, if functional traits are correlated with the way species respond to environmental change, we would expect greater temporal variability in the production of individual functions. In addition, if patterns of trait distributions differ across taxonomic groups or ecosystem types, this would be informative for understanding how multifunctioning in different communities would be affected by environmental change or landscape fragmentation.

Spatial insurance and habitat loss in spatially explicit metacommunities

All current models of spatial insurance, including Chapter 4 of this thesis, model space implicitly, assuming that dispersal is equal between all patches in the metacommunity. Yet, real metacommunities are explicitly arranged in space, and this affects how organisms move between habitat patches. Habitat patches may vary in their proximity to other patches in the metacommunity, and dispersal is likely to be lower in patches that are isolated in space. Furthermore, because patches are not all equally connected, the strength of spatial insurance will be affected by the amount of environmental heterogeneity present in proximal patches. Further research is needed to understand how the pattern of metacommunity network structure affects the way communities respond to environmental change.

Using spatially explicit models can allow us to directly explore how habitat loss fragments landscapes and how this affects the dynamics and functioning of metacommunities. In collaboration with Bronwyn Rayfield and Andrew Gonzalez, I asked how the spatial pattern of habitat loss affects the robustness of the spatial insurance effects in fragmented regional metacommunities (Thompson et al. see Appendix F). In this paper, we modelled the ability of dispersal to provide spatial insurance in spatially explicit metacommunities as habitat patches were sequentially lost, resulting in the gradual fragmentation of the metacommunity. We found that the spatial insurance effects on biodiversity, productivity, and productivity stability are most sensitive to losses of patches with high betweenness centrality, that is, patches that were most important for maintaining connectivity within the metacommunity. These results suggest that conservation efforts should prioritize habitat patches with high betweenness centrality, as these patches facilitate the spatial insurance effects of biodiversity.

Spatial insurance in directionally changing environments

More research is needed to consider the role of spatial insurance in directionally changing environments. As I showed in Chapter 3, directional changes, like climate warming, that occur at the regional metacommunity scale, have the potential to erode spatial insurance effects by synchronizing population and community dynamics. However, if habitats span a large climate gradient, as in Chapter 5, dispersal allows species to shift their ranges and track their climate niches even though warming is directional and affects all habitats equally. This allows for spatial insurance, where the greatest biodiversity is retained when dispersal rates are intermediate, while productivity is highest and most stable when dispersal rates are intermediate to high (Fig. 6-1). I suggest that the spatial insurance hypothesis is more general than originally suggested (Loreau et al. 2003, Gonzalez et al. 2009); dispersal has the potential to provide spatial insurance in environments that are fluctuating or changing directionally. However, whether spatial insurance occurs in these situations will depend on the patterns of environmental heterogeneity and whether habitats are distributed over a gradient of the environmental variable that is changing. Further work is needed to formalize this theory, outlining the potential for, and limitations of, spatial insurance to provide stability and preserve biodiversity in the context of all types of environmental change.

OVERALL CONCLUSIONS

This thesis demonstrates how dispersal of species between habitats is a key process that mediates the response of ecosystems to complex environmental change. This work builds on the idea of spatial insurance (Loreau et al. 2003, Gonzalez et al. 2009), providing an empirical test (Chapters 2 & 3), incorporating multiple ecosystem functions (Chapters 2 & 4), extending spatial insurance to directionally changing environments (Chapters 3 & 5), and introducing its effect on community predictability (Chapter 5). As a whole, this thesis has advanced our knowledge of how spatial insurance occurs in natural ecosystems experiencing realistic environmental change. Still, more work is needed to understand the potential and limitations of this theory, especially where evolutionary processes are at play (Thuiller et al. 2013). However, these findings suggest that managing landscapes to maintain connectivity is a viable strategy for preserving the biodiversity, functioning, stability, and predictability of ecosystems in changing climates.

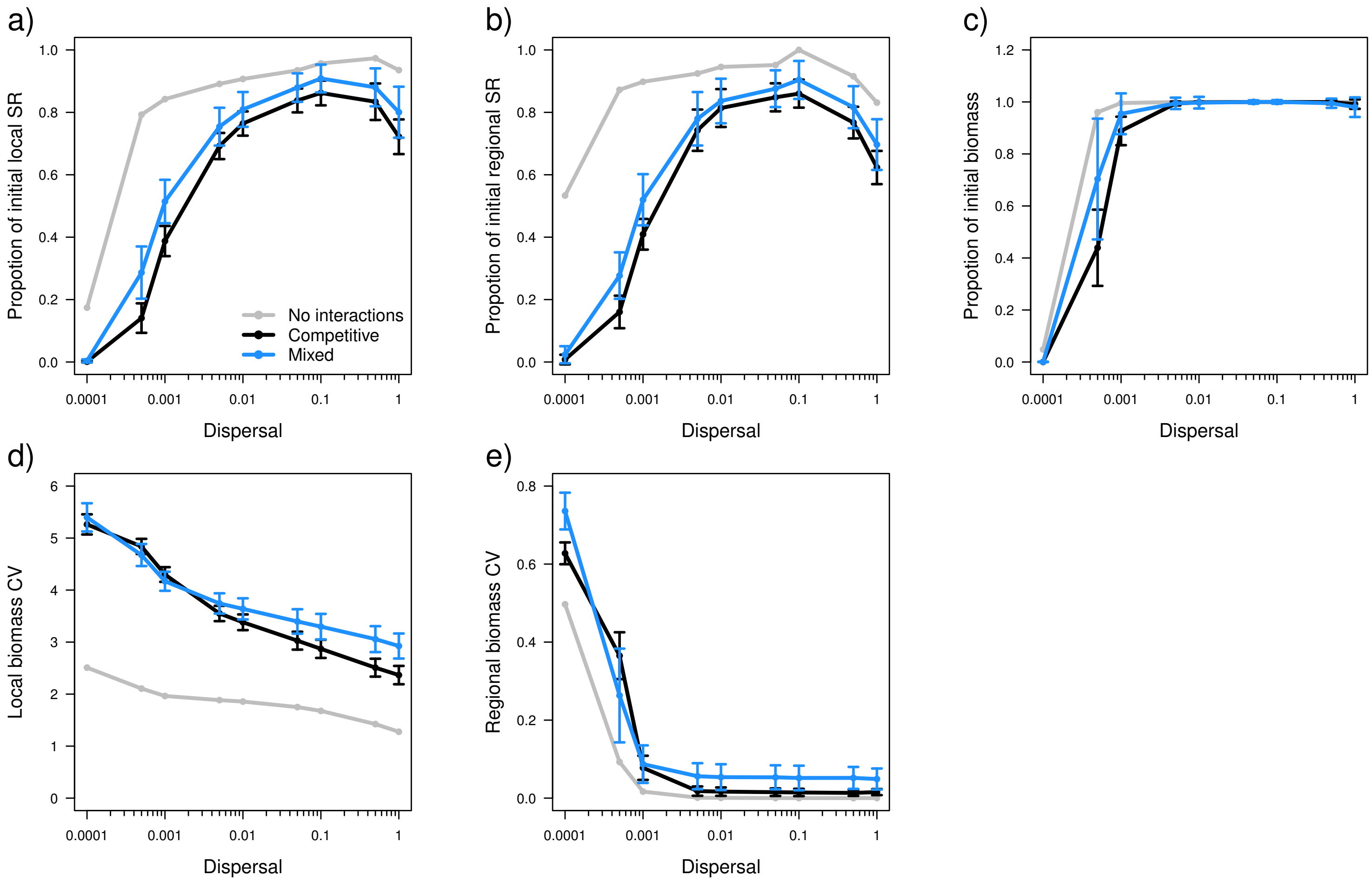

Figure 6-1. Spatial insurance in lanscapes durring directional environmental change. The relationship between the rate of dispersal and the proportion of initial species richness (a – local, b – regional) and biomass (c) that is retained after the range shift in the model from Chapter 5. Panels d and e show this relationship for the temporal variability (CV) of biomass during the range shift at local and regional scales. One standard deviation around the mean, based on 50 replicates is shown.

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APPENDIX A

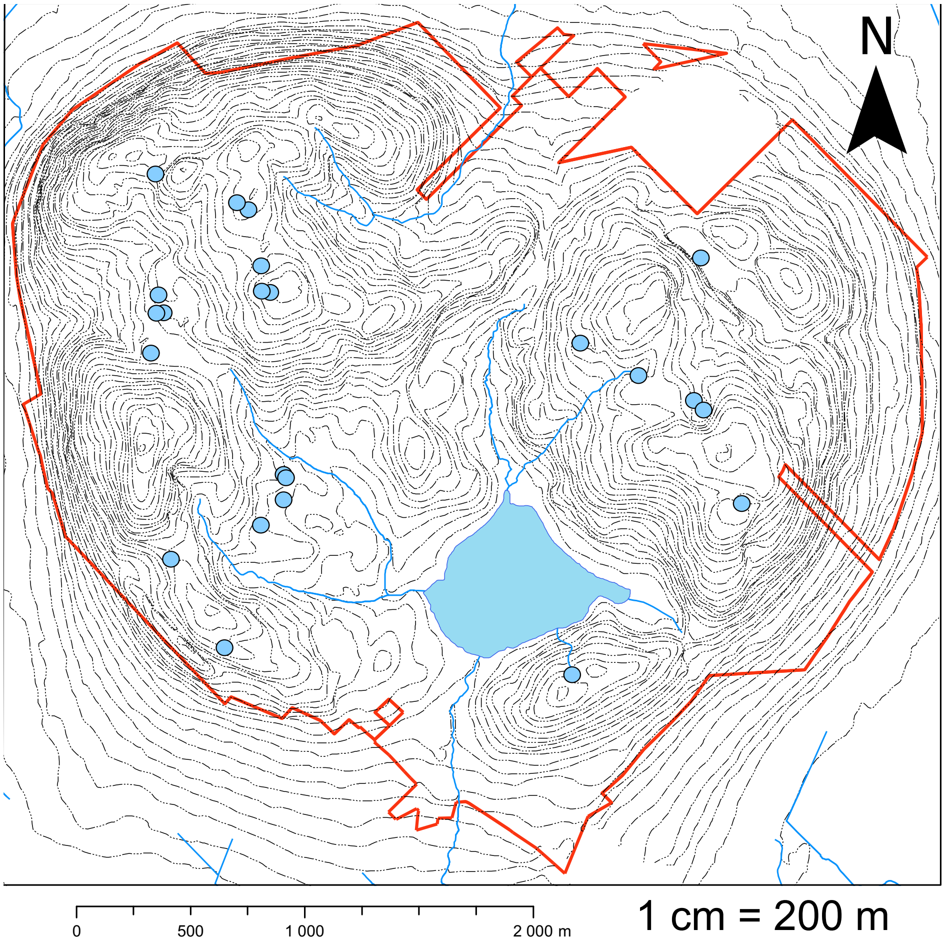

Figure A-1. The location of the 23 ponds on Mont St. Hilaire. The red outline marks the Gault Nature Reserve border. Map courtesy of Gault Nature Reserve.

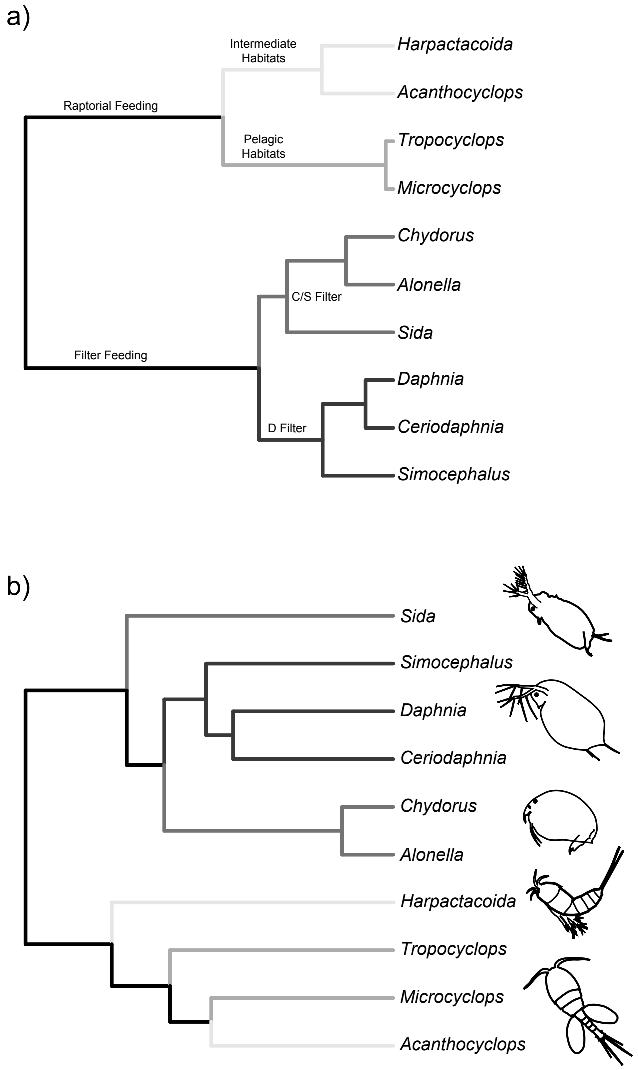

Figure A-2. Dendrograms indicating the functional (a) and phylogenetic (b) relationships between the zooplankton in the Mont St. Hilaire ponds. All five traits were used to create the functional dendrogram (a) and we have marked traits that divide clearly across the main functional bifurcations. The four functional groups selected from the trait dendrogram (a) are distinguished by shade and these are retained in the phylogenetic tree (b).

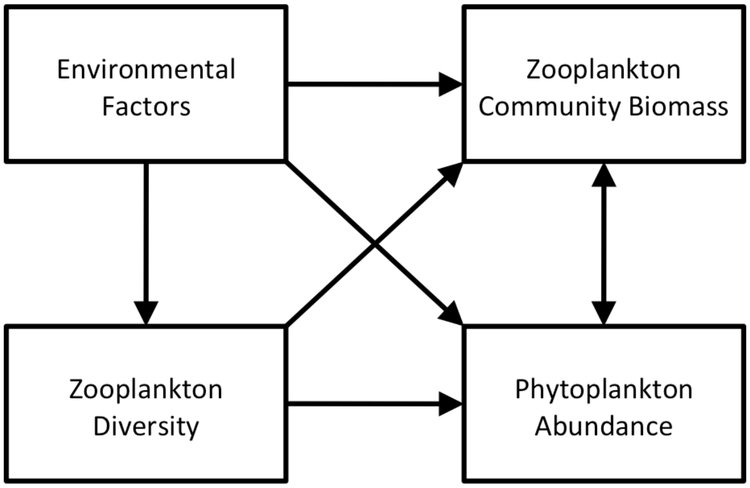

Figure A-3. The hypothesized paths by which zooplankton diversity and environmental factors could affect the two ecosystem functions. Note: because the link between phytoplankton abundance and zooplankton biomass is a trophic link, the direction of the arrow between these variables changes depending on which one we are trying to predict.

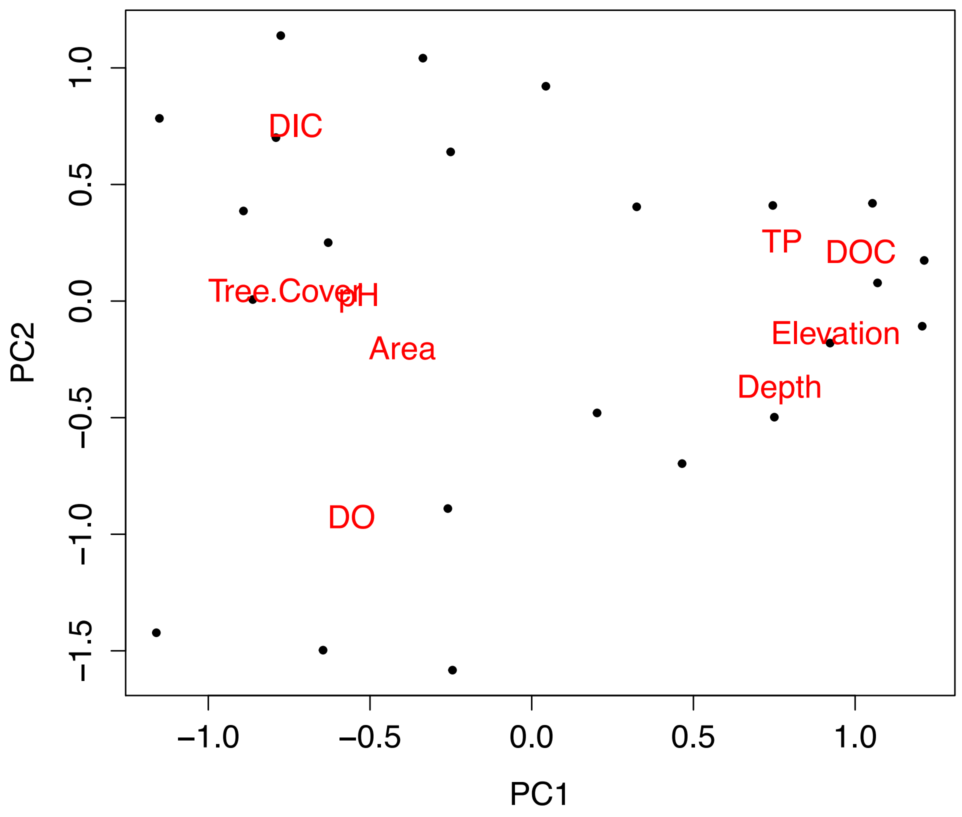

Figure A-4. PCA of the 9 environmental variables. The black dots mark the position of the ponds in multivariate environmental space. All variables were standardized to a mean of zero and a standard deviation of one prior to calculating the PCA.

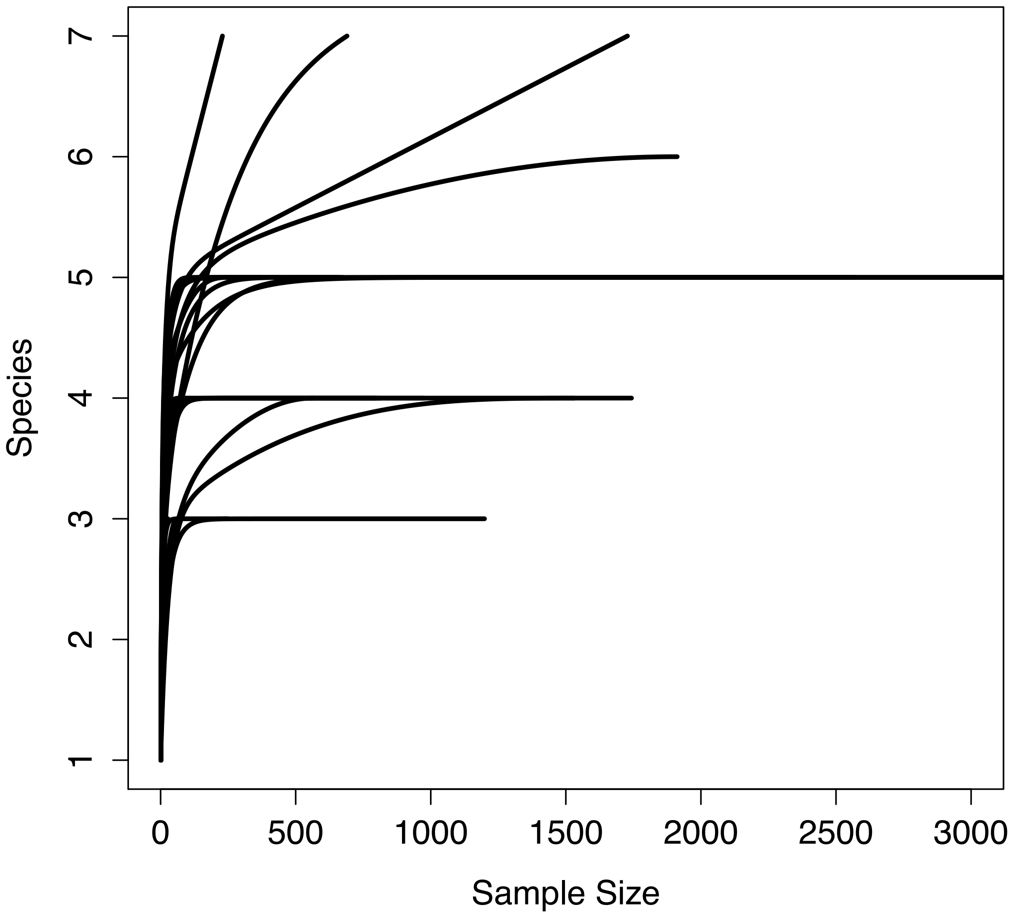

Figure A-5. Rarefaction curves estimating the relationship between species richness and the number of individuals identified in a sample for the 23 ponds.

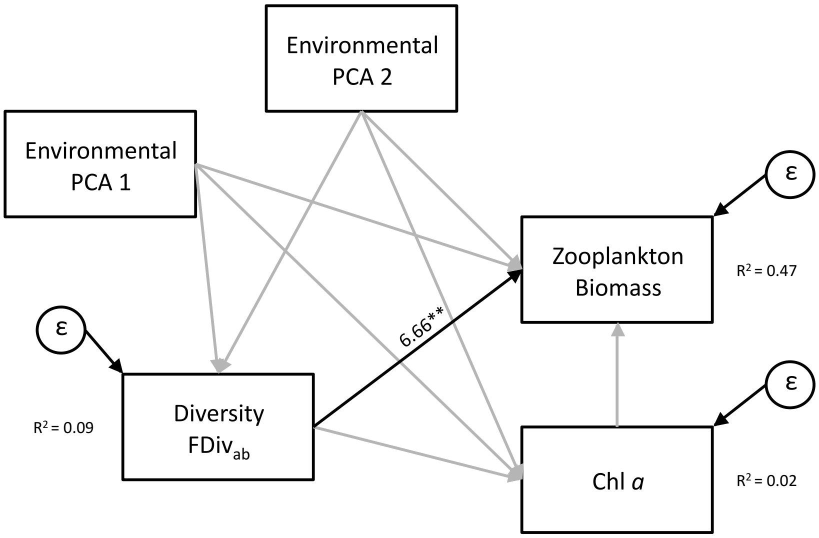

Figure A-6. Structural equation model to predict zooplankton biomass. This model is not the most parsimonious, but is shown because it includes all parameter types (zooplankton biomass, diversity, chlorophyll *a*, and environmental variables). Significant paths (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) and their unstandardized parameter estimations are shown in black. Non-significant paths are shown in grey. Epsilons indicate error in endogenous variables. This diagram demonstrates that diversity was the most significant predictor of zooplankton biomass and was retained as significant when pathways from the environmental variables were included, as was the case in all models.

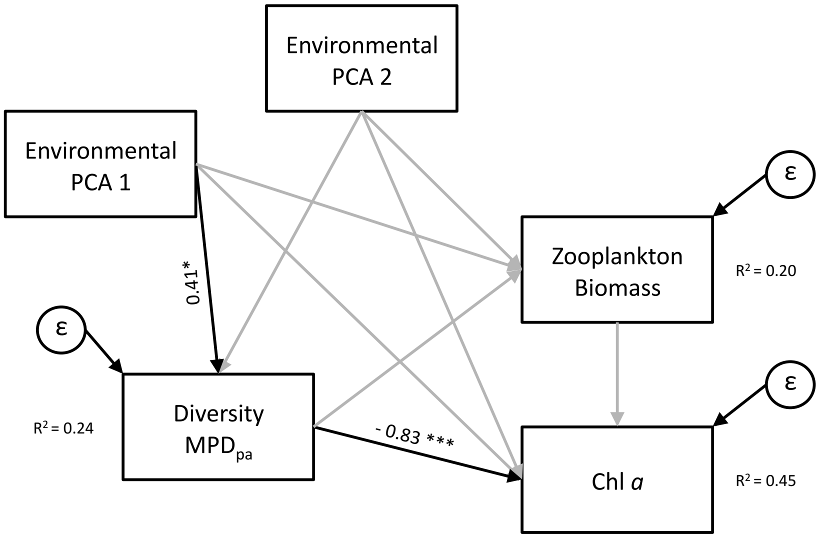

Figure A-7. Structural equation model to predict chlorophyll *a*. This model is not the most parsimonious, but is shown because it includes all parameter types (chlorophyll *a*, zooplankton biomass, diversity, and environmental variables). Significant paths (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) and their unstandardized parameter estimations are shown in black. Epsilons indicate error in endogenous variables. Non-significant paths are shown in grey. This diagram demonstrates that diversity was the most significant predictor of chlorophyll *a* and was retained as significant when pathways from the environmental variables were included, as was the case in all models.

Table A-1. Structural equation models for predicting zooplankton community biomass ranked in increasing order of AIC. Zooplankton community biomass (Z.bmass) and chlorophyll *a* (chl) were ln transformed. The environmental variables selected through multiple regression (Env) were elevation, DIC, and log TP. PCA refers to the first two axes of a PCA of all standardized environmental variables. The χ^2 test provides a test of how well the model fits the data. Models with *p*-values >0.05 are considered to be a reasonable fit to the data. Models are saturated when paths are specified between all variables and are considered to fit the data perfectly (Grace 2006).

	Model	AIC	χ^2	d.f.	*P* value
1	Z.bmass ~ FDiv_{ab}	37	0	0	saturated
2	Z.bmass ~ FDiv_{ab} + chl	103	0	0	saturated
3	Z.bmass ~ chl	146	0	0	saturated
4	Z.bmass ~ FDiv_{ab} + PCA FDiv_{ab} ~ PCA	151	0	1	1.000
5	Z.bmass ~ PCA	189	0	0	saturated
6	Z.bmass ~ FDiv_{ab} + PCA + chl FDiv_{ab} ~ PCA chl ~ FDiv_{ab} + PCA	221	0	1	1.000
7	Z.bmass ~ FDiv_{ab} + Env FDiv_{ab} ~ Env	234	4.03	2	0.134
8	Z.bmass ~ PCA + chl chl ~ PCA	261	0	1	1.000
9	Z.bmass ~ Env	272	0	0	saturated
10	Z.bmass ~ FDiv_{ab} + Env + chl FDiv_{ab} ~ Env chl ~ FDiv_{ab} + Env	304	4.03	2	0.134
11	Z.bmass ~ Env + chl chl ~ Env	342	4.02	2	0.134

Table A-2. Structural equation models for predicting chlorophyll *a* ranked in increasing order of AIC. Zooplankton community biomass (Z.bmass), chlorophyll *a* (chl), and total phosphorous (TP) were ln transformed. The environmental variables selected through multiple regression (Env) were % tree cover, DIC, log area, log depth, pH, and log DOC. PCA refers to the first two axes of a PCA of all standardized environmental variables. The χ^2 test provides a test of how well the model fits the data. Models with *p*-values >0.05 are considered to be a reasonable fit to the data.

	Model	AIC	χ^2	d.f.	*P* value
1	chl ~ MPD$_{pa}$	114	0	0	saturated
2	chl ~ TP	133	0	0	saturated
3	chl ~ Z.bmass	146	0	0	saturated
4	chl ~ MPD$_{pa}$ + TP MPD$_{pa}$ ~ TP	173	0	0	saturated
5	chl ~ PCA	177	0	0	saturated
6	chl ~ MPD$_{pa}$ + Z.bmass Z.bmass ~ MPD$_{pa}$	197	0	0	saturated
7	chl ~ MPD$_{pa}$ + PCA MPD$_{pa}$ ~ PCA	222	0	1	1.000
8	chl ~ PCA + Z.bmass Z.bmass ~ PCA	256	0	1	1.000
9	chl ~ MPD$_{pa}$ + TP MPD$_{pa}$ ~ TP Z.bmass ~ MPD$_{pa}$ + TP	258	0	0	saturated
10	chl ~ MPD$_{pa}$ + PCA + Z.bmass MPD$_{pa}$ ~ PCA Z.bmass ~ MPD$_{pa}$ + PCA	305	0	1	1.000
11	chl ~ Env	515	0	0	saturated
12	chl ~ MPD$_{pa}$ + Env MPD$_{pa}$ ~ Env	567	14.41	6	0.017
13	chl ~ Env + Z.bmass Z.bmass ~ Env	600	15.41	6	0.017
14	chl ~ MPD$_{pa}$ + Env +Z.bmass MPD$_{pa}$ ~ Env Z.bmass ~ MPD$_{pa}$ + Env	648	15.41	6	0.017

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APPENDIX B

I used UPGMA agglomerative clustering (Borcard et al. 2011) to determine that the zooplankton communities in the ponds on Mont St. Hilaire clustered into three general groups depending on whether they were dominated by *Daphnia* species, cyclopoid copepod species, or ostracods (Fig. B-1).

Redundancy analysis (RDA), with Hellinger transformed zooplankton biomass counts (Legendre and Anderson 1999, Legendre and Gallagher 2001), was used to determine which environmental variables were informative in explaining variation in the zooplankton community compositions. Forward selection of the environmental variables in the RDA was preformed by using permutations and AIC with the ordistep function in *vegan* (Oksanen et al. 2011). From this, I determined that the compositional differences were explained by variation in pond depth, and the concentration of dissolved organic carbon (DOC), and the concentration of chlorophyll *a* (chl *a*) (Fig. B-2). However, the association between chl *a* and zooplankton community composition is due to the top down control of phytoplankton by zooplankton which is dependent on community composition, as identified in Chapter 2. Therefore, I consider the zooplankton community composition to be primarily determined by pond depth and DOC.

Various spatial modeling techniques, including multivariate trend-surface analysis and PCNM (Borcard et al. 2011), were used to describe the spatial network of ponds. The amount of variation in zooplankton community composition that was explained by the variables from these spatial modeling techniques was compared using redundancy analysis, but none performed better than basic latitude and longitude.

Variation partitioning using the *vegan* package (Oksanen et al. 2011) was used to compare the variation in zooplankton community composition that was explained by environmental (depth and DOC) and spatial variables (latitude and longitude). The environmental variables explained a significant amount of variation in zooplankton community composition but the spatial variables were not informative (Table B-1). This is indicative of a species sorting metacommunity, where dispersal rates are high enough so that the community compositions are determined by the environmental conditions in the ponds, but not so high to homogenize closely related ponds through mass effects (Cottenie 2005).

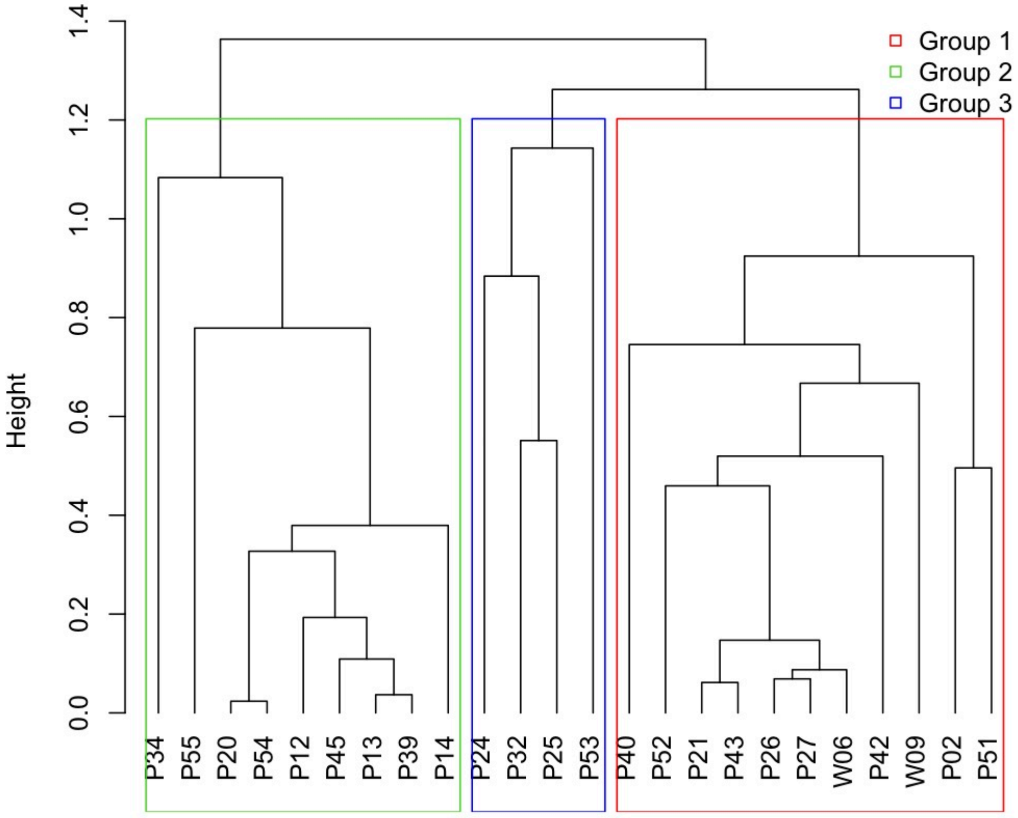

Figure B-1. Dendrogram of pond groupings based on UPGMA average agglomerative clustering of the crustacean zooplankton community composition in 23 fishless ponds on Mont St. Hilaire. Green ponds are dominated by *Daphnia spp.*, blue ponds are dominated by copepods, and red ponds are dominated by ostracods and one species of copepod.

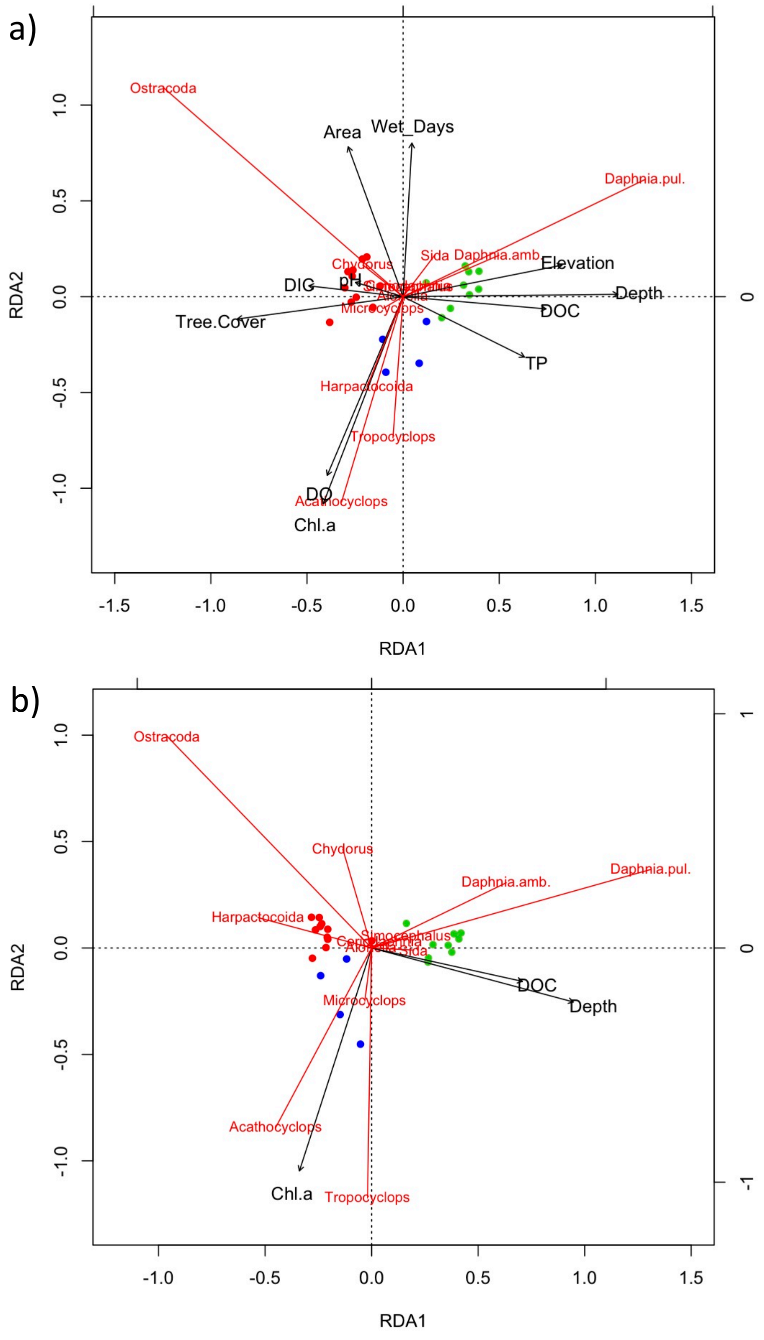

Figure B-2. Redundancy analysis (RDA) of zooplankton community composition constrained by all environmental variables (a) and a reduced set based on a forward selection (b). Individual pond community compositions are represented by the dots corresponding to their zooplankton community grouping. Scaling 1 is used in both plots.

Table B-1. Variation partitioning and associated *P* values for the zooplankton community composition. Zooplankton community variation is partitioned into that which can be explained by the environmental and spatial (latitude and longitude) variables.

	Variation explained	*p*-value
[E+S]	0.284	**0.0391**
[E]	0.156	0.138
[S]	0.005	0.361
[E|S]	0.279	**0.0376**
[S|E]	0.128	0.063
[E□ S]	<0	
1- [E+S]	0.716	

Notes: [E+S] is the total variation explained by both the environment and spatial variables. [E] is the total variatin explained by the environmental variables. [S] is the variation explained by the spatial variables. [E|S] is the variation explained by the environment when the spatial variables have been constrained. [S|E] is the variation explained by the spatial variables when the environmental variables have been constrained. [E□ S] is the variation explained that is shared by the environmental and spatial variables. 1- [E+S] is the unexplained variation.

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APPENDIX C

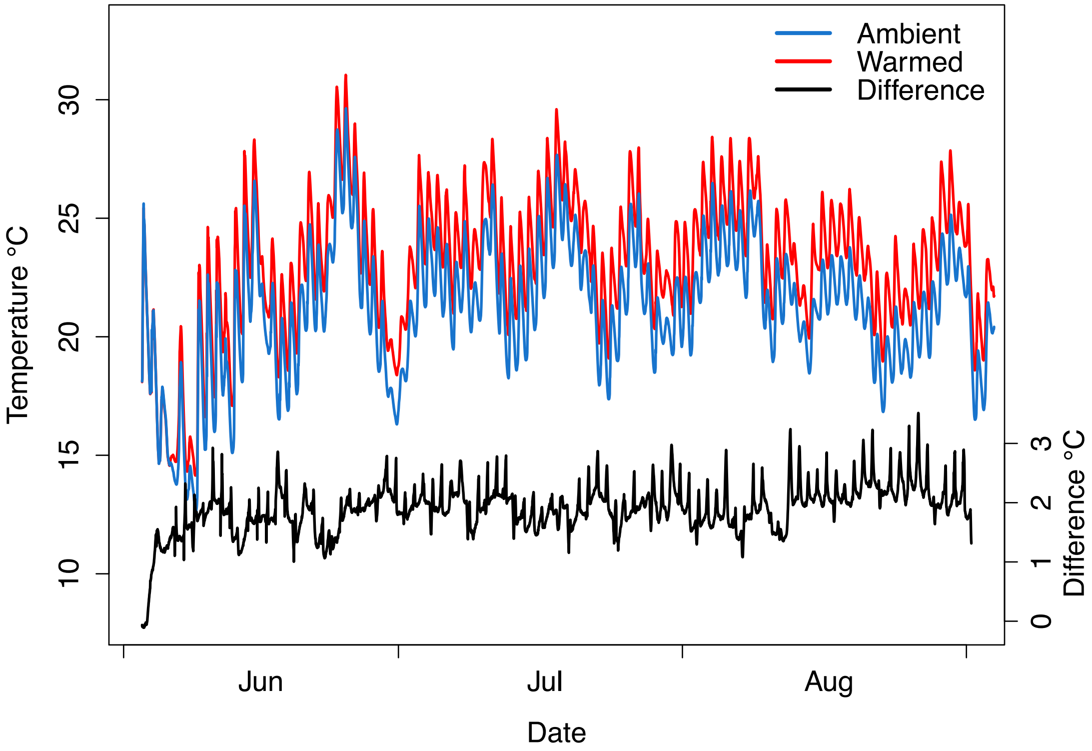

Figure C-1. Average water temperatures in the ambient (blue) and warmed mesocosms (red) over the course of the experiment. The difference between the two treatments is shown in the black line and corresponds to the right hand y-axis. Standard deviations across replicates are not shown, but were 0.48°C for ambient mesocosms and 0.30°C for warmed mesocosms.

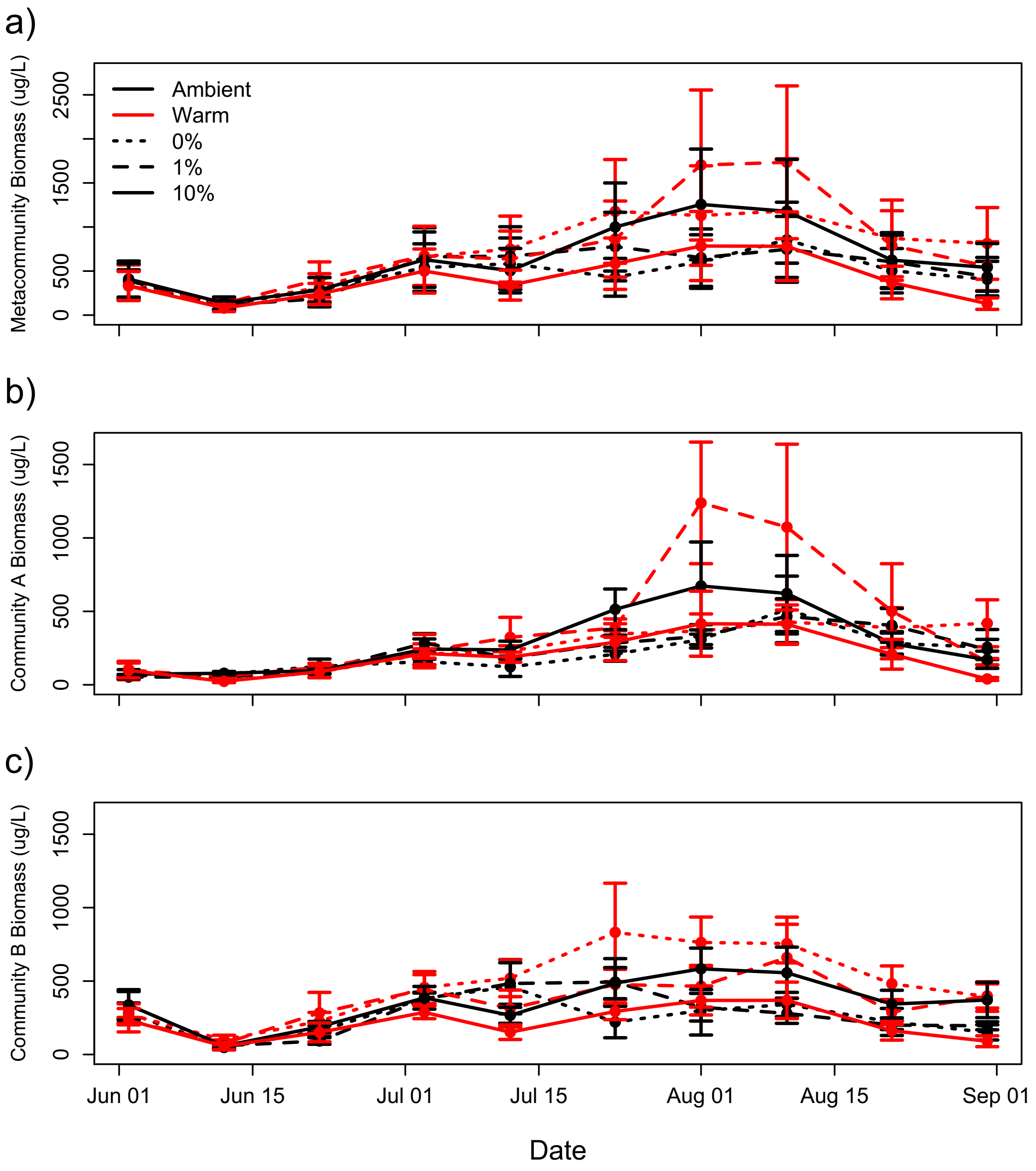

Figure C-2. Metacommunity (a) and local community (b-c) biomass over the course of the experiment. Error bars represent one standard error around the mean. Treatments began to diverge by at least one standard error on July 12. All reported treatment effects on community composition and stability are based on data from July 12 onwards.

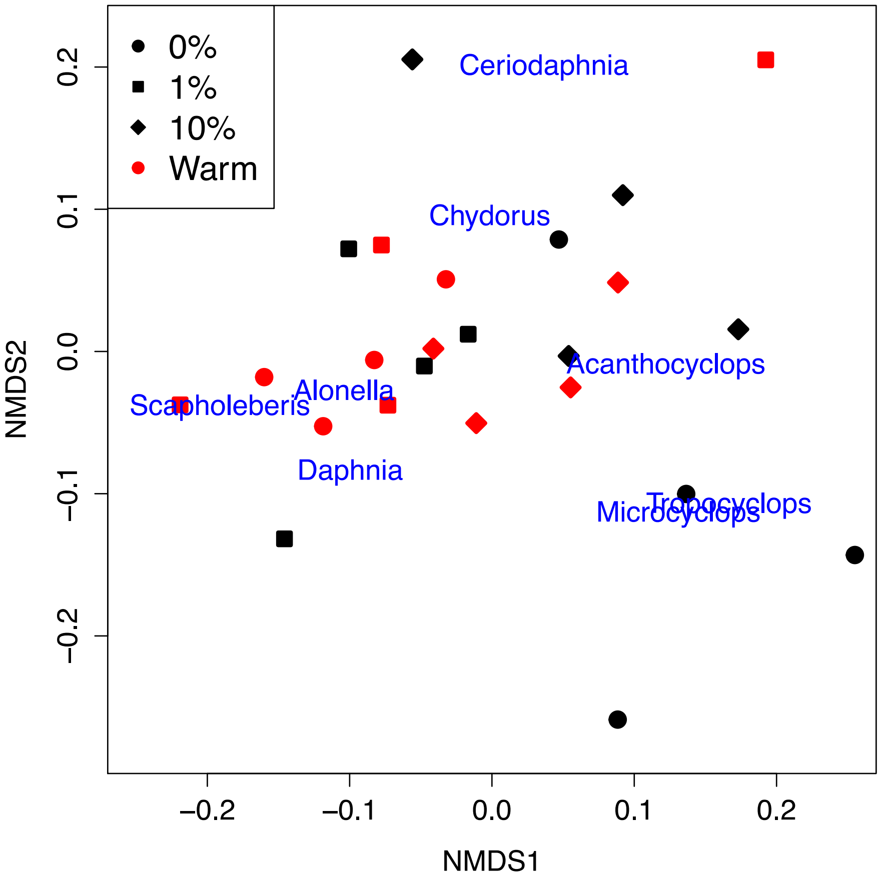

Figure C-3. Nonmetric multidimensional scaling of metacommunity (averaged across sampling dates) compositional differences. Each metacommunity is represented by a single point. Dispersal rate is indicated by the shape (0% – circle, 1% – square, 10% – diamond) and the warming treatment is indicated by the colour (ambient – black, warmed – red). NMDS stress = 0.134.

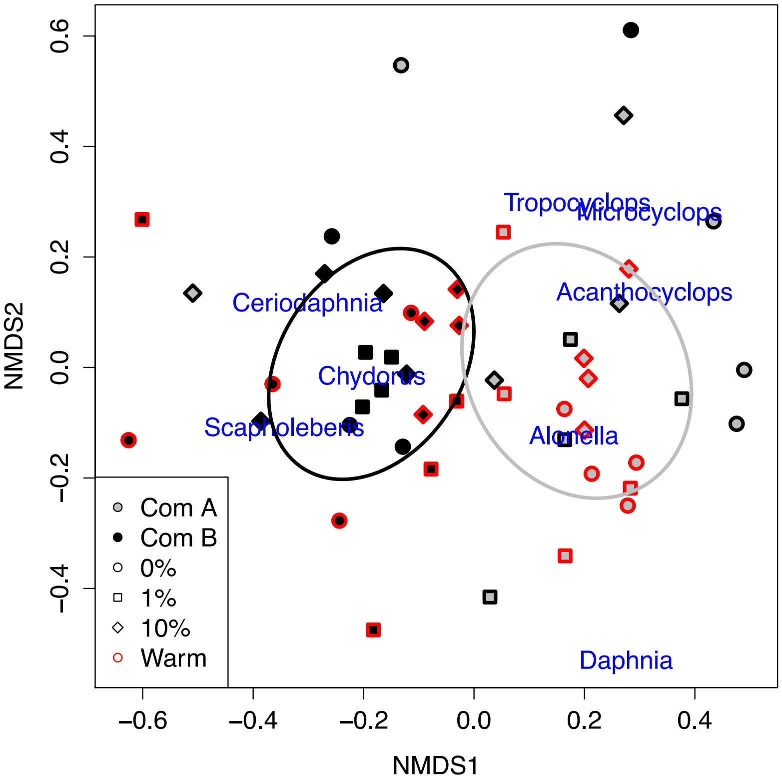

Figure C-4. Nonmetric multidimensional scaling of local community (averaged across sampling dates) compositional differences. Each local community is represented by a single point. Community type is indicated by the inner colour (Com A – grey, Com B – black), dispersal rate is indicated by the shape (0% – circle, 1% – square, 10% – diamond) and the warming treatment is indicated by the border colour (ambient – black, warmed – red). The ellipses represent 1 standard deviation around the mean community composition for each local community type. NMDS stress = 0.147.

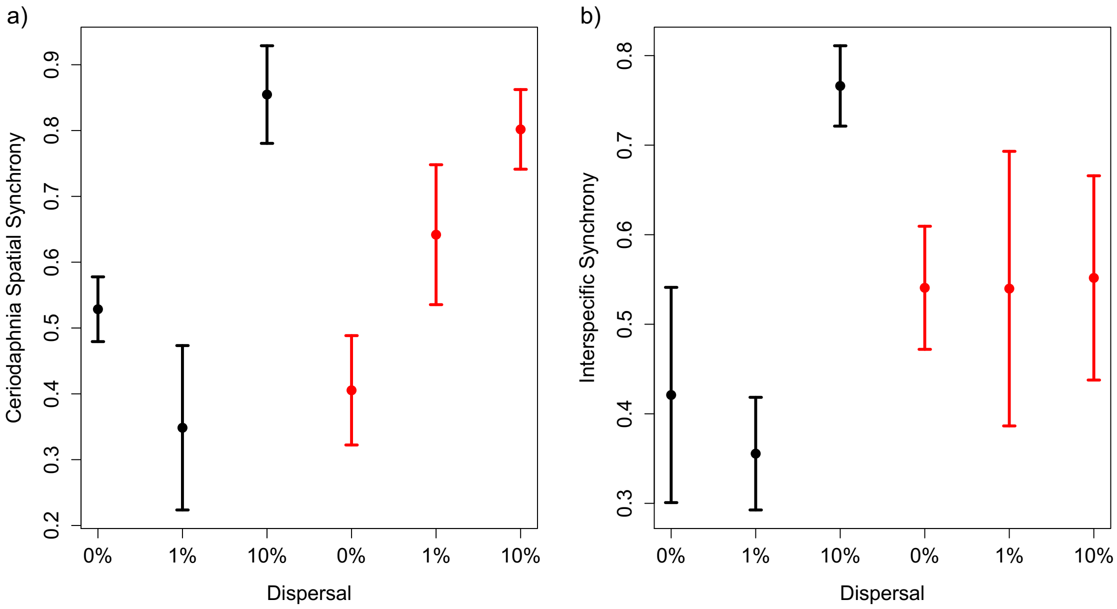

Figure C-5. Ceriodaphnia spatial synchrony (a) and metacommunity interspecific synchrony (b) in ambient (black) and warmed (red) treatments, crossed with the three dispersal treatments (0%, 1%, and 10%). Error bars represent 1 standard error around the mean (n=4).

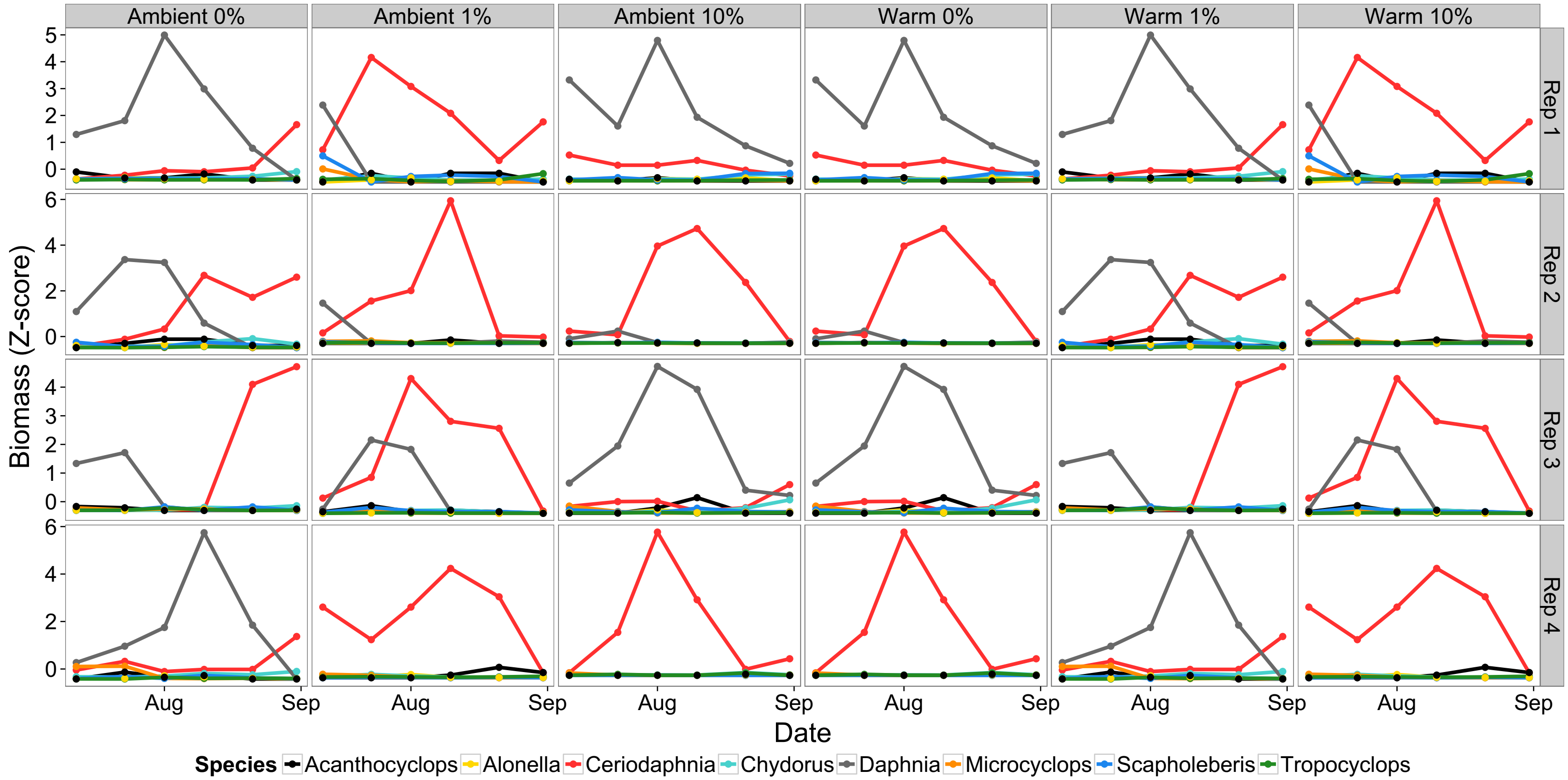

Figure C-6. Biomass (standardized) time series of each species in each community A replicate. Treatment combinations are ordered by column.

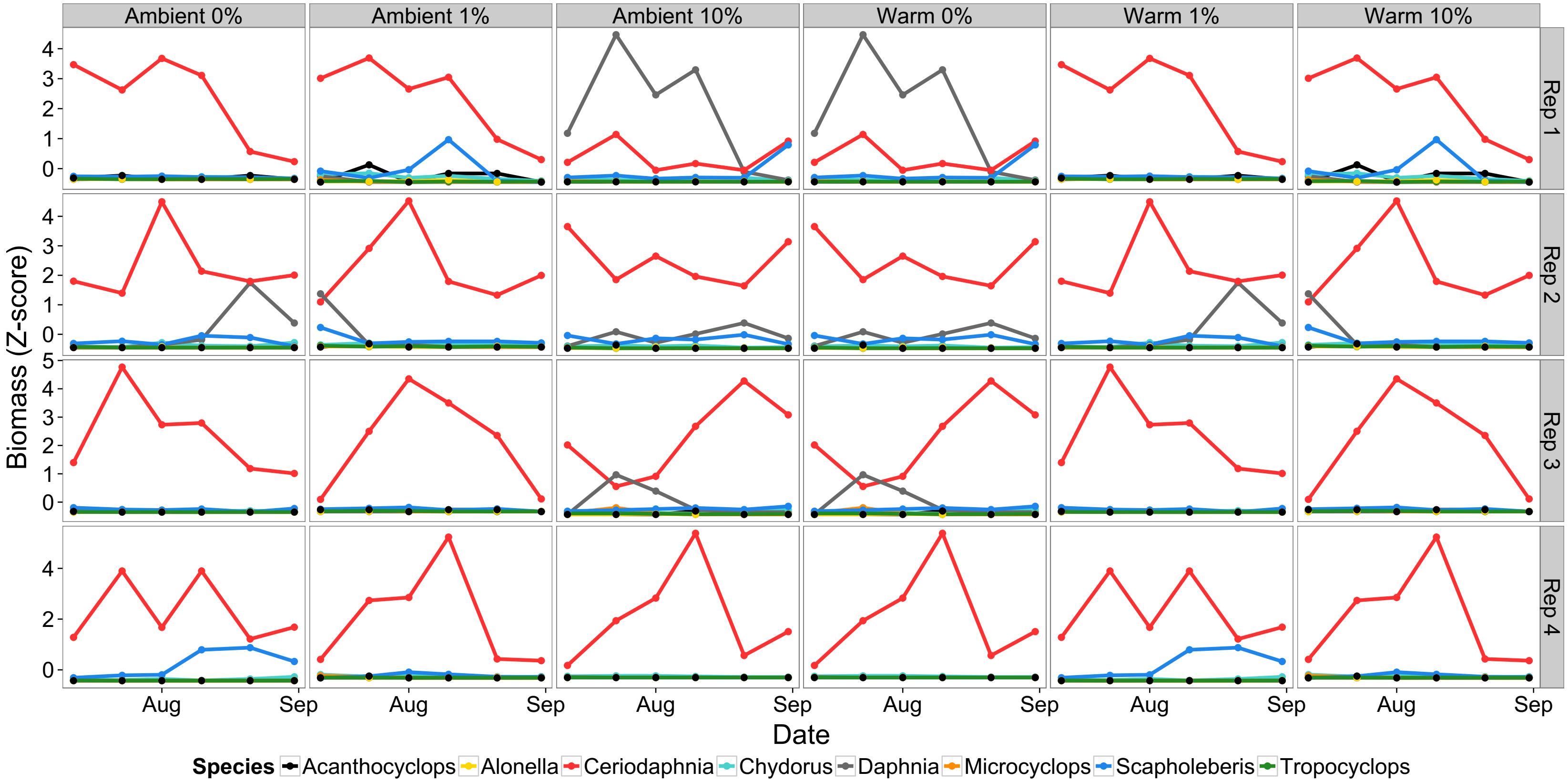

Figure C-7. Biomass (standardized) time series of each species in each community B replicate. Treatment combinations are ordered by column.

Table C-1. Individual genus response to treatments at the metacommunity level. Estimates, standard errors, *t*-values, and *p*-values are based on linear models on log transformed biomass averaged across sample dates. A constant of 1 was added to all values prior to log transforming.

Genus		Estimate	Std error	*t*-value	*p*-value
Daphnia	Intercept	3.35	0.46	7.32	**0.000**
	Dispersal L	-1.08	0.79	-1.36	0.191
	Dispersal Q	-1.01	0.79	-1.28	0.218
	Warming	0.87	0.65	1.34	0.197
	Dispersal L * Warming	-0.63	1.12	-0.56	0.582
	Dispersal Q * Warming	0.67	1.12	0.60	0.556
Ceriodaphnia	Intercept	6.21	0.19	33.32	**0.000**
	Dispersal L	0.59	0.32	1.84	0.082
	Dispersal Q	0.03	0.32	0.10	0.922
	Warming	-0.05	0.26	-0.19	0.850
	Dispersal L * Warming	-1.00	0.46	-2.19	**0.042**
	Dispersal Q * Warming	-0.05	0.46	-0.12	0.906
Chydorus	Intercept	2.26	0.10	23.33	**0.000**
	Dispersal L	-0.01	0.17	-0.06	0.951
	Dispersal Q	-0.09	0.17	-0.54	0.593
	Warming	0.61	0.14	4.48	**0.000**
	Dispersal L * Warming	-0.57	0.24	-2.42	**0.027**
	Dispersal Q * Warming	-0.03	0.24	-0.14	0.891
Microcyclops	Intercept	2.28	0.18	12.74	**0.000**
	Dispersal L	-0.95	0.31	-3.05	**0.007**
	Dispersal Q	0.62	0.31	1.98	0.063
	Warming	-0.46	0.25	-1.80	0.089
	Dispersal L * Warming	0.86	0.44	1.96	0.066
	Dispersal Q * Warming	-0.58	0.44	-1.32	0.204
Tropocyclops	Intercept	1.82	0.15	12.19	**0.000**
	Dispersal L	-0.89	0.26	-3.45	**0.003**
	Dispersal Q	0.38	0.26	1.45	0.163
	Warming	-0.36	0.21	-1.71	0.105
	Dispersal L * Warming	0.93	0.37	2.53	**0.021**
	Dispersal Q * Warming	-0.43	0.37	-1.18	0.253
Scapholeberis	Intercept	3.10	0.25	12.55	**0.000**
	Dispersal L	0.28	0.43	0.65	0.521
	Dispersal Q	-0.57	0.43	-1.33	0.200
	Warming	0.04	0.35	0.10	0.919
	Dispersal L * Warming	-0.89	0.60	-1.46	0.160
	Dispersal Q * Warming	0.96	0.60	1.59	0.130
Alonella	Intercept	1.03	0.12	8.49	**0.000**
	Dispersal L	-0.06	0.21	-0.28	0.782
	Dispersal Q	-0.44	0.21	-2.11	**0.050**
	Warming	0.59	0.17	3.41	**0.003**
	Dispersal L * Warming	-0.23	0.30	-0.79	0.439
	Dispersal Q * Warming	0.40	0.30	1.35	0.193
Acanthocyclops	Intercept	1.91	0.24	8.07	**0.000**
	Dispersal L	-0.24	0.41	-0.58	0.568
	Dispersal Q	0.01	0.41	0.02	0.986
	Warming	0.34	0.33	1.02	0.321
	Dispersal L * Warming	0.02	0.58	0.04	0.971
	Dispersal Q * Warming	0.56	0.58	0.96	0.349

Table C-2. Median concentrations for total phosphorous (TP), total nitrogen (TN), dissolved organic carbon (DOC), and dissolved inorganic chemistry (DIC) by community type and for ambient and warmed treatments. Water chemistry measurements from mid experiment (June 27 or July 19) and at the end of the experiment (August 31) are shown. The range (min – max) of concentrations is indicated in brackets. Note that the estimates for TP and TN from August 31 are based on reduced sample size because 25 of 48 samples were lost.

Variable	Date	Community A	Community B	Ambient	Warmed
TP (µg L^{-1})	June 27	16.5 (10.8 – 25.1)	22.9 (14.6 – 64.3)	21.6 (12.7 – 64.3)	17.8 (10.8 – 48.3)
	August 31	38.3 (21.8 – 56.9)	25.2 (13.4 – 88.1)	34.3 (13.4 – 88.1)	31.4 (18.6 – 86.7)
TN (mg L^{-1})	June 27	0.41 (0.31 – 0.87)	0.49 (0.34 – 0.69)	0.45 (0.31 – 0.87)	0.44 (0.34 – 0.69)
	August 31	0.61 (0.39 – 0.85)	0.54 (0.21 – 0.74)	0.55 (0.21 – 0.85)	0.58 (0.44 – 0.74)
DOC (mg L^{-1})	July 19	27.4 (8.0 – 53.8)	25.8 (10.6 – 33.9)	28.2 (8.0 – 53.8)	26.8 (8.1 – 33.9)
	August 31	30.8 (8.3 – 213.1)	16.0 (9.6 – 100.0)	22.4 (8.3 – 213.1)	23.7 (10.5 – 99.0)
DIC (mg L^{-1})	July 19	12.7 (6.7 – 14.7)	10.5 (7.2 – 13.8)	11.4 (7.2 – 14.0)	11.6 (6.7 – 14.7)
	August 31	11.3 (7.7 – 14.7)	7.5 (3.6 – 11.2)	9.0 (3.6 – 12.4)	10.7 (5.3 – 14.7)

Table C-3. Genus-specific population synchrony relationships with metacommunity biomass variability.

Genus	Estimate	Std error	*t*-value	*p*-value
Daphnia	-0.02	0.17	-0.110	0.914
Ceriodaphnia	0.46	0.11	4.043	**<0.001**
Chydorus	-0.25	0.16	-1.580	0.128
Microcyclops	0.54	0.21	2.645	0.015
Tropocyclops	0.17	0.17	0.975	0.340
Scapholeberis	-0.03	0.17	-0.158	0.876
Alonella	-0.17	0.20	-0.846	0.407
Acanthocyclops	-0.22	0.17	-1.323	0.200

APPENDIX D

THE ROBUSTNESS OF THE SPATIAL INSURANCE EFFECT TO VARIATION IN INTERSPECIFIC DISPERSAL RATES

Our model assumes equal dispersal rates across all species, but our results are robust to relaxing this assumption. Here we show the results for species richness, productivity, and productivity CV (Fig. D-1) and multifunction (Fig. D-2) when dispersal rates vary across species. For this, dispersal rates were drawn from two beta distributions with different shape parameters (Fig. D-1a). In the 5,5 beta distribution, dispersal rates are normally distributed around the mean. In the 2,5 beta distribution, dispersal rates are skewed towards lower rates. These distributions are centred around and scaled to the given dispersal rate a such that,

$$a_i = a\,\frac{\beta_i}{\bar{\beta}}$$

where β_i is the value for species i drawn from the beta distribution, and a is the average rate of dispersal. We compare the results obtained with these two beta distributions with the case when all species have equal dispersal rates (Beta distribution – none). Allowing variation in interspecific dispersal rates results in quantitative differences in the response variables, but does not change the general shape of the relationship with dispersal. For example local and regional richness (Fig. D-1b,c) still peak at low to intermediate dispersal rates (a = 0.005 – 0.01), but lower levels of richness are maintained than the case with equal dispersal rates across species (e.g. a = 0.1). There is little overall effect on productivity (Fig. D-1d-f). Likewise, there are quantitative differences in multifunction (Fig. D-2), but the general shape of the relationship with dispersal does not change when interspecific dispersal rates differ. For, example, local and regional multifunction still peaks at low to intermediate dispersal rates (a = 0.005 – 0.01) but these peaks are slightly supressed when interspecific dispersal rates vary (e.g. beta distribution 2,5)

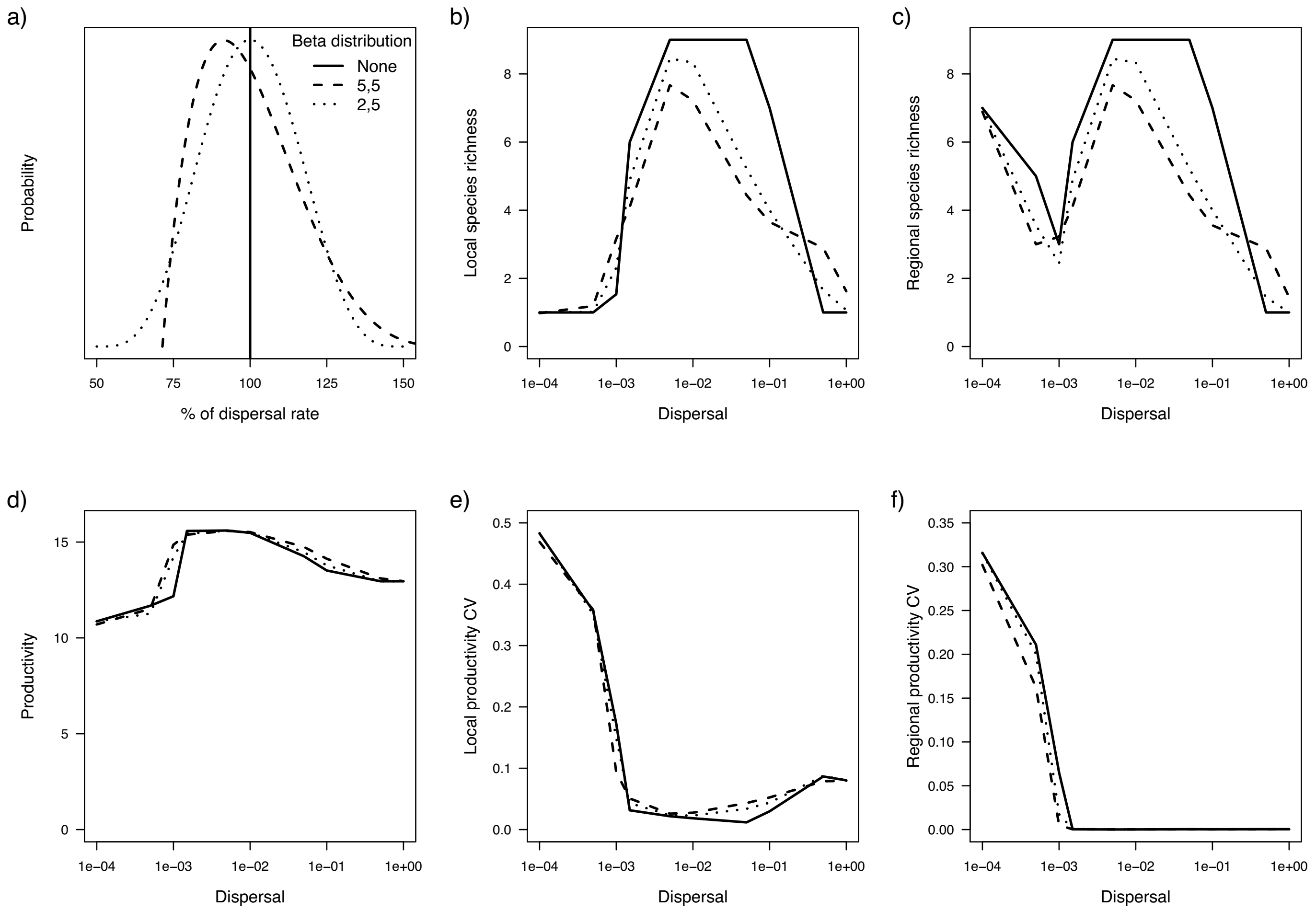

Figure D-1. The spatial insurance model results when dispersal rates vary across species. Panel a illustrates the shape of the two beta distributions from which dispersal rates are drawn as a percentage of the mean dispersal rate *a*. The relationship between the mean dispersal rate and species richness (local – b; regional – c), productivity (d), and productivity coefficient of variation (local – e; regional –f) are shown. One standard deviation around the mean for 10 replicate distributions is shown.

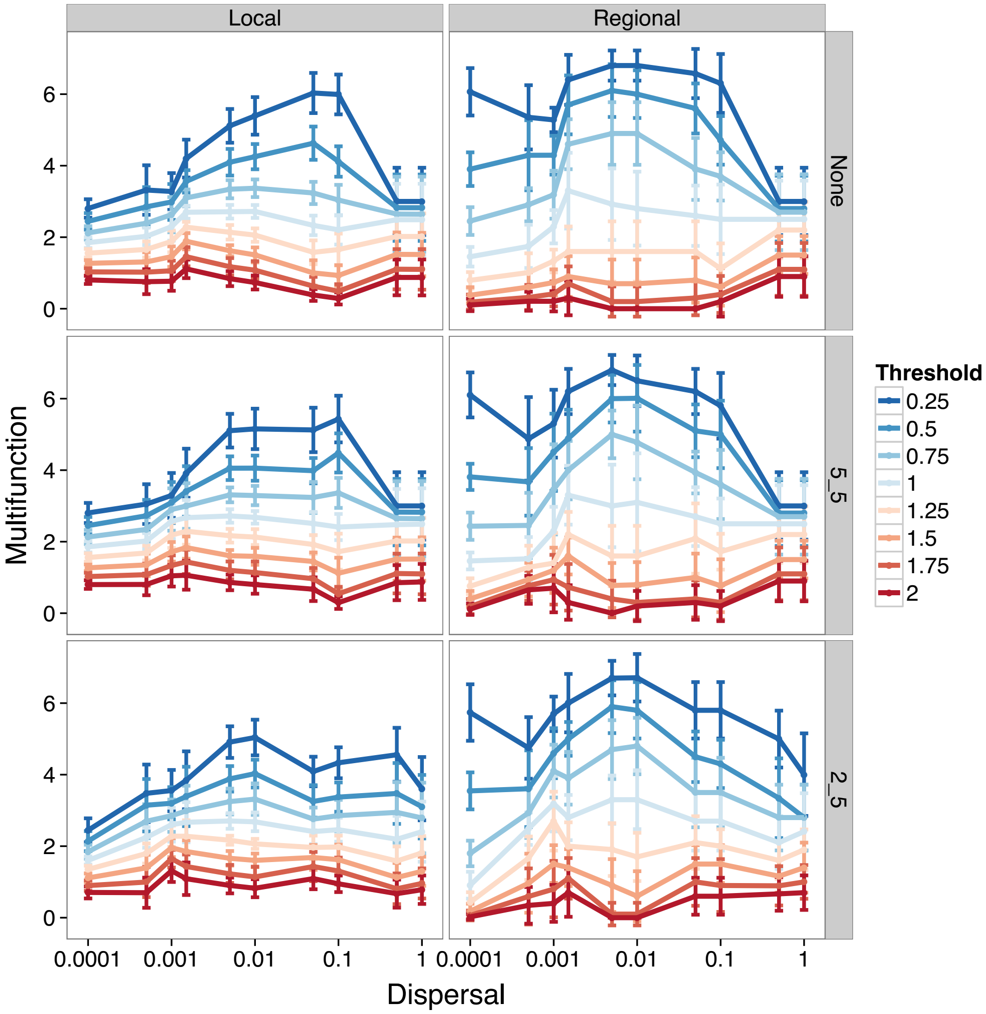

Figure D-2. The relationship between multifunction and the rate of dispersal, at local and regional scales. The rows show the three cases of interspecific variation in dispersal rate. Results are based on a single replicate for each interspecific dispersal variation case. One standard deviation around the mean value from 10 replicate draws of functional traits with a functional overlap of 0.5 is shown.

THE OF ROBUSTNESS OF SPATIAL INSURANCE EFFECTS TO VARIATION IN NUMBER OF PATCHES AND SPECIES

The manuscript shows results from metacommunities consisting of 9 species and 30 patches but the spatial insurance effects of biodiversity are robust to changing these parameter values. Here we show the results for species richness, productivity, and productivity CV (Fig. D-3) and multifunction (Fig. D-4) for 3, 9, and 15 species in of 5, 15, and 30 patches. Changing the number of species and patches results in quantitative differences in the response variables, but does not change the general shape of the relationship with dispersal. The greatest deviation in results occurs when the number of species exceeds the number of patches because each species does not always have a patch where it is the most competitive species (Fig. D-3a,b); in this case, local and regional richness peaks at higher levels of dispersal (e.g. richness peaks at a = 0.1 for the case of 15 species and 5 patches). Productivity and stability (Fig. D-3c-e) and multifunction (Fig. D-4) show smaller differences across cases.

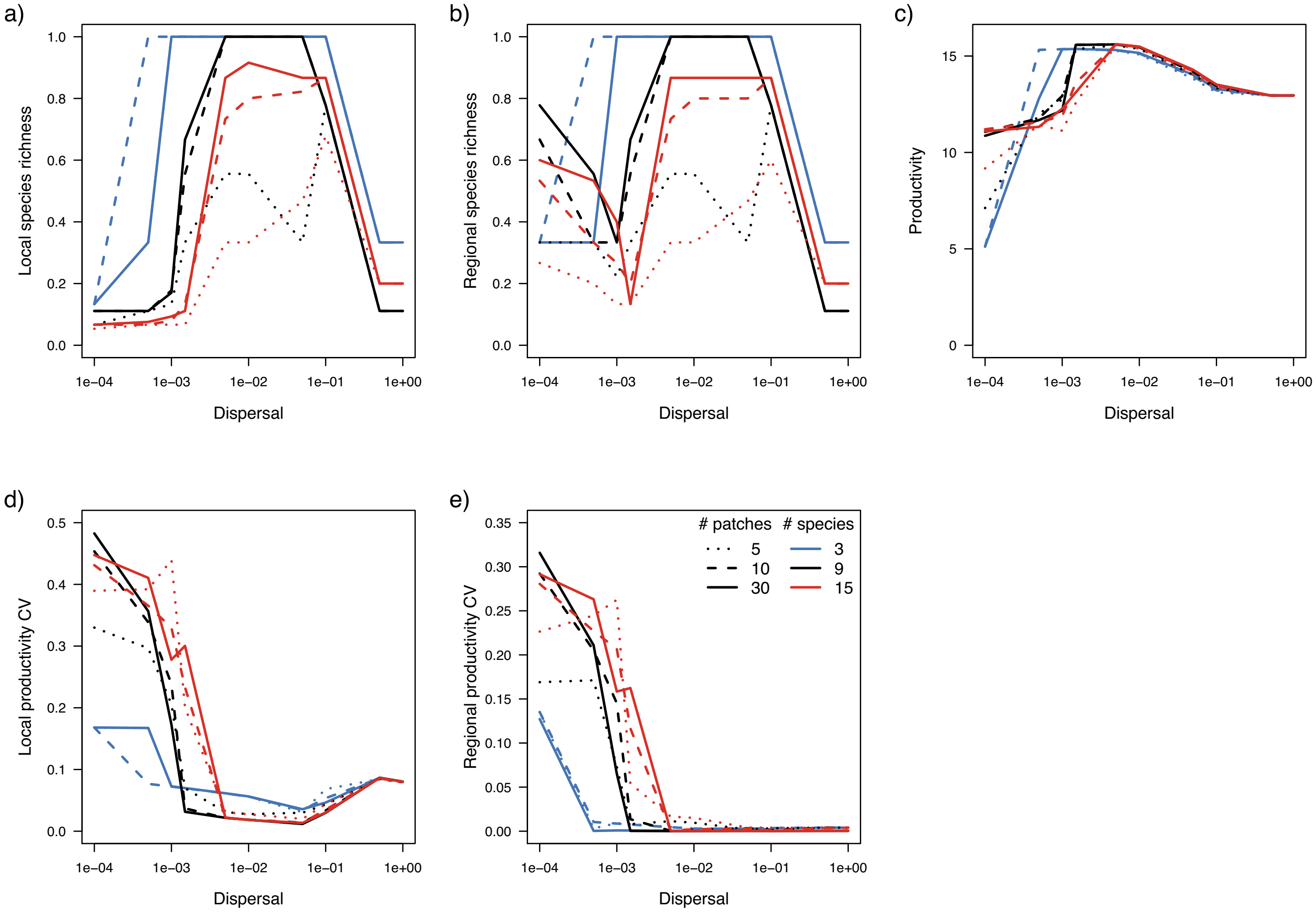

Figure D-3. The spatial insurance model results for 3, 9, and 15 species in 5, 10, and 30 patches. The relationship between the mean dispersal rate and the proportion of total species richness (local – a; regional – b), productivity (c), and productivity coefficient of variation (local – d; regional –e) are shown.

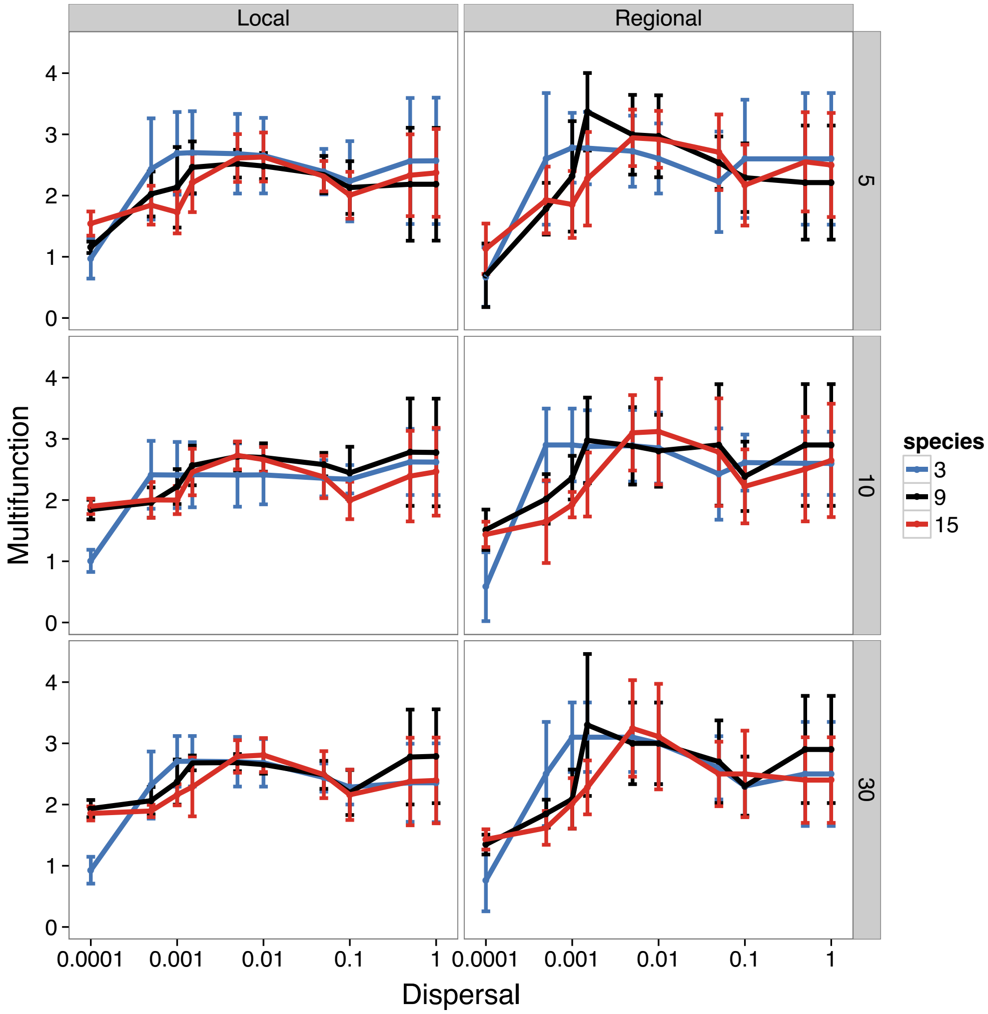

Figure D-4. The relationship between multifunction and the rate of dispersal, at local and regional scales in metacommunities that vary in their number of patches (rows) and species (colours). One standard deviation around the mean value from 10 replicate draws of functional traits with a functional overlap of 0.5 and a threshold of 1 is shown.

DEMONSTRATION OF ROBUSTNESS OF SPATIAL INSURANCE TO VARIATION IN NUMBER OF ECOSYSTEM FUNCTIONS

The manuscript shows results for seven ecosystem functions but the spatial insurance effects of biodiversity are robust to changing these parameters. Here we show the number of functions that are simultaneously produced when species are able to contribute to 3, 7, 11, and 15 functions when the functional overlap is 0.5 (Fig. D-5). Changing the number of functions does not change the shape of the relationship between multifunction and dispersal.

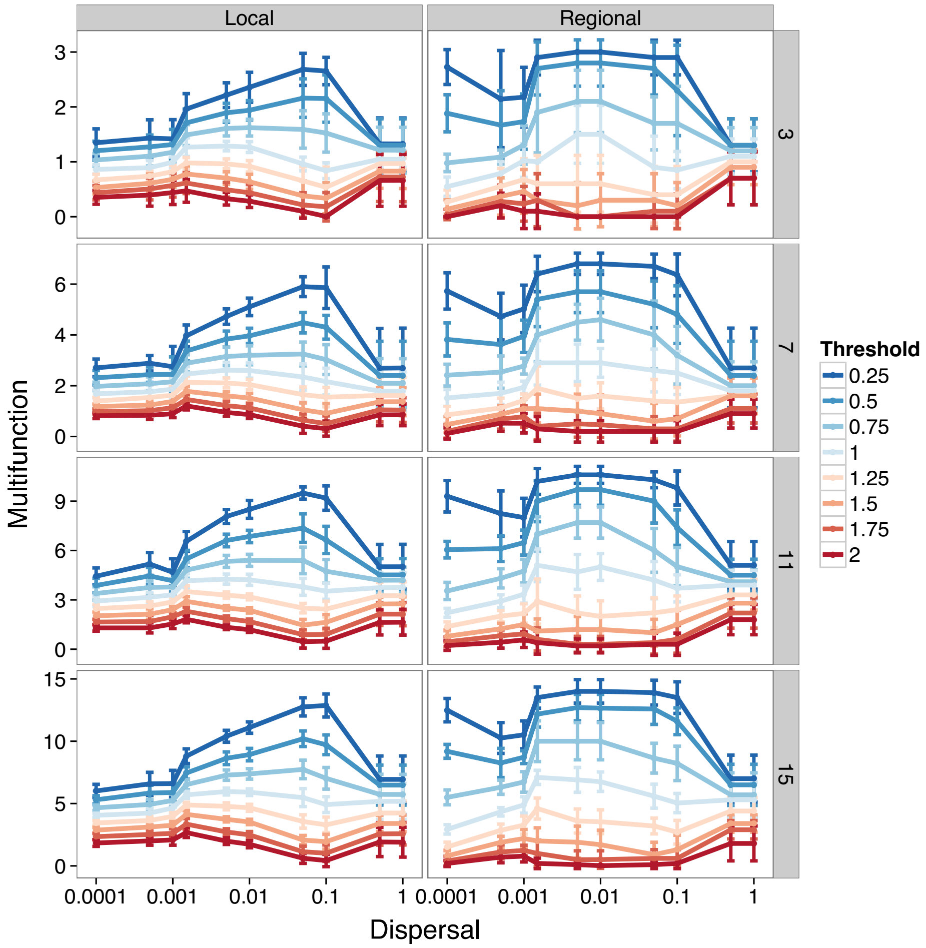

Figure D-5. The relationship between multifunction and the rate of dispersal, at local and regional scales. The rows each show this relationship when a different number of functions are modelled (3, 5, 11, and 15). One standard deviation around the mean value from 10 replicates is shown.

COMPARISON OF LOCAL VS. REGIONAL MULTIFUNCTION

Here we show the relationship between local and regional multifunction over the full range of dispersal rates (colours), levels of functional overlap (size of circles) and thresholds (panels; Fig. D-6). Intermediate dispersal rates (yellow and orange colours) tend to result in the greatest multifunction at both scales, especially when thresholds are less than 1. Regional multifunction is always greater than, or equal to, local multifunction when the threshold is less than 1, but this reverses as thresholds increase beyond 1. Communities with high functional overlap produce more local and regional multifunction when thresholds are below 1, but this reverses as thresholds increase beyond 1.

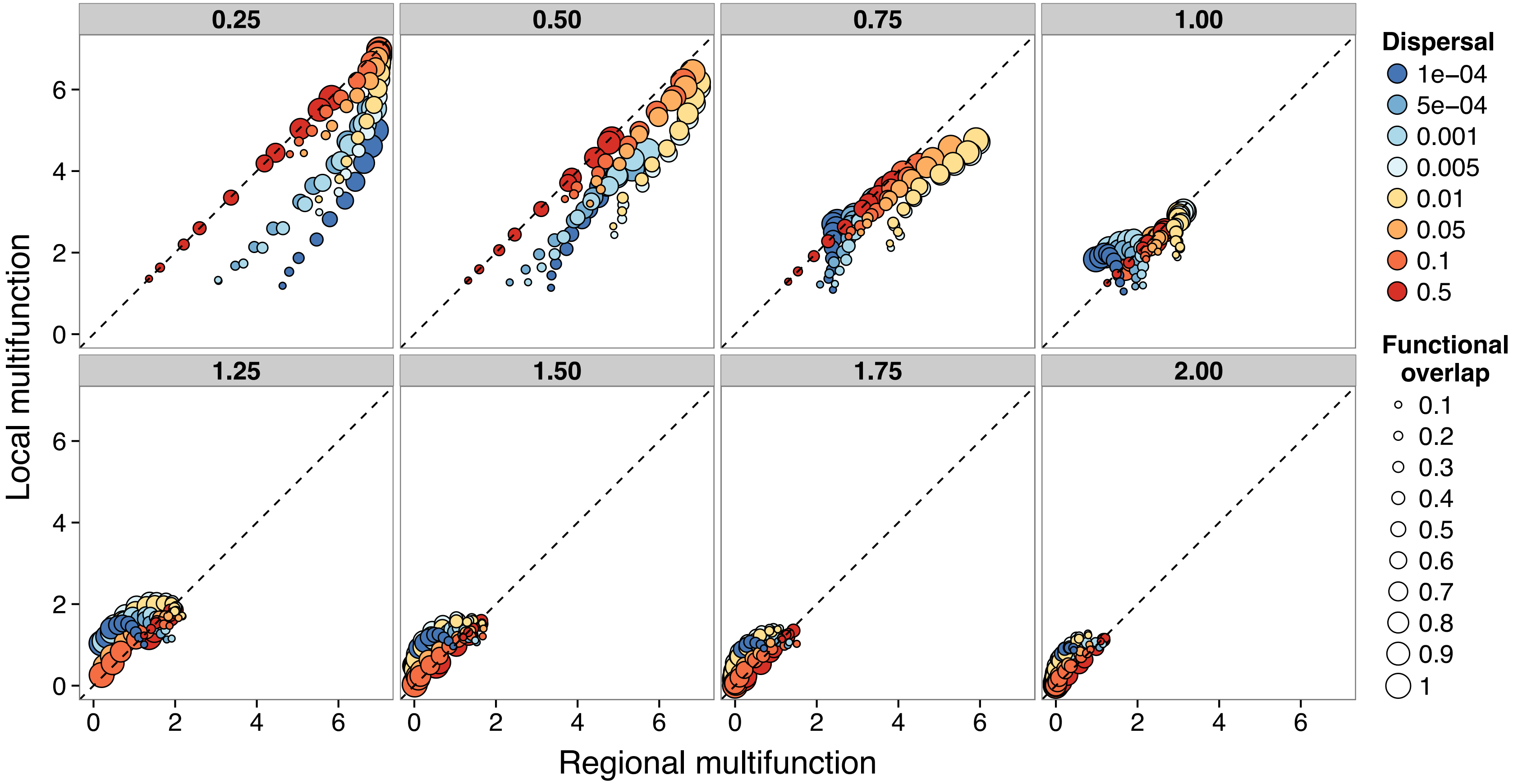

Figure D-6. The relationship between multifunction at local and regional scales over a range of thresholds for production (panels). The colour indicates the dispersal rate and the size of the circle indicates the functional overlap of the community. The dashed 1:1 line indicates when multifunction is the same at both scales. Mean values from 100 replicates are shown.

COMPARISON OF DIVERSITY MULTIFUNCTION RELATIONSHIP OVER ALL LEVELS OF FUNCTIONAL OVERLAP AND PRODUCTION THRESHOLDS

Here we show the relationship between species richness and local and regional multifunction over the full range of functional overlap and production thresholds (Fig. D-7). Dispersal mediates this relationship in all cases, but how this is realized depends on both parameters. The non-linear effects of dispersal on this relationship are most evident when production thresholds are low, because it is possible to obtain higher levels of multifunction.

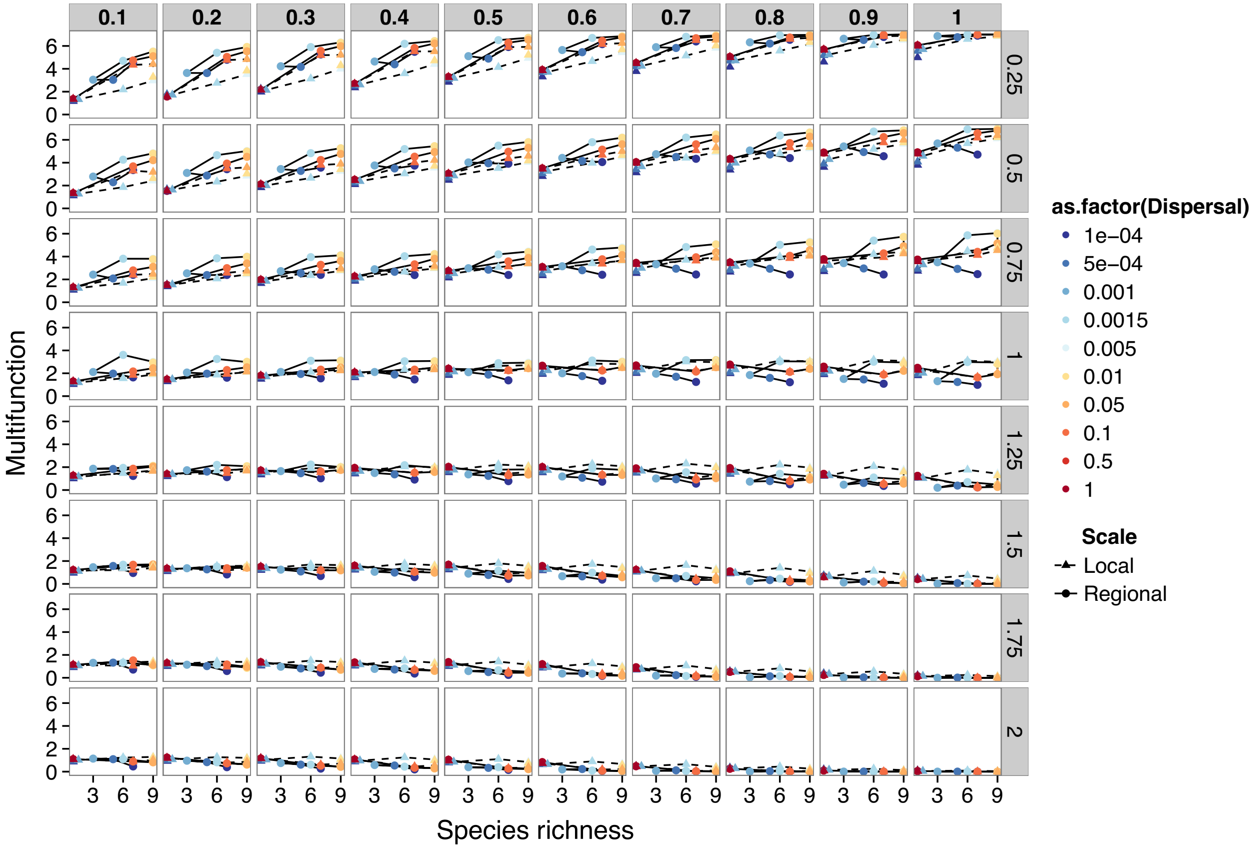

Figure D-7. The relationship between species richness and multifunction at local and regional scales over all levels of functional overlap (columns) and thresholds for production (rows). Dispersal rates are indicated by the colour of the points (blue – low, red – high) and the lines connect the points in order of dispersal. Mean values from 100 replicates are shown.

COMPARISON OF LOCAL VS. REGIONAL MULTIFUNCTION VARIABILITY

Here we show the relationship between local and regional multifunction variability (SD) over the full range of dispersal rates (colours), levels of functional overlap (size of circles) and thresholds (panels; Fig. D-8). Local multifunction variability is higher than regional multifunction variability except when dispersal is low ($a \leq 0.001$). Dispersal rates that are at least intermediate ($a \geq 0.005$) result in stable regional multifunction. Intermediate dispersal rates result in the most variable local multifunction ($a = 0.01$). The effect of functional overlap on multifunction variability depends on the scale, threshold, and rate of dispersal.

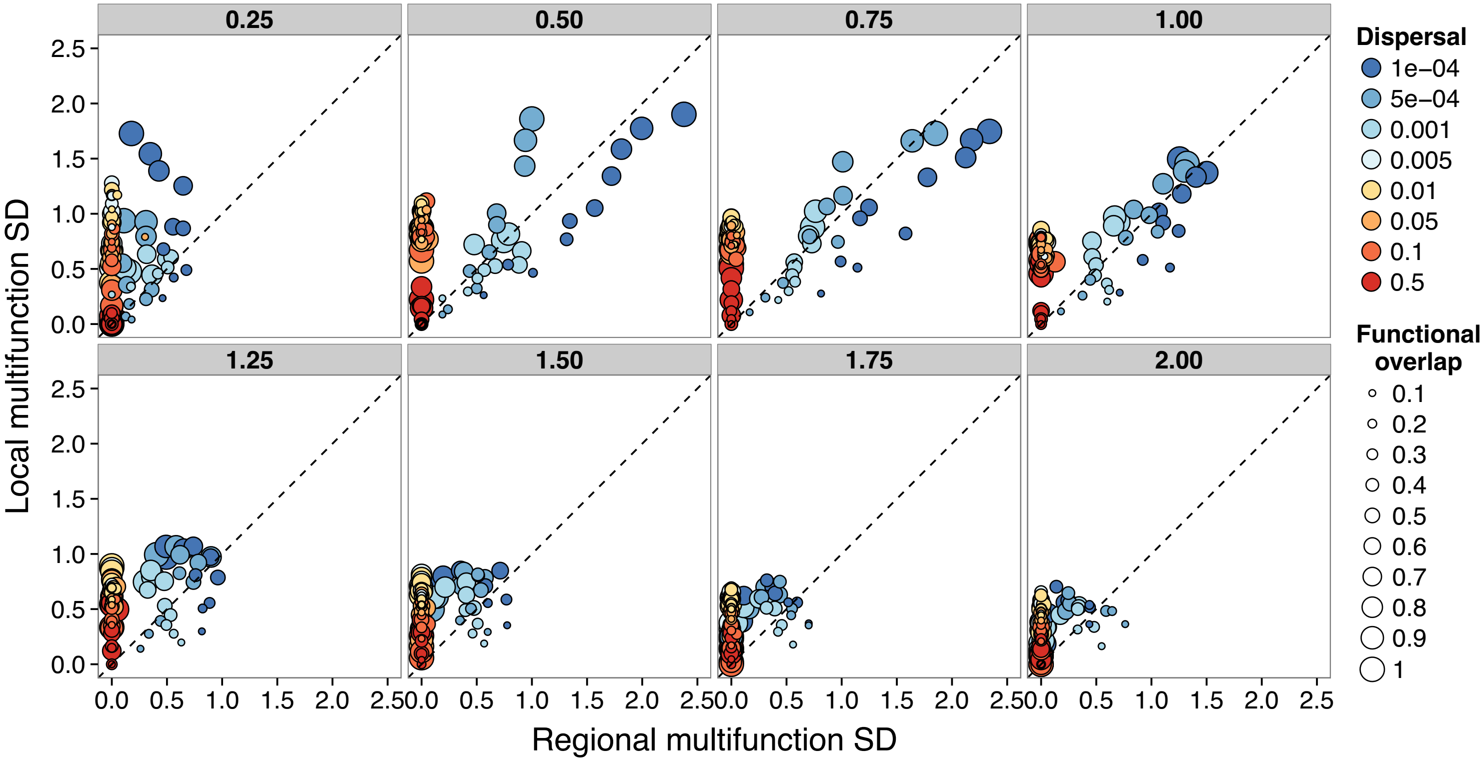

Figure D-8. The relationship between multifunction variability (CV) at local and regional scales over a range of thresholds for production (panels). The colour indicates the dispersal rate and the size of the circle indicates the functional overlap of the community. The dashed 1:1 line indicates when multifunction variability is the same at both scales. Mean values from 100 replicates are shown.

APPENDIX E

MEASURES OF PREDICTION ACCURACY

Here we present two additional measures of prediction accuracy, the correct classification rate and the true skill statistic (Fig. E-1). These measures are based on presence-absence comparisons of our predicted and realized communities (Fielding and Bell 1997, Allouche et al. 2006), in comparison to the multivariate abundance based community distance used to calculate the Bray-Curtis similarity (Fitzpatrick et al. 2011).

The correct classification rate measures the proportion of presence absence predictions that match the realized distributions, averaged across all species (Fielding and Bell 1997). This measure has a high accuracy rate because it is boosted by the high rate of sites where species are absent in both the predicted and realized communities.

The true skill statistic provides a presence-absence measure of accuracy the is corrected for the number of correct classifications that are expected to occur by chance (Allouche et al. 2006). It ranges been -1 and 1, with positive values indicating predictions that are more accurate than we would expect by chance. In comparison to the kappa statistic, it provides a measure of accuracy that is independent of the prevalence of species on the landscape.

The overall classification rate and the true skill statistic both exhibit the same overall unimodal relationship (Fig. E-1) with dispersal that we see for the Bray-Curtis similarity (Fig. 5-2). Quantitative differences are seen in the shape of the unimodal peaks, but these do not change the overall conclusions reported in the manuscript.

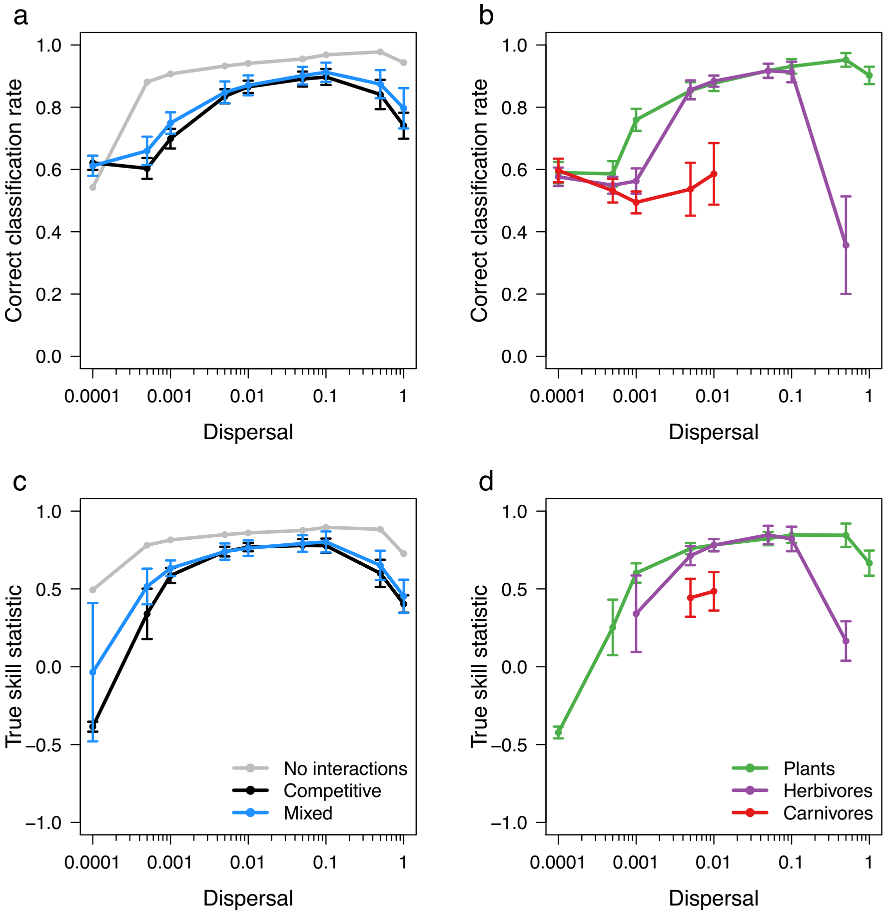

Figure E-1. The relationship between the rate of dispersal and the correct classification rate (a, b) and the true skill statistic (c, d). Panels a and c show this relationship in communities with no interactions (grey), competitive interactions (black), and mixed interactions (blue). Panels b and d show this relationship across three trophic levels. One standard deviation around the mean, based on 50 replicates is shown.

TYPES OF PREDICTION INACCURACY

The false discovery rate (the compliment of the positive predictive power) is the proportion of sites where species were predicted to be present but were not, while false negative rate is the proportion of sites where species were predicted to be absent but were actually present (Benjamini and Hochberg 1995, Fielding and Bell 1997).

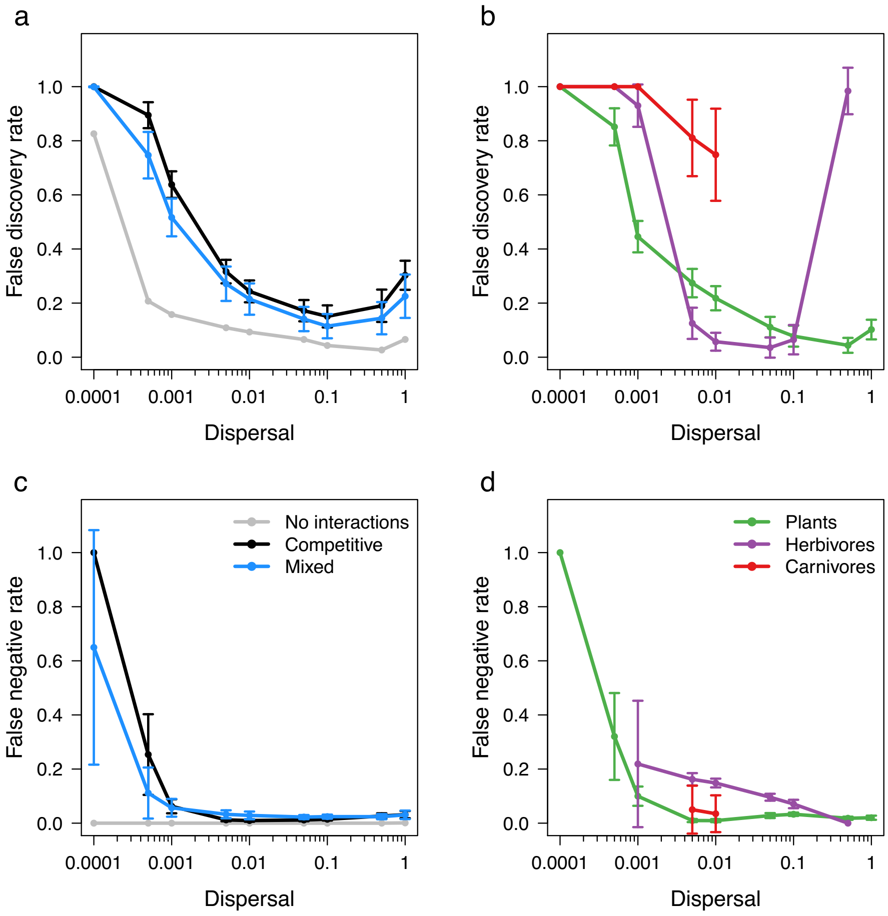

Figure E-2. The relationship between the rate of dispersal and the false discovery rate (a, b) and the false negative rate (c, d). Panels a and c show this relationship in communities with no interactions (grey), competitive interactions (black), and mixed interactions (blue). Panels b and d show this relationship across three trophic levels. One standard deviation around the mean, based on 50 replicates is shown.

THE ROBUSTNESS OF OUR RESULTS TO CHANGING THE OVERALL STRENGTH OF BIOTIC INTERACTIONS

The shape of the relationship between dispersal and prediction accuracy is robust over a range of interaction strengths. To show this, we compare the shape of the relationship between dispersal and Bray-Curtis similarity when we vary the strength of the biotic interactions using a scaling factor (1, 3, 5, 7, and 9x). We see that the overall shape of this relationship remains unchanged regardless of the type of interaction (Fig. E-3). The tri-trophic communities cannot persist when interaction strengths become too strong, but over the range where they do persist, the shape of the relationship between dispersal and Bray-Curtis similarity is consistent.

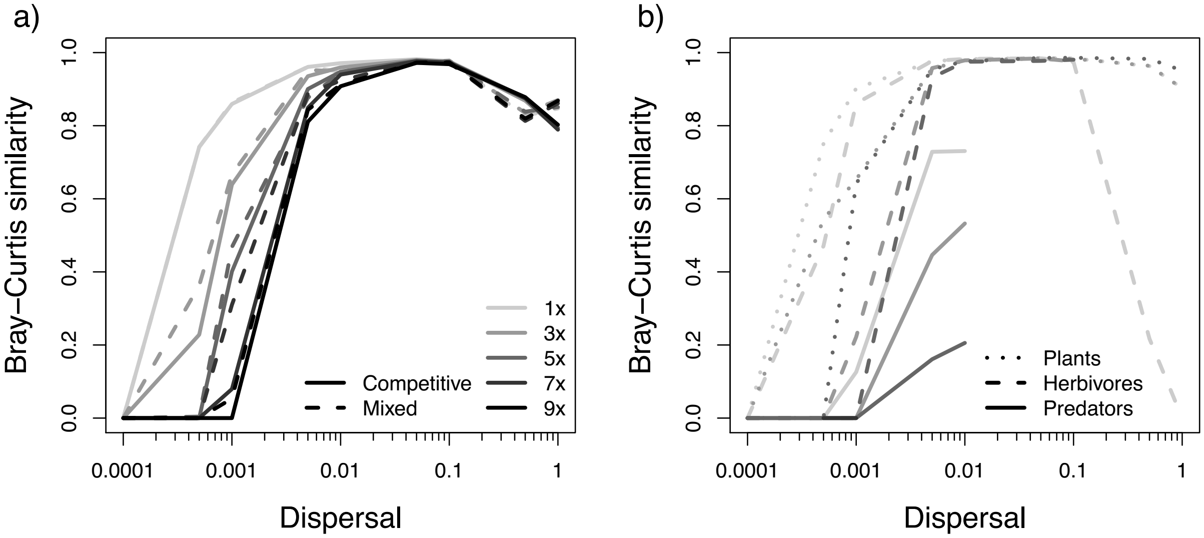

Figure E-3. A comparison in the shape of the relationship between the rate of dispersal and prediction accuracy (Bray-Curtis) over a range of interaction strengths (1, 3, 5, 7, and 9x the base strength; increasing with the shade of lines). The mean value based on 5 replicates is shown, error bars are omitted for clarity.

THE ROBUSTNESS OF OUR RESULTS TO VARIATION IN INTERSPECIFIC DISPERSAL RATES AND CLIMATE NICHE BREADTH

Our model assumes that all species disperse at the same rate and have the same climate niche breadth. Here we show that allowing interspecific variation in dispersal rates and niche breadth does not qualitatively change the relationship between dispersal and the accuracy of our predictions for a competitive community (Fig. E-4). We modelled interspecific variation in dispersal rates by drawing dispersal rates from a normal distribution centered around the given dispersal rate *a* with a standard deviation of *a*/5. We modelled interspecific variation in climate niche breadth by altering the value of σ in equation 2, which defines the width of the climate niche breadth. For this, values of σ were drawn from a normal distribution with a mean of 50 (the values previously used for all species) and a standard deviation of 10. Allowing for interspecific variation in dispersal rates and niche breadth resulted in minor deviations from the case when these values were uniform across all species, which did not change the overall relationship between dispersal and prediction accuracy (Fig. E-4).

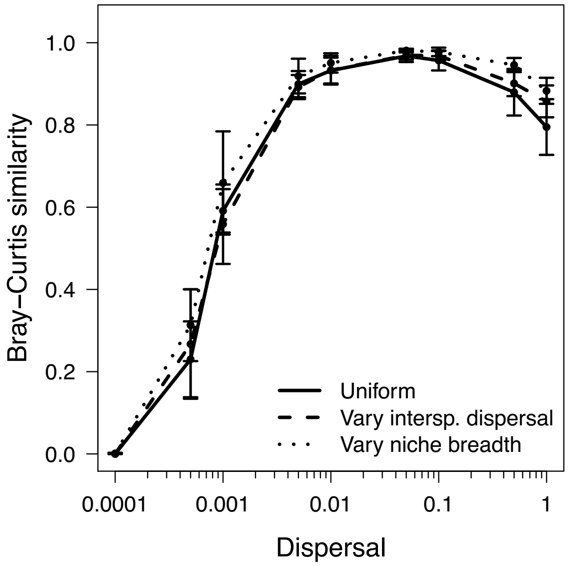

Figure E-4. A comparison in the shape of the relationship between the rate of dispersal and prediction accuracy (Bray-Curtis) in competitive communities with interspecific variation in dispersal rates (dashed lines), interspecific variation in niche breadth (dotted lines), and uniform dispersal and niche breadth (solid lines). One standard deviation around the mean, based on 5 replicates is shown.

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APPENDIX F – ROBUSTNESS OF THE SPATIAL INSURANCE EFFECTS OF BIODIVERSITY TO HABITAT LOSS

This manuscript is under consideration for publication in an academic journal: Patrick L. Thompson*, Bronwyn Rayfield*, & Andrew Gonzalez. *Evolutionary Ecology Research*.

*These authors contributed equally to this manuscript.

ABSTRACT

Question: How do spatial patterns of habitat loss affect the robustness of the insurance effects of biodiversity in fragmented landscapes? Does the underlying pattern of habitat connectivity in metacommunities play a role in maintaining biodiversity and ecosystem function in the face of habitat loss?

Background: Individual habitat patches can be ranked in terms of their contribution to the connectivity of the metacommunity. The betweenness centrality of a patch quantifies its role as a stepping-stone for individuals dispersing within the metacommunity.

Mathematical method: We analyzed a spatially explicit version of the resource competition metacommunity model. We simulated habitat loss in metacommunity networks composed of habitat patches connected by links for dispersal.

Key assumptions: Species differ in their environmental preferences. Local environmental conditions fluctuate asynchronously so that species must disperse in order to persist and maintain productivity. Habitat patches are lost sequentially, resulting in gradual fragmentation of the metacommunity.

Conclusions: Habitat loss reduces the spatial insurance effects of biodiversity by preventing species from dispersing to environmentally suitable areas. The robustness of metacommunities to habitat loss decreases dramatically when the patches with high betweenness centrality are lost. Metacommunities are generally most robust when the pattern of habitat connectivity is random and when the habitat patches that are lost have low betweenness centrality.

INTRODUCTION

Destruction of natural habitat is the major direct cause of biodiversity declines worldwide (IUCN 2014) and is projected to increase over the next century (Millennium Ecosystem Assessment 2005, IUCN 2014). The fragmentation of remaining habitat and the spatial arrangement of the surrounding landscape can compound the effects of habitat destruction, resulting in further biodiversity loss over time. For example, habitat isolation is one consequence of habitat fragmentation that is known to drive biodiversity loss (Hanski et al. 2013, Dobert et al. 2014) because it increases rates of local extinction and reduces rates of re-colonization. Patterns of landscape fragmentation are typically the result of both habitat loss and fragmentation, which have interdependent effects on biodiversity (Didham et al. 2012).

Loss of biodiversity in fragmented landscapes may also impact ecosystem function and erode associated ecosystem services essential for human well-being (Gonzalez et al. 2009, 2011, Cardinale et al. 2012, Hooper et al. 2012, Balvanera et al. 2014). For example, local biodiversity loss can reduce the efficiency with which communities convert nutrients into plant biomass (Cardinale et al. 2011), which has implications for a wide range of ecosystem services such as carbon storage and primary productivity (Kremen 2005). Moreover, biodiversity loss may decrease the stability of ecosystem functioning (Cardinale et al. 2012) resulting in ecosystems with more variable aggregate biomass through time (Gonzalez and Loreau 2009, Hector et al. 2010).

Maintaining functional connectivity, or the ability of species to disperse among habitat fragments may slow biodiversity loss and so mitigate the negative impacts of habitat loss and fragmentation (Loreau et al. 2003, Staddon et al. 2010, Hanski 2011). The spatial insurance hypothesis posits that dispersal mediates diversity at local and regional scales and so directly affects the function and stability of ecosystems in single habitat fragments, and across many fragments, at the scale of the landscape (Loreau et al. 2003, Gonzalez et al. 2009). Our ability to effectively manage fragmented landscapes requires that we understand how habitat loss erodes the role connectivity plays in maintaining biodiversity and ecosystem functioning.

Patterns of landscape fragmentation can be modeled as spatial networks (Fagan and Calabrese 2006, Dale and Fortin 2010, Gonzalez et al. 2011), wherein nodes represent habitat patches and links represent dispersal potential or pathways. The structure of habitat networks depends on the spatial distribution of links among nodes (Rayfield et al. 2011) and has been shown to affect ecological dynamics of the resident species (e.g. Ranta et al. 2008, Holland and Hastings 2008, Economo and Keitt 2010, Gilarranz and Bascompte 2012). One important aspect of network structure is the degree to which links are regularly or randomly distributed among the nodes. Ranta et al. (2008) found that increasing the randomness of links among populations reduced synchrony of the population fluctuations. Holland and Hastings (2008) also found that randomizing the structure of habitat networks reduced synchrony among predator-prey dynamics across the network.

Another important measure of network structure is patch centrality (Carroll et al. 2011). Centrality metrics rank the importance of habitat patches (or links) based on their local or regional position within the network (Bunn et al. 2000, Estrada and Bodin 2008, Carroll et al. 2011). For example, betweenness centrality (Freeman 1977) identifies habitat patches that are used as stepping stones to facilitate movement across the entire network. Protecting patches with high betweenness centrality can have a disproportionately large effect on maintaining regional landscape connectivity. Crucially, local biodiversity can be higher in habitat patches with high regional centrality because they are more accessible to species distributed in different regions of the landscape (Economo and Keitt 2010).

The structure of habitat networks can define the robustness of fragmented landscapes to further habitat loss (reviewed in Gonzalez et al. 2011). Robustness is generally attributed to network structures that maintain connectivity even when some nodes are removed (Albert et al. 2000, Dunne et al. 2002). Many networks are sensitive to the selective loss of the most connected nodes yet robust to the random loss of nodes (Cohen and Havlin 2010). We hypothesise that robust landscapes are able to maintain levels of biodiversity and ecosystem function despite the loss of some habitat patches. However, the impact of losing any given habitat patch will depend on its local biodiversity and centrality. To assess robustness involves simulating different patterns of habitat loss by sequentially removing patches based on different criteria such as their area (Urban and Keitt 2001) or centrality (Estrada and Bodin 2008). We examine the robustness of metacommunities, or networks of local communities embedded in fragmented landscapes (Economo and Keitt 2008, 2010), across a range of network structures spanning regular to random patterns of connectivity (Holland and Hastings 2008). We are interested in the degree to which habitat network structure can mediate impacts of habitat loss on biodiversity and ecosystem functioning. We simulate different patterns of habitat loss in these fragmented landscapes by using different node removal sequences that target randomly, strongly, or weakly connected nodes based on their betweenness centrality. We show that biodiversity and ecosystem function are sensitive to habitat loss and that patch centrality is a key measure mediating the robustness of the spatial insurance hypothesis in fragmented landscapes (Dunne et al. 2002).

METHODS

Resource competition metacommunity model

We modelled habitat loss in metacommunity networks using a resource competition model previously used to develop the spatial insurance hypothesis (Loreau et al. 2003, Gonzalez et al. 2009). The metacommunity networks consist of M habitat patches connected by $2*M$ links. Habitat patches are represented as dimensionless points with fixed locations on a ring with a radius of one (Fig. F-1). Each link has an associated length corresponding to the Euclidean distance between the locations of the connected patches. The networks were constructed first as regular lattices, where each patch was connected to its first and second order nearest neighbours. A given percentage of links were then randomly rewired to create random network structures that had a variety of shortcuts across the ring of habitat patches (Holland and Hastings 2008).

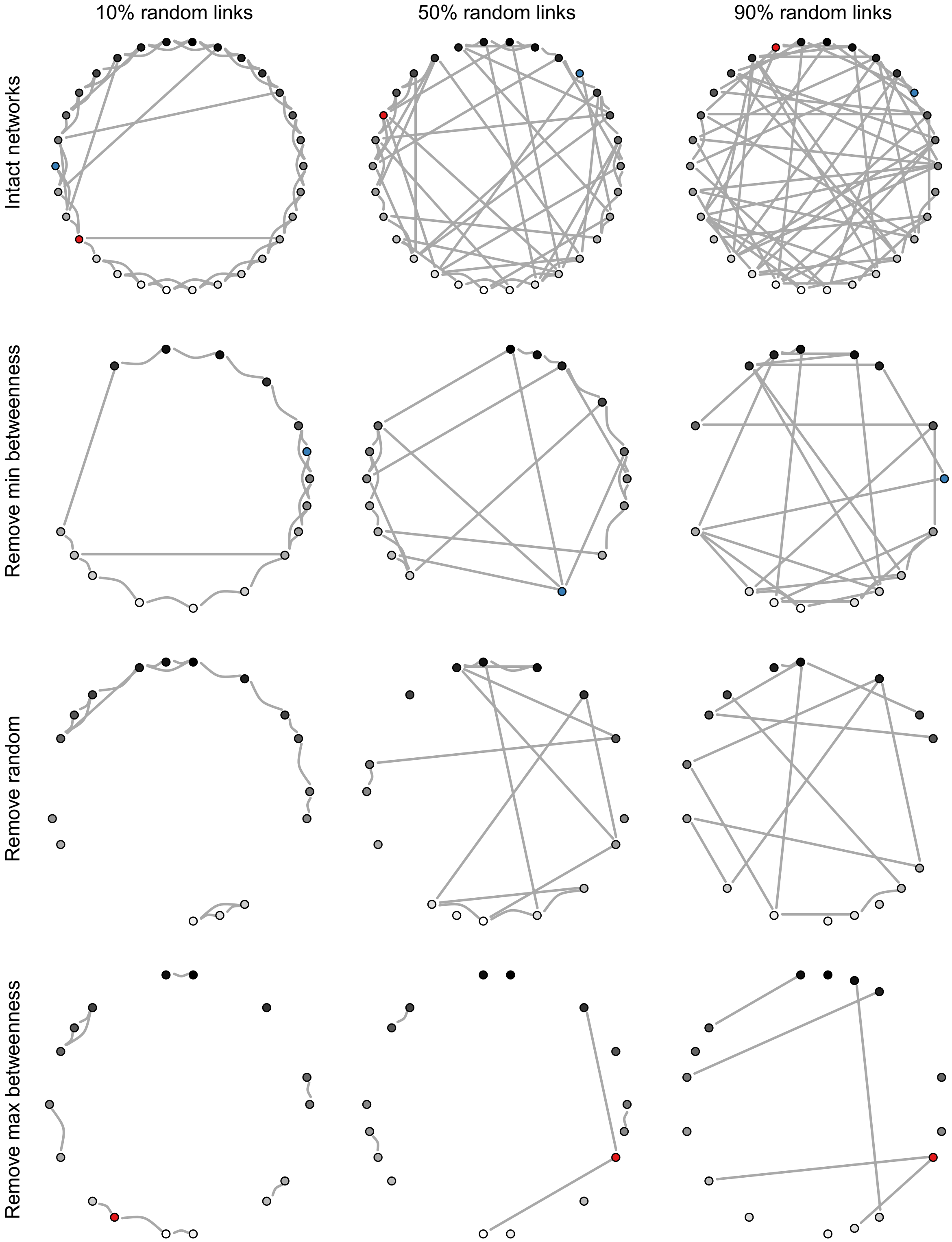
10% random links
50% random links
90% random links
Intact networks
Remove min betweenness
Remove random
Remove max betweenness

Figure F-1. Example metacommunity networks with 10, 50, and 90% random links. Metacommunities are shown as intact networks, and after 14 patches have been removed based on the three removal sequences: removing the patch with the minimum betweenness centrality, removing a random patch, and removing the patch with the maximum betweenness centrality. First and second order neighbour links are shown with curved lines for clarity, but distances are calculated based on Euclidean (straight-line) links. The next patch to be deleted in each of the centrality removal sequences is shown in blue (min betweenness) or red (max betweenness). The autocorrelated environmental conditions (*t* = 1) are illustrated by the gray scale of the patches.

The metacommunity dynamics are determined by the following equations governing resource competition:

$$\text{1)}\quad \frac{dN_{ij}(t)}{dt} = N_{ij}(t)\left[ec_{ij}(t)R_j(t) - m\right] + A_{ij}(t) - aN_{ij}(t)$$

$$\text{2)}\quad \frac{dR_j(t)}{dt} = I - lR_j(t) - R_j(t)\sum_i^S c_{ij}(t)N_{ij}(t)$$

where $N_{ij}(t)$ is the biomass of species i and $R_j(t)$ is the abundance of a single limiting resource in patch j at time t. We assume that there are S species in the metacommunity. They compete for a single limiting resource $R_j(t)$, and $c_{ij}(t)$ is the consumption of that resource by species i in patch j at time t. All species convert the resource into new biomass with an efficiency of e and die at a rate of m. $A_{ij}(t)$ is the amount of biomass of species i that arrives in patch j through immigration at time t. We assume that a given proportion of the biomass of each species is lost to emigration at each time step t, which is determined by the dispersal rate a. I is the rate of resource input, and l is the rate of resource loss.

Dispersal occurs via the network links and decreases with distance from source patch such that:

$$\text{3)}\quad A_{ij}(t) = aN_{ij}(t)\sum_{k\neq j}^{M}\frac{\exp\left(-Ld_{kj}\right)}{\sum_{f\neq k}^{M}\exp\left(-Ld_{kf}\right)}$$

where $A_{ij}(t)$ is the biomass of species i immigrating to patch j at time t. This is dependant upon the shortest network distance (computed as the weighted shortest path based on link length) between source patch k and the destination patch j. The distance dependence limitation L determines the strength of the exponential decrease in dispersal with distance d_{kj}. Because we assume equal emigration from all patches, the proportion of dispersing biomass to patch j from patch k is also dependant upon the distance from patch k to each other patch f. If patch j loses all connections with other patches in the network, $A_{ij}(t)$ will be equal to zero. We assume that emigration continues once patches become isolated, but that this biomass is lost from the metacommunity.

The environmental conditions E_j in each patch j fluctuate through time (e.g. temperature), following a sinusoid with a period T such that:

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

We assume that the initial conditions $Einit_j$ span a regular gradient between zero and one, but are autocorrelated (Moran's I = 0.43)(Moran 1950) in space so that the environments $E_j(t)$ in nearby patches are similar at any time t (Fig. F-1). We assume that the consumption rate $c_{ij}(t)$ of species i is determined by the match between its environmental optimum H_i and the local environmental conditions $E_j(t)$ such that:

$$5)\quad c_{ij}(t) = \frac{1.5|H_i - E_j(t)|}{10}$$

where the environmental optima H_i of the S species are equally spaced across the range of environmental conditions.

Landscape fragmentation simulations

We simulated 30-patch networks with nine species and the following model parameters: $e = 0.2$, $m = 0.2$, $I = 150$, $l = 10$, $N_{ij}(t = 1) = 10$, and $R_j(t = 1) = 9$. We set an extinction threshold to be $N_{ij} = 0.1$; populations below this were assumed extinct with a biomass of zero. We used the Euler method with $\Delta t = 0.08$ to approximate continuous dynamics. Each environmental fluctuation had a period $T = 40\,000$, which was chosen to be large enough to cause competitive exclusion of all but one species if there is no dispersal. We set the dispersal rate to be $a = 0.01$, a rate that allows for tracking of local environmental conditions. This allowed all species to persist in all patches, with maximum community biomass, and minimal temporal variation of biomass at both local and regional scales (Loreau et al. 2003, Gonzalez et al. 2009). This provides a best-case scenario with which to examine the impacts of different habitat loss sequences.

We compared networks that varied in the proportion of links that were randomly rewired (10, 30, 50, 70, and 90%) and a spatially implicit case, as a baseline reference, where dispersal was equal between all patches in the metacommunity. The spatially implicit networks match those that have been previously used to demonstrate the spatial insurance hypothesis (Loreau et al.

2003, Gonzalez et al. 2009). In the spatially explicit networks, distance dependent limitation *L* was set to 1.

Habitat loss

Each simulation ran for 100 000 time steps to allow initial transient dynamics to subside. We then simulated habitat loss by removing a single patch from the network, as well as its connections to other patches, every 20 000 time steps until only two patches remained. We compared three patch removal sequences: removing the patch with the lowest betweenness centrality, removing a random patch, and removing the patch with the highest betweenness centrality (Fig. F-1). The links connected to the patch were also removed. The betweenness centrality of a patch is computed as the proportion of shortest paths between all pairs of patches that include that patch (Freeman 1977, White and Borgatti 1994). Shortest paths were weighted by link lengths. Habitat patches with high betweenness centrality can be considered as key stepping-stones as they are included in the largest number of shortest paths. Betweenness centrality was recalculated each time a patch was removed to account for the effect of removing that patch on the betweenness centrality of patches in the remaining network. Only the random removal sequence could be used for the spatially implicit networks.

Response variables and analysis

All response variables were calculated based on sampled data taken every 1000 time steps, excluding the first 100 000 time steps. The number of connected components in each metacommunity was calculated to track changes to the network structure. A connected component is defined as a subset of patches in the metacommunity that are all either directly or indirectly connected. Patches in different components are not connected and therefore would not be able exchange individuals during metacommunity simulations.

Species richness and community biomass were calculated at both local and regional scales. Here we only present the mean local community biomass because regional biomass is lost with every patch removal, and so does not reflect the response of the metacommunity to patch removal. The temporal coefficient of variation (CV) of community biomass was calculated, both locally and regionally, for time steps between each patch removal. All reported variables are based on 100 replicate simulations, each with a new randomly generated network as an initial condition.

We calculated network robustness as the proportion of patches removed that is required to change each response variable beyond a given threshold (Dunne et al. 2002). These thresholds were: ≥50% of initial species richness, ≥75% of initial mean local biomass, and when local and regional biomass CV was ≤ 0.1 and 0.05 respectively. These threshold values were chosen to emphasize differences between networks and patch removal sequences.

All analyses, and simulations were conducted in *R* version 3.1.1 (R Development Core Team 2014) with networks generated using the *iGraph* package version 0.7.1 (Csardi and Nepusz 2006).

RESULTS

Connected components

The number of connected components had a unimodal shape in both the maximum betweenness and random patch removal sequences (Fig. F-2); initially increasing due to the removal of patches that bridge two or more connected components and subsequently decreasing as single-patch components were removed. The maximum betweenness patch removal sequence resulted in the largest numbers of connected components (up to 11 components) for the smallest fraction of patches removed (50% of patches) across all levels of link randomness. The network remained intact as a single connected component under the minimum betweenness patch removal sequence.

Species richness

Local and regional species richness declined from 9 to 1 species as patches were removed (Fig. F-3), and species loss occurred with fewer patch deletions in the spatially explicit metacommunities than in the spatially implicit case. The decline in species richness was most gradual in the minimum betweenness removal sequence and most rapid in the maximum betweenness removal sequence. Loss of species richness was similar at both local and regional scales, but the decreases

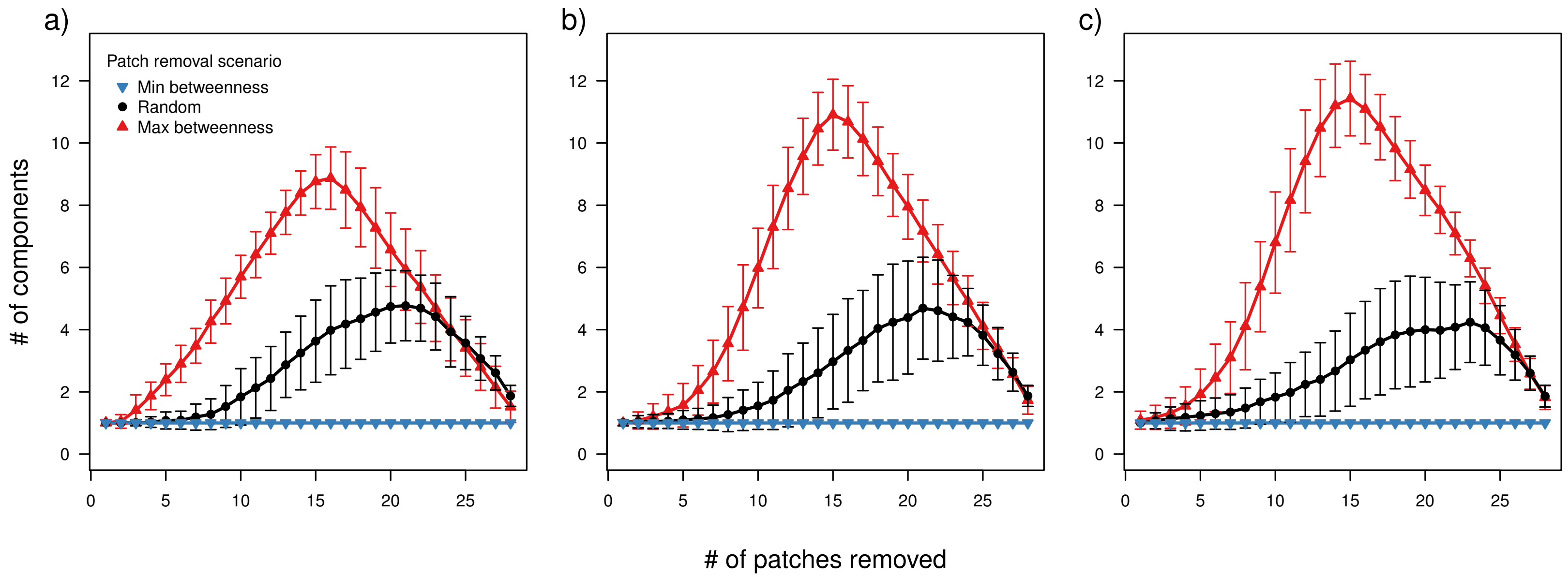

Figure F-2. The number of connected components resulting from the removal of patches in the three removal sequences (blue – min betweenness patch removed; black – random patch removed; red – max betweenness patch removed) in metacommunity networks with 10 (A), 50 (B) and 90 (C) percent random links. Error bars represent ± 1 standard deviation around the mean for 100 replicate networks.

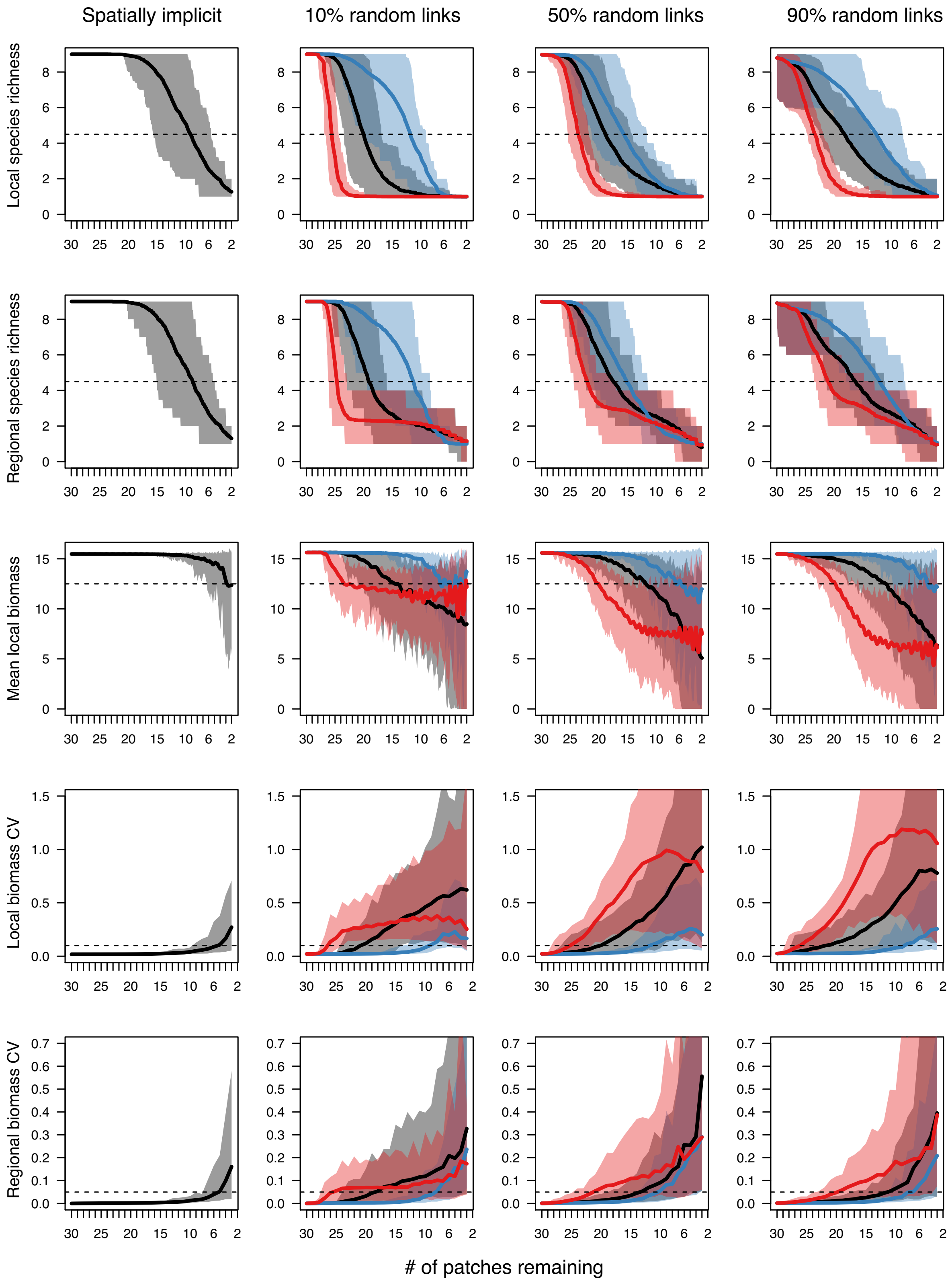
Spatially implicit
10% random links
50% random links
90% random links
Local species richness
Regional species richness
Mean local biomass
Local biomass CV
Regional biomass CV
0
2
4
6
8
5
10
15
0.0
0.5
1.0
1.5
0.1
0.2
0.3
0.4
0.5
0.6
0.7
30
25
20
15
10
6
2
# of patches remaining

Figure F-3. The change in the five response variables (local species richness, regional species richness, mean local biomass, local biomass CV, and regional biomass CV) as patches are removed from spatially implicit metacommunity networks and spatially explicit metacommunity networks with 10, 50, and 90% random links. Mean values (lines) and 95% quantiles (shaded areas) from 100 replicate networks are shown for the three removal sequences (blue – min betweenness patch removed; black – random patch removed; red – max betweenness patch removed). The threshold value for calculating robustness, seen in Fig. F-4, for each response variable is indicated with the dashed line.

were slightly greater at local scales, especially under the maximum betweenness removal sequence.

Species richness robustness was lower in the spatially explicit metacommunities compared to the spatially implicit case; the latter retained more than half the species until 75% of the patches had been removed (Fig. F4a,b). Local and regional species richness robustness followed the same general patterns with removal sequence and link randomness but differences among removal sequences were greater for local richness. The minimum betweenness removal sequence was most robust, retaining more than half of the species regionally until an average of 63% of the patches had been removed in the 10% random link networks. The maximum betweenness sequence was least robust, with removal of an average of 22% of the patches resulting in the loss of half of regional species richness in the 10% random link networks. The random removal sequence had intermediate robustness, with removal of an average of 39% of the patches resulting in the loss of half the species regionally in the 10% random link networks. Robustness increased with link randomness in the random and maximum betweenness patch removal sequences, but robustness showed a unimodal dip in the minimum betweenness removal sequence. The greatest difference in species richness robustness across the removal sequences occurred when link randomness was low.

Biomass

Mean local biomass declined as patches were removed (Fig. F-3), and biomass began to decline with fewer patch deletions in the spatially explicit metacommunities than in the spatially implicit case. The initial biomass was most robust in the minimum betweenness patch removal sequence and was the least robust in the maximum betweenness sequence. However, although biomass began to decline after only a few patches were removed in the maximum betweenness removal sequence, this decline slowed so that biomass remained at a relatively constant level as the remaining patches were removed. This asymptote occurred with fewer patch deletions under low link randomness, resulting in a negative relationship between final biomass and link randomness (Fig. F-3). This asymptote did not occur in the random removal sequence, and once biomass began to decline it did so relatively constantly as further patches were removed. Therefore, unless

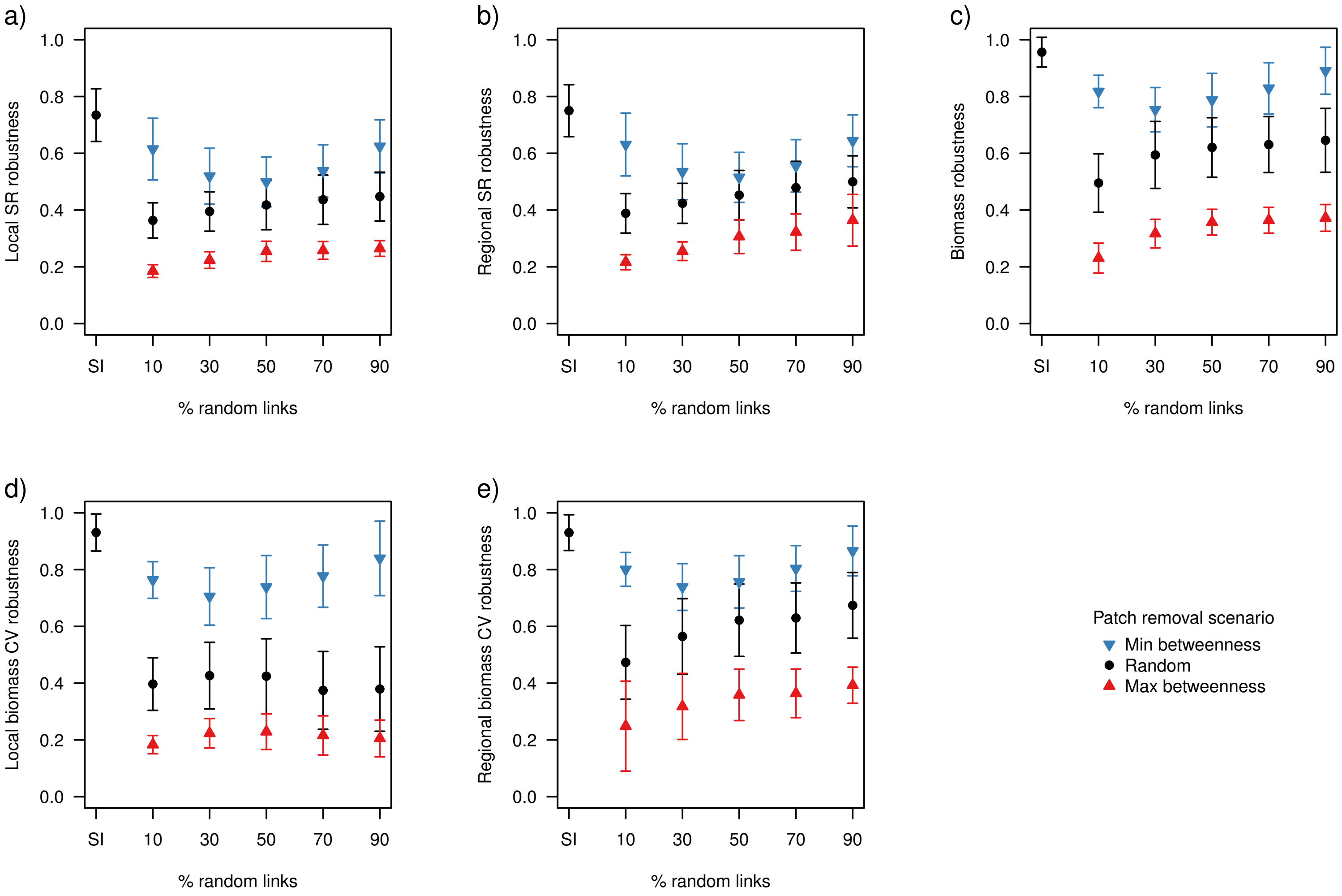

Figure F-4. Robustness for (a) local and (b) regional species richness (c) mean local biomass, and (d) local and (e) regional biomass CV across metacommunity link randomness. SI indicates the spatially implicit metacommunities. Error bars represent ± 1 standard deviation around the mean based on 100 replicate networks.

networks had high link randomness (90%), the final biomass when only two patches remained was higher in the maximum betweenness removal sequence than in the random removal sequence. The decline in biomass only reached an asymptote in the minimum betweenness removal sequence in networks with low link randomness (10%), and in all cases the highest biomass was retained in the minimum betweenness removal sequence. Biomass robustness showed similar patterns to species richness robustness but the unimodal dip of the minimum betweenness sequence was less pronounced (Fig. F-4c).

Local biomass variability (CV) increased as patches were removed (Fig. F-3), and this increase was greater in the spatially explicit metacommunities than in the spatially implicit case. The maximum betweenness removal sequence showed sharp increases in local biomass variability with the removal of only a few patches, but these increases slowed, and then local biomass CV declined as subsequent patches were removed. As with biomass, this result occurred with fewer patch deletions in networks that had low link randomness, resulting in a positive relationship between final biomass CV and link randomness (Fig. F-3). The random patch removal sequence was less sensitive to initial patch deletion, but increases in biomass variability were more consistent, only saturating in networks with high link randomness (90%). Therefore, the final biomass CV, once all but two patches had been removed, was highest with the random patch removal sequence except in networks with high link randomness (90%). Initial patch removals had little effect on local biomass CV in the minimum betweenness removal sequence. In this case, biomass variability only became noticeable after half the patches had been removed. These increases tended to saturate at low CV, especially when link randomness was not high (< 90%). The minimum betweenness removal sequence always resulted in the lowest local biomass variability. Local biomass CV robustness showed similar patterns to mean biomass robustness but robustness did not increase with link randomness in the random and maximum betweenness removal sequences (Fig. F-4d).

Regional biomass variability (CV) was always lower than local biomass variability (Fig. F-3). Unlike local biomass CV, increases in regional biomass variability did not reach an asymptote as patches were removed. In addition, the minimum betweenness removal sequence resulted in similar or higher regional biomass variability than the maximum betweenness removal sequence, when only a few patches remained (<6) and when network links were not highly random (<90%). Regional biomass CV robustness showed similar patterns to mean biomass robustness (Fig. F-4e).

DISCUSSION

The diversity and ecosystem function of metacommunities in this study are more robust to the loss of random or least-connected habitat patches than of highly connected habitat patches. Fragility to the loss of highly connected nodes is a common property of many real-world networks (Dunne et al. 2002, Cohen and Havlin 2010). As expected, the more connected a habitat patch is, the more disruptive its loss will be to species' dispersal and, consequently, to the diversity and functioning of the metacommunity network. Previous assessments of landscape robustness have found that different node removal criteria have different effects on various aspects of the network structure, such as network diameter (Urban and Keitt 2001), network modularity (Albert et al. 2013), size of the largest connected component, and network cliqueishness (Estrada and Bodin 2008). Our study goes further than these assessments by demonstrating both the structural and the functional consequences of habitat loss in fragmented landscapes.

The robustness of our metacommunities to habitat loss depends on the degree to which the removal of the patches disrupts the connectivity of the landscape. Because the local environmental conditions are constantly changing, diversity and productivity can only be maintained when species are able to track favourable conditions through dispersal (Loreau et al. 2003, Gonzalez et al. 2009). When habitat loss reduces landscape connectivity, species become restricted to subsets of the remaining patches. These subsets, or connected components, of the metacommunity contain only part of the environmental range of the intact metacommunity, and so species are unable to track their environmental optima as the local conditions change over time. As a result, species diversity and biomass decline, and biomass becomes more temporally variable because species are trapped in habitat patches and are forced to fluctuate in response to local environmental conditions. The metacommunity is least robust to the removal of patches with the highest betweenness centrality because their removal causes the most abrupt changes to the connectivity of the habitat network. In the example shown in Fig. F-1 (10% random links), the removal of a single patch with the highest betweenness disconnects the bottom-left region. Furthermore, removing 50% of the patches with the highest betweenness centrality results in a metacommunity of 15 remaining patches that is isolated into, on average, nine subgroups, each comprised of one or two neighboring habitat patches (Fig. F2a). In comparison, the metacommunity is most robust to the removal of patches with low betweenness centrality because network connectivity is always preserved, regardless of the number of patches removed (as shown in Fig. F-1 and Fig. F-2). However, although the metacommunities are structurally robust to the minimum betweenness removal sequence (at least in terms of the number of connected components; Fig. F-2), patches can become more isolated if they are only connected to other patches by long pathways. This isolation reduces the amount of dispersal to these patches, with negative consequences for diversity and productivity. Patch isolation is responsible for the reduced functional robustness of these networks compared to the spatially implicit metacommunities, the case where all patches remain equally connected.

The initial distribution of links among habitat patches in fragmented landscapes has a weak ability to buffer biodiversity and ecosystem functioning against habitat loss. Our results show a trend of positive correlation between the randomness of network links and functional robustness (Fig. F-4). This result is consistent with the effects of link randomness on population (Ranta et al. 2008) and predator-prey synchrony (Holland and Hastings 2008). However, the positive effects of link randomness are small compared to the negative effects of removing patches with high betweenness centrality. Furthermore, the positive effects of link randomness on functional robustness are not caused by structural robustness because the number of connected components increases with link randomness (Fig. F-2). Rather, link structure affects metacommunity network robustness because it determines how much environmental heterogeneity is retained in the connected components as habitat is lost. Components containing subsets of patches that are more environmentally heterogeneous are able to sustain more diversity and function because there is better opportunity to track changes in the environment through dispersal among patches. The environments in our metacommunities are spatially autocorrelated so the environmental heterogeneity of connected patches increases with network randomness, resulting in the increased robustness of these networks. There is, however, a benefit to having a less random link structure during the minimum patch betweenness removal sequence. In this removal sequence, the remaining patches are connected so the full range of environmental heterogeneity is always accessible. The benefit of networks with low link randomness is that most links are between patches with similar environments, so conditions are generally favourable for dispersing individuals requiring an environment that matches their trait optimum. Therefore, the sensitivity of metacommunity robustness to link randomness depends on the spatial autocorrelation of local environments (Moran 1953).

Our model is an obvious simplification of the dynamics of real metacommunities, but our approach allows us to identify how habitat loss will affect the spatial maintenance of biodiversity and ecosystem function (Chesson 2000a, Loreau et al. 2003, Gonzalez et al. 2009). Other coexistence mechanisms that we did not model, such as the temporal storage effect (Chesson 2000b), non linear response to environmental fluctuations (Levins 1979), or species that specialize on different resources (Tilman 1990), would likely increase metacommunity robustness to habitat loss. We chose conditions that maximized the spatial insurance effects of diversity on ecosystem function by fixing dispersal rate, maintaining the asynchrony of local environmental conditions, and modeling species with environmental optima that are evenly spaced across the environmental range. However, spatial insurance will still occur as long as (1) the metacommunity is connected via dispersal, (2) local environmental variation is not completely spatially synchronous, and (3) species exhibit differential responses to these environmental conditions (Gonzalez et al. 2009). We have extended previous study of the spatial insurance hypothesis by studying the role that network connectivity plays in the robustness of spatially explicit metacommunities. Our networks are still idealized models of real habitat networks embedded in fragmented landscapes, but we have shown that the core mechanisms of the spatial insurance hypothesis are retained when dispersal is limited by the constraints of dispersal distance and network structure.

The use of current network approaches in conservation biology promises to accelerate our understanding of biodiversity change and our ability to mitigate its impacts on ecosystem function. A recent application of network approaches to conservation is the design of ecosystem networks for sustainable landscapes (Opdam et al. 2006, Vos et al. 2008). Ecosystem networks are composed of mixed ecosystem types (e.g., forest, wetland, grassland etc.) linked into a spatially coherent network through the movement of organisms and resources (Opdam et al. 2006). Our model captures the essential features of ecosystem networks, and our results point to the value of a network perspective for the management of highly fragmented landscapes for biodiversity and associated ecosystem services. For example, we might manage patch centrality in a network of forest patches to sustain networks of pollinators required for pollination services, or complex communities of natural enemies for pest control in agricultural landscapes. Recent experimental results further strengthen the science of ecosystem networks (Tewksbury et al. 2002, Brudvig et al. 2009, Staddon et al. 2010, Chisholm et al. 2010) and stress the value of ecological corridors as a practical means of maintaining landscape connectivity and the spatial insurance effects of biodiversity.

CONCLUSION

Our analysis demonstrates how habitat loss within fragmented landscapes can reduce biodiversity and ecosystem function by eroding spatial insurance effects of biodiversity. The impact of habitat loss depends on the degree to which species can track their environmentally optimal conditions within the habitat patches that remain. The loss of patches with high betweenness centrality hinders the ability of species to relocate to environmentally suitable habitat patches. The underlying distribution of links in metacommunity networks determines how habitat loss reduces the range of environmental heterogeneity in the residual network. It is the connectivity and heterogeneity of the landscape that governs how much biodiversity can be maintained and the degree to which this diversity can buffer environmental change. Together, these results suggest that robustness of fragmented landscapes to ongoing habitat loss can be maintained if conservation strategies focus on protecting or restoring landscape connectivity.

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