Coexistence in a Warm and Patchy World

by

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A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy
Department of Ecology and Evolutionary Biology
University of Toronto

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Abstract

For the many species that rely on patchily distributed resources, patterns of coexistence and diversity are the product of local abiotic and biotic interactions and inter-patch dispersal. Understanding the multi-scale drivers of coexistence in patchy landscapes has become increasingly pressing, as habitat fragmentation makes the world patchier, and warming threatens to disrupt biological processes across spatial scales. In my thesis, I use meta-analytic, observational and experimental approaches to understand how local species interactions and dispersal shape diversity in patchy landscapes, and how warming disrupts these dynamics.

In Chapter 1, I review metacommunity experiments to identify when common experimental approaches that homogenize metacommunities fail to test existing theory, and outline how emerging theory on the invasion criterion, food webs and priority effects could be used to help reveal the mechanisms underlying observed responses. In Chapter 2, I use dispersal and anti-predator traits of specialist milkweed herbivores to predict species’ distributions across a patchy landscape and test the importance of local top-down pressure in mediating classic biogeographic relationships. In Chapter 3, I test predictions about the impact of warming on plant-herbivore interactions and the importance of species’ arrival order and demonstrate how warming strengthens trophic interactions, amplifies priority effects and alters the interspecific differences in dispersal that determine arrival order. In Chapter 4, I test the combined impact of
warming-induced changes to local competitive interactions and dispersal on metacommunity diversity, and show that positive local effects of warming, combined with the risk of moving across the matrix, can produce unexpected interactive effects of temperature and connectivity on metacommunity diversity.

By describing and implementing novel approaches that provide better tests of metacommunity theory, and applying a multi-scale approach to climate change research, my thesis informs our understanding of how natural and anthropogenic processes shape diversity in patchy landscapes.
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A desire to understand the processes that maintain biological diversity and allow species to coexist has long motivated ecological research; we want to know why species live where they do, and how so many species are able to live together (Grinnell 1917; Hutchinson 1959). Decades of theoretical and empirical work has revealed how organisms’ interactions with their local abiotic and biotic environments (MacArthur 1958; Paine 1969; Shmida & Wilson 1985; Chesson 2000), and their movements across the landscape (MacArthur & Wilson 1967; Levins 1969; Hubbell 2001; Leibold et al. 2004), shape the ecological patterns we see in nature. Unfortunately, this deeper understanding of the processes that structure communities has coincided with two major anthropogenic global changes that threaten to disrupt these very dynamics. As humans modify and destroy essential habitat, forcing species to navigate increasingly fragmented landscapes, an already heterogeneous world is becoming even patchier (Fahrig 2003). And as greenhouse gas emissions raise global temperatures, evidence is accumulating that warming can fundamentally alter the physiological and ecological processes that drive patterns of persistence and coexistence (Parmesan & Yohe 2003; Gilman et al. 2010; Urban 2015). These joint anthropogenic pressures necessitate a more complete understanding of the drivers of coexistence in patchy landscapes, and deeper insight into how warming disrupts ecological processes across spatial scales. These are the two aims of my thesis.

Here, I use meta-analytic, observational and experimental approaches to understand how local species interactions and dispersal together shape diversity in patchy landscapes (Chapters 2 and 3), and to predict how climate change will disrupt these dynamics (Chapters 4 and 5). The first half of my thesis builds on an extensive body of research describing the mechanisms through which species coexist in spatially structured environments. The second half of my thesis uses emerging insights into the effects of temperature on metabolic rates, species interactions and dispersal to investigate the multi-scale effects of warming in patchy landscapes. Below, I outline the ideas and evidence that motivated this research.
Coexistence in spatially structured environments

The integration of ecological processes across spatial scales has been elusive since the inception of modern ecological research (Loreau & Mouquet 1999). As ecology emerged as a rigorous scientific discipline over half a century ago, two separate bodies of research focused at different spatial scales developed in parallel, with surprisingly little integration (Mouquet & Loreau 2002; Losos & Ricklefs 2009). First, a major thrust of early ecological work concentrated on the suite of local processes that manifest from a species’ interactions with its immediate abiotic and biotic environment and govern local coexistence within a community (MacArthur 1958; Connell 1961; Paine 1966; Schoener 1974). Early theory described the niche as a species’ place or role in the local abiotic and biotic landscape (Grinnell 1917; Elton 1927), or the local abiotic and biotic axes that jointly determine population persistence (Hutchinson 1957; MacArthur & Levins 1967). Early experiments emphasized the role of abiotic gradients such as light, moisture and nutrients in shaping species persistence and distributions (Southward 1958; Whittaker 1960). Likewise, the recognition that the competitive and consumptive dynamics that play out the local scale are major drivers of ecological patterns led to much of the foundational theoretical (Paine 1966; MacArthur & Levins 1967) and empirical research (Gause 1932; MacArthur 1958; Connell 1961; Paine 1966) that still informs ecological inquiry today. These advances indelibly shaped ecologists’ worldview by laying the foundations for decades of work examining the local processes that drive organisms’ local persistence, performance and interactions.

Meanwhile, the joint observations that species often occupy discrete islands of habitat imbedded within a non-habitat matrix, and that rates of movement between these local communities can play a major role in shaping their diversity, led to a separate body of contemporaneous research (MacArthur & Wilson 1967; Simberloff 1974). The Theory of Island Biogeography describes how a balance between colonisations and extinctions drives diversity in island systems (MacArthur & Wilson 1967). Decreasing extinction rates with increasing island size, combined with increasing colonization rates with increasing proximity to a mainland source, determine the equilibrium number of species on a given island, and result in high diversity on large, well-connected islands (MacArthur & Wilson 1967). In contrast to local theories that strongly emphasized species’ differences, The Theory of Island Biogeography considered species to be ecologically equivalent, and has served as a precursor to subsequent neutral theories of
coexistence (Hubbell 2001). Concurrently, the development of metapopulation models describing how continuous extinctions and recolonizations of populations within local habitat patches scale up to shape regional population dynamics also drew attention to the ecological dynamics playing out in patchy landscapes (Levins 1969). These spatially-centred theories of ecological dynamics in patchy environments have become major touchstones in the field of ecology, and continued theoretical expansion to incorporate additional subtleties such as the positive relationship between island isolation and extinction rates (Brown & Kodric-Brown 1977) and the integration of competitive (Tilman 1994) and trophic dynamics (Gravel et al. 2011) have expanded their scope and applicability. Likewise, empirical work testing this theory in a wide variety of patchy systems exemplify the continued relevance of early models describing the ecologically dynamics that play out in patchy environments (Losos & Ricklefs 2009; Harvey & MacDougall 2014; Jones et al. 2015).

Insights into competitive and consumptive interactions occurring at the local scale, and species’ movement across the landscape occurring at the regional scale, form the foundation on which modern ecological research was built, and yet these two bodies of work were initially poorly integrated. Indeed, ‘MacArthur’s Paradox’ describes the disconnect between Robert MacArthur’s niche-based theories of local coexistence and his neutral theory of island biogeography (Schoener 1983; Loreau & Mouquet 1999). However, the decades that followed saw a major discussion about the disparate and joint roles of local and regional processes in structuring communities (Cornell & Lawton 1992; Holt 1993). As efforts grew to integrate ecological processes across local and regional scales, emerging theory revealed how dispersal between local patches modifies local outcomes through a variety of mechanisms that bridge the local-regional gap: mass effects that allow incoming colonists to support sink populations (Shmida & Wilson 1985; Pulliam 1988), competition-colonization trade-offs that allow inferior competitors to persist through continued colonization of new patches (Tilman 1994), and neutral species interactions in which stochastic speciation, extinction and dispersal events structure alpha and beta diversity across landscapes (Hubbell 2001). This progress in integrating the joint impacts of local interactions and dispersal spurred a renewed effort to summarize the coexistence mechanisms that operate in patchy landscapes, and gave rise to the field of metacommunity ecology (Wilson 1992; Leibold et al. 2004; Holyoak et al. 2005).
A metacommunity consists of a group of local communities that are connected by dispersing individuals (Leibold et al. 2004; Holyoak et al. 2005). Within local communities, species interact frequently enough to affect one another’s demographic rates, while across local communities, the rate of movement of individuals between patches is high enough to affect regional coexistence outcomes, but low enough to prevent discrete patches from acting as a single community of regularly interacting individuals (Leibold et al. 2004). The metacommunity concept thus hinges on the central idea that processes operating at two discrete scales have important consequences for coexistence and diversity: local processes such as competition and predation, along with the regional process of dispersal. As with metapopulations, these two discrete scales of organization can cause local and regional scale extinction or coexistence outcomes to diverge (Levins 1969; Leibold et al. 2004). For example, frequent colonization of unfavourable patches can maintain coexistence at the regional scale despite deterministic extinctions at the local scale (Shmida & Wilson 1985). Metacommunity theory describes the suite of coexistence mechanisms that operate uniquely in patchy environments and that rely on both local processes and dispersal (Leibold et al. 2004; Holyoak et al. 2005). These mechanisms have been grouped into four paradigms that form the theoretical framework for metacommunity ecology: patch dynamics, mass effects, species sorting and neutral dynamics (Leibold et al. 2004; Holyoak et al. 2005; Table S2.1). This metacommunity framework has been remarkably successful in summarizing and stimulating a wealth of theoretical predictions about how dispersal affects metacommunity diversity (e.g. Mouquet and Loreau 2003; Gilbert 2012; Haegeman and Loreau 2014). Concomitantly, the two decades since the framework was introduced have seen a rapid rise in empirical work investigating the joint role of local processes and dispersal in shaping diversity (Cadotte 2006; Logue et al. 2011). This developing body of research has made major strides in moving ecological work beyond the local scale to highlight how spatial structure, connectivity and dispersal drive ecological patterns.

Despite the promise of linking local and regional coexistence mechanisms to observed relationships between connectivity and diversity, however, progress in this field has been hindered by a mismatch between theory that synthesizes local and regional processes, and empirical research that has faced challenges in incorporating complexity across scales. This is in large part because several key characteristics of natural metacommunities that contribute to
regional coexistence are extremely difficult to incorporate into empirical research. For example, differences in dispersal ability among species competing across a landscape of habitat patches permit competition-colonization trade-offs to maintain weak competitors (Tilman 1994; Cadotte 2007). Likewise, these dispersal differences determine which species arrives first at a local patch, which can have major implications for the trajectory of community assembly (Chase 2003; Fukami 2015). Local trophic interactions can also fundamentally alter the relationship between dispersal and diversity by dampening the role of spatial processes in determining species’ distributions (Kneitel & Miller 2003; Haegeman & Loreau 2014). The complexities that arise from heterogeneity in dispersal and trophic interactions are, unsurprisingly, difficult to incorporate in to empirical tests. This has produced major gaps in our understanding how local and regional process shape the metacommunity patterns observed in nature.

The first half of my thesis is focused on filling these gaps by solidifying links between the local and regional processes that shape coexistence in patchy landscapes. In Chapter 1, I review 20 years of metacommunity experiments, discuss why a mismatch between theory and experimental work has arisen in this field, and propose new approaches that are designed to align metacommunity theory with empirical work and test emerging questions about species coexistence in patchy landscapes (Grainger & Gilbert 2016). In Chapter 2, I use an observational study to demonstrate how interspecific differences in dispersal and predator-resistance can be used to predict the joint effects of local trophic interactions, patch size and patch connectivity in driving species’ distributions across a patchy landscape (Grainger et al. 2017). Together, these chapters strengthen and expand empirical links between the local species interactions and dispersal dynamics that jointly shape metacommunities.

Local and regional responses to warming

As we enter an era characterized by anthropogenically driven increases in global temperatures, a comprehensive understanding of the processes that shape ecological communities will be essential for determining when and how warming will disrupt these dynamics and set ecological communities on unrecognizable and irreversible trajectories. While there is mounting evidence that warming fundamentally alters both local competitive and trophic dynamics (Tylianakis et al. 2008; O’Connor 2009; Gilman et al. 2010), and the rate at which species move between local
communities (O'Connor et al. 2007; Travis et al. 2013), the joint effects of warming on local interactions and dispersal have only recently begun to be explored (Limberger et al. 2014; Thompson et al. 2015; Salt et al. 2016). Instead, climate change research has largely focused on species’ responses at very small local scales (Walker et al. 2006; Gruner et al. 2017), or range shifts and extinctions at very large continental scales (Parmesan & Yohe 2003; Thomas et al. 2006). This is despite the fact that the fates of many species may hang in the balance of processes operating at the mesoscale (Urban et al. 2012a). Fortunately, an integration of insights from metabolic theory that describes the local effects of warming on organisms, populations and communities, with emerging evidence for the role of warming in shaping dispersal rates, can provide a promising path forward for understanding responses to climate change in a spatially complex world (Urban et al. 2012b; Gilbert & O’Connor 2013).

For ectotherms, temperature governs biological processes at the most basic molecular level, by determining rates of enzyme activity and cellular function (Gillooly et al. 2001). The temperature-dependence of metabolic rates has been recognized for over a century (Arrhenius 1889), and has come to be understood as a general rule that can be applied across much of the tree of life (Brown et al. 2004). By dictating the rate and timing of organisms’ emergence, growth, feeding, reproduction and death, temperature governs ecological processes more fundamentally, and potentially more predictably, than any other environmental factor (Brown et al. 2004; Savage et al. 2004; Dell et al. 2011). As the earth’s changing climate has triggered a renewed interest in the role of temperature in mediating biological processes, research has revealed how organismal responses to temperature scale up through levels of biological organization to shape processes at population (Amarasekare & Savage 2012) and community levels (O’Connor 2009). Indeed, the positive impact of temperature on biological rates, which results in increased performance up to a species-specific thermal optimum, has been recognized as a consistent response in ectotherms (Dell et al. 2011) that can predict species’ performance across a temperature gradient (Amarasekare & Savage 2012). Going a step further, recent research has demonstrated how the disparity between the temperature-dependence of photosynthesis and respiration can cause consumers to outpace their autotrophic resources, which leads to stronger top-down control and eventual consumer population crashes (O’Connor et al. 2011; Gilbert et al. 2014). These theoretical insights that are emerging from metabolic
theory to describe the temperature-dependence of species interactions provide a powerful tool to predict and test local community responses to a changing climate.

While the myriad impacts of temperature on local-scale ecological processes have been the focus of a rapidly growing body of research, the role of temperature in mediating dispersal rates has received much less attention. This is despite the evidence that temperature can impact dispersal rates through a wide variety of direct and indirect pathways (Travis et al. 2013). For example, warming-induced changes in behavior, habitat quality and species interactions have been shown to both induce and inhibit dispersal (Altermatt et al. 2008; McCauley & Mabry 2011; Travis et al. 2013). Organisms that respond strongly to environmental cues for dispersal, such as insects, should be especially affected by warming that alters local conditions and population dynamics (Zera & Denno 1997; Travis et al. 2013). Changes in the propensity and ability of organisms to move between habitat patches could have major implications for metacommunity processes driven by inter-patch movement (Gilbert & O’Connor 2013). However, the implications of temperature-dependent dispersal rates on metacommunity dynamics remain almost entirely unexplored (but see Altermatt et al. (2008)).

Despite recent calls to move global change ecology research beyond local communities by considering the effect of warming on processes operating at the metacommunity scale, integrating warming effects across spatial scales remains challenging (Urban et al. 2012a; Gilbert & O’Connor 2013). Through interactive and independent impacts on local interactions and dispersal, warming is likely to have cascading effects that alter individual, population, community and metacommunity processes in complex ways. For example, warming could alter both the order in which species arrive at a local site by changing dispersal rates, while also changing the impact of arrival order on coexistence outcomes by altering competitive dynamics. Or, by accelerating local resource-consumer dynamics, warming could increase the importance of connectivity to neighboring patches containing additional resources. Despite strong evidence for the impacts of warming at the local scale, and emerging evidence of temperature effects on dispersal, the combined effects of temperature on local interactions and dispersal remains an open question.
CHAPTER 1: GENERAL INTRODUCTION

The second half of my thesis is focused on filling these gaps in our understanding of how temperature impacts ecological dynamics in patchy landscapes. In Chapter 4, I test predictions about the impact of warming on plant-herbivore interactions, and demonstrate how these shifts alter both dispersal rates and the importance of species’ arrival order (Grainger et al. In press). In Chapter 5, I use experimental metacommunities to test the combined impact of warming-induced changes to local competitive interactions and dispersal on species performance and diversity (Grainger & Gilbert 2017).

Thesis overview

In this thesis, I investigate how local species interactions and dispersal shape diversity and coexistence in patchy landscapes, and how warming alters these processes. To do this, I critically review the literature and propose empirical approaches for testing metacommunity theory (Chapter 2), sample natural metacommunities (Chapter 3), and conduct controlled experiments in the lab (Chapter 4) and field (Chapter 5). For my empirical chapters, I use the small suite of insects that specialize on patchily distributed common milkweed plants (Asclepias syriaca L.) as a model metacommunity. Although each chapter was written as a stand-alone paper, the four projects are linked by my overarching goal of understanding the drivers and disrupters of coexistence in an increasingly warm and patchy world.

References


CHAPTER 1: GENERAL INTRODUCTION


CHAPTER 1: GENERAL INTRODUCTION


Chapter 2: Dispersal and diversity in experimental metacommunities: linking theory and practice


Abstract

There has been a recent rise in the number of experiments investigating the effect of dispersal on diversity, with many of the predictions for these tests derived from metacommunity theory. Despite the promise of linking observed relationships between dispersal and diversity to underlying metacommunity processes, empirical studies have faced challenges in providing robust tests of theory. We review experimental studies that have tested how dispersal affects metacommunity diversity to determine why shortcomings emerge, and to provide a framework for empirical tests of theory that capture the processes structuring diversity in natural metacommunities. We first summarize recent experimental work to outline trends in results and to highlight common methods that cause a misalignment between empirical studies and the processes described by theory. We then identify the undesired implications of three widely used experimental methods that homogenize metacommunity structure or species traits, and present alternative methods that have been used to successfully integrate experiments and theory in a biologically relevant way. Finally, we present methodological and theoretical insights from three related ecological fields (coexistence, food web and priority effects theory) that, if integrated into metacommunity experiments, could help isolate the independent and joint effects of local interactions and dispersal on diversity, and reveal the mechanisms underlying observed dispersal-diversity patterns. Together, these methods can provide stronger tests of existing theory and stimulate new theoretical explorations.

Introduction

A central goal in ecology is to understand the processes that maintain biodiversity (Chesson 2000; Hubbell 2001). The growth of metacommunity ecology over the past several decades represents a major advance toward this goal; by describing processes through which local species interactions and dispersal together determine the diversity of species living in spatially
structured environments, metacommunity research has helped move ecology beyond the local scale (Levins & Culver 1971; Shmida & Wilson 1985; Holt 1993; Holyoak et al. 2005). These processes have been grouped into four paradigms that form the theoretical framework for metacommunity ecology, and are distinguished by differences in the roles of habitat heterogeneity, competitive asymmetries and dispersal rates in structuring local and regional coexistence (Appendix A Table S2.1; Leibold et al. (2004); Holyoak et al. (2005)).

Since this conceptual synthesis of metacommunity ecology (Leibold et al. 2004), theoretical work in this field has expanded on these classic paradigms to provide a more nuanced understanding of the processes that structure metacommunities. For instance, the growing recognition that aspects of multiple paradigms are likely to characterize any given system has led to calls for research that integrates across paradigms to include multiple metacommunity coexistence mechanisms (Holyoak et al. 2005; Logue et al. 2011; Winegardner et al. 2012). Likewise, recent theory has begun to incorporate links between metacommunity dynamics and ecosystem function (Massol et al. 2011), and to investigate how complex processes such as evolutionary dynamics (Urban et al. 2008; Vanoverbeke et al. 2015) and asymmetric dispersal in dendritic networks (Altermatt 2013) shape metacommunities.

One core focus in metacommunity ecology that has received increased attention in recent years is the relationship between inter-patch dispersal rate and metacommunity diversity (Kneitel & Miller 2003; Cadotte 2006a; Howeth & Leibold 2010b). As theory describing this relationship has developed (Loreau & Mouquet 1999; Mouquet & Loreau 2003; Altermatt et al. 2011; Pillai et al. 2011; Gilbert 2012; Haegeman & Loreau 2014), there has been a rapid rise in the number of studies using microcosm, mesocosm and field experiments to empirically test the effect of dispersal on diversity at the alpha (within-patch), beta (between-patch) and gamma (metacommunity-wide) scales (Appendix A Fig. S2.1). Together, this growing body of theoretical and experimental work has demonstrated that dispersal strongly shapes coexistence and diversity in metacommunities (Mouquet & Loreau 2003; Cadotte 2006b).

Despite efforts to link observed relationships between dispersal and diversity to underlying processes, experimental investigations have faced unique challenges in creating empirical tests that elucidate the processes that are described by theory and observed in natural conditions.
metacommunities. This is in part because the homogenization of dispersal rates, starting communities and environmental conditions across patches - which would normally be considered rigorous experimental design - can impede the mechanisms that allow coexistence and shape metacommunity diversity. Likewise, diversity in metacommunities is often shaped by multiple coexistence mechanisms acting at several spatial scales on species with unknown competitive and trophic interactions, which makes a mechanistic interpretation of experimental results difficult. This inherent complexity necessitates creative methods and novel approaches to help untangle how and why dispersal impacts metacommunity diversity.

Here we provide a review of metacommunity experiments that investigate the relationship between dispersal and diversity in order to highlight ways in which experimental approaches could be improved to provide more robust tests of theory. We clarify how three commonly-used experimental methods prevent tests of metacommunity processes by eliminating interspecific and inter-patch differences, and highlight alternative but under-utilised methods that researchers have developed to overcome these issues. We then review techniques and insights emerging from related ecological fields (coexistence, food web and priority effects theory) that could facilitate a more mechanistic understanding of the relationship between dispersal and diversity. Despite the challenges facing metacommunity empiricists, thoughtful experimental approaches that incorporate heterogeneity and integrate emerging theory promise to untangle complex processes and strengthen the link between theory and empirical work in this rapidly growing field.

**Literature review**

We conducted a review of published experiments testing the relationship between dispersal and diversity in metacommunities, and summarized the results obtained (Fig. 2.1) and the methods used (Fig. 2.2) by these studies. We included experiments that manipulated either the rate at which individuals move between habitat patches or the connectivity of patches, and measured the resulting effect on species diversity at the local (alpha or \( \alpha \)), inter-patch (beta or \( \beta \)) or regional (gamma or \( \gamma \)) scales (see Appendix A for detailed search methods and inclusion criteria). We included multispecies (\( \geq 3 \)) studies that had two or more levels of dispersal (including any no-dispersal controls). We excluded seed rain and species addition experiments
where colonists came from an external species pool and no information on species establishment post-colonization was provided. We also excluded fragmentation studies that only compared diversity in fragments to diversity in continuous habitat, and experiments focused solely on the effect of dispersal on recovery after severe disturbance. Fifty studies met our criteria and were included; all of these studies were published within the last twenty years, and 24 were published within the last five years. These experiments ranged from highly controlled lab experiments that used artificial species assemblages, to semi-natural outdoor mesocosms, to field experiments conducted *in situ* in grasslands, bromeliads, pitcher plants or moss patches. A table of all included studies is available on the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.nq853> (Grainger & Gilbert 2016).

**Summary of experimental hypotheses and results**

Although a variety of organisms and experimental methods were used in these studies, the stated hypothesis for the effect of dispersal on local (alpha) diversity was fairly consistent across studies. Most authors hypothesized a hump-shaped relationship between dispersal and alpha diversity, as predicted by a commonly-cited model of source-sink metacommunities (Mouquet & Loreau 2003). However, only six of the 30 studies that quantified alpha diversity across three or more dispersal treatments actually detected a hump-shaped relationship (Fig. 2.1). This may be in part because the assumptions of Mouquet and Loreau’s (2003) model (e.g., heterogeneous patches, one trophic level) were not met by most studies, and altering competitive dynamics or adding trophic interactions can have important implications for the dispersal-diversity relationship (Gilbert 2012; Haegeman & Loreau 2014). In particular, certain experimental choices may be more likely to produce this relationship; all six studies that detected a unimodal relationship did so under conditions with no predators, and with each patch initially containing a different local community (Kneitel & Miller 2003; Matthiessen & Hillebrand 2006; Howeth & Leibold 2010b; Matthiessen *et al.* 2010b; Severin *et al.* 2013). The implications of these and other experimental methods on the dispersal-diversity relationship are described in the sections below.

 Gamma diversity likewise exhibited a variety of relationships with dispersal, including positive, negative and no effect (Fig. 2.1); however these results showed no consistent association with
the experimental methods used. The relationship between dispersal and beta diversity was consistently negative, as predicted if dispersal between patches facilitates the homogenization of local communities (Fig. 2.1).

Figure 2.1 Summary of results reported by experimental studies included in our literature review. Bars indicate the effect of increasing dispersal on local (alpha) richness, between-patch similarity (beta diversity) and regional (gamma) richness. See Grainger and Gilbert (2016) for a full list of included experiments and their corresponding results.

**Summary of experimental methods**

The variety of relationships between dispersal and alpha and gamma diversity detected in metacommunity studies suggests that there may be underlying differences in the systems studied.
or the methods used. Indeed, our review of the methods employed by these studies revealed that while some methods were highly consistent across studies, others varied markedly. We focus on methods that may have undesired implications for understanding the mechanisms underlying dispersal-diversity relationships (Fig. 2.2). As in previous discussions of this topic (Cadotte 2006b; Logue et al. 2011), we noted the prevalence of the following experimental choices that impact how closely experiments match natural metacommunities and/or theory: a strong preference for using aquatic microcosms and mesocosms (70% of studies); precluding mass effects and species sorting by using homogeneous patches (36% of studies); precluding the detection of hump-shaped responses by including only two levels of dispersal (30% of studies); and failing to report all levels of diversity ($\alpha$, $\beta$, $\gamma$) despite requiring all measures to distinguish underlying mechanisms that structure diversity (66% of studies) (Fig. 2.2). We do not focus on these shortcomings, as they have been well-described elsewhere (Holyoak et al. 2005; Cadotte 2006a; Logue et al. 2011).

An additional, and underappreciated, concern for metacommunity research arises from the common application of experimental methods that are inappropriate for detecting or even allowing metacommunity processes that drive the dispersal-diversity relationship. In particular, metacommunity diversity can be structured and maintained by heterogeneity at a number of organisational levels including interspecific differences in dispersal ability, heterogeneity in local interactions that arises from only a subset of species being present at each patch, and differences in colonization rates between patches caused by directional dispersal. Although these sources of heterogeneity have been shown to be important in structuring metacommunity diversity in both theoretical work and natural metacommunities, common experimental methods eliminate them. Below, we outline the challenge of incorporating these aspects of metacommunity heterogeneity and highlight research that has advanced the field by finding creative ways to incorporate them.
Figure 2.2 Summary of methods used in experimental studies included in our literature review. The most commonly used method is highlighted in grey. Patch heterogeneity: manipulated heterogeneity = the experiment included some type of controlled inter-patch heterogeneity (e.g. disturbance, nutrients); homogenous = all patches had the same environmental conditions; natural variation = experiment used natural patches that presumably differed in some environmental conditions. Dispersal levels: the number of levels of dispersal (e.g. low dispersal, high dispersal) included in the experiment, including any no-dispersal controls. Scales of diversity: the diversity metrics that were reported. A = alpha; B = beta; G = gamma (see Appendix A for details). Dispersal methods: manual transfer = transferred water containing aquatic organisms between patches or transferred organisms between patches; corridors = terrestrial habitat connecting patches; tubes = tubes connecting patches through which aquatic organisms can pass; distance = manipulated inter-patch distances and allowed organisms to move freely between patches. Control: type of control used for dispersal treatment (e.g. isolated patches with no dispersal). Starting communities: identical starting communities = all patches started with the same suite of species; natural patches = the species assemblage of each patch was (or was sourced from) a patch in a natural metacommunity; species manipulation = each patch was seeded with a different suite of species; natural colonization = patches were left open to be colonized. Network structure: whether or not experiments tested for effects of network structure or directional dispersal. Trophic level: whether or not diversity results included species from more than one trophic level. See Grainger and Gilbert (2016) for a full list of included experiments and their corresponding results.
Incorporating metacommunity heterogeneity

Interspecific differences in dispersal

Differences in dispersal ability among species can permit coexistence in patchy environments through mechanisms such as a competition-colonization trade-off or the stabilization of trophic dynamics (Taylor 1990; Tilman 1994). Such interspecific dispersal differences result from different dispersal modes (active, passive and differences in vectors), dispersal abilities, or methods of habitat selection. These differences are an important feature of natural metacommunities (De Bie et al. 2012; Jones et al. 2015) that can have major effects on local and regional coexistence and diversity (Amarasekare 2010; Resetarits & Silberbush 2016). However, the most common method of manipulating dispersal (used by 42% of the studies reviewed here) eliminates these differences; researcher-mediated bulk dispersal involves the transfer of part of a community among patches, for example a volume of water containing a portion of the community in aquatic studies (Fig. 2.2). Although bulk dispersal increases tractability, it allows only species abundances to generate interspecific differences in dispersal within each dispersal treatment. This homogenization precludes any metacommunity coexistence mechanism that relies on interspecific differences in dispersal. Additionally, while bulk dispersal may mimic a specific type of inter-patch dispersal in aquatic ecosystems resulting from splashing (Kneitel & Miller 2003), it is likely a poor proxy for total dispersal for organisms that disperse actively, are carried passively by wind, or move via hydrological connections (Vanschoenwinkel et al. 2008; Altermatt & Ebert 2010; Pellowe-Wagstaff & Simonis 2014).

While some studies have acknowledged the shortcomings of homogenizing dispersal among species (Matthiessen et al. 2010a; Carrara et al. 2012), others have gone even further to preserve individual species’ differences in dispersal. These latter studies have used treatments that alter dispersal by varying either inter-patch distance (Chase et al. 2010), the presence or length of inter-patch connection tubes (Cadotte 2006b; Davies et al. 2009) or corridors (Gonzalez et al. 1998), or the frequency of propagule rains (Matthiessen & Hillebrand 2006; Matthiessen et al. 2010b) (Fig. 2.2). These treatments promote more natural dispersal among patches and increase experimental realism and adherence to common theoretical assumptions; as a result, these approaches provide some of best tests of the effect of dispersal on diversity. For example, one
study that allowed semi-natural dispersal among patches demonstrated that while only the strongest disperser was able to colonize patches in low dispersal treatments, resulting in low diversity, weaker dispersers dominated the metacommunity in high dispersal treatments (Matthiessen & Hillebrand 2006).

Another common but extreme treatment that removes the advantage of superior dispersers is a completely isolated ‘control’ treatment (Fig. 2.2). While several studies have appropriately used this type of treatment to test for rescue effects (Gonzalez et al. 1998; Chisholm et al. 2011), this control can be problematic for researchers attempting to understand the effect of dispersal on diversity via spatial coexistence mechanisms such as a competition-colonization trade-off, or to predict how dispersal influences the relative abundance of species regionally. In these cases, theory predicts the performance of good dispersers increases as metacommunity connectivity decreases, but that this advantage disappears completely when local communities become totally isolated. Thus, going from very low connectivity to an isolated control with zero connectivity reverses expectations for the relative success of good dispersers. In such cases an isolated control is effectively the opposite treatment of very low connectivity, rather than the next most isolated treatment. Although isolated controls serve a valuable purpose for certain experimental questions, such as clarifying competitive or consumptive dynamics in the absence of dispersal (Shurin 2001), researchers should interpret results from no-dispersal controls carefully and within the context of theory.

**Heterogeneous starting communities**

Underlying three of the most common hypotheses for dispersal-diversity studies is the assumption that patches within a metacommunity vary in the identity of their constituent species. When dispersal limitation prevents species from colonizing suitable habitat, increasing dispersal has a positive effect on alpha diversity (Gonzalez et al. 1998). Similarly, a decline in diversity at very high dispersal rates can result from a dominant competitor or predator reaching all sites, or from increased synchrony (Taylor 1990; Mouquet & Loreau 2003; Gilbert 2012). Finally, beta diversity is predicted to decline as dispersal increases because local communities become more similar in species composition as species reach all patches. Intuitively and mechanistically, it is evident from these hypotheses that an experiment that starts each patch
with an identical local suite of species will produce vastly different results from an experiment in which patches differ in their initial species composition.

Although the impact that starting community composition may have on the likelihood of experimental outcomes adhering to theoretical predictions is rarely discussed, it is noteworthy that all six of the studies that found a hump-shape relationship between dispersal and alpha diversity used patches that started with different communities (Fig. 2.1; Kneitel and Miller (2003); Cadotte (2006b); Matthiessen and Hillebrand (2006); Howeth and Leibold (2010b); Matthiessen et al. (2010b); Severin et al. (2013)). Indeed, the impact of starting communities on experimental outcomes was explored empirically by Cadotte (2006b); by creating metacommunities that differed in whether patches initially had identical or different species composition, he demonstrated that a hump-shaped relationship between dispersal and local diversity was only found in metacommunities that had different starting communities. However, despite the apparent importance of varying composition among patches at the outset of experiments, 28% of the studies reviewed here used identical starting communities in each patch (Fig. 2.2). Of the studies that used different communities, 27 used initial starting communities that were created from a natural community in some way (patches were composed of species drawn from natural patches, pooled sources or natural colonization) and presumably had unquantified inter-patch differences in species composition. Only seven studies used intentionally different starting communities by systematically varying species composition in each patch. Such studies highlight the advantage of this method. For example, Matthiessen and Hillebrand (2006) found that final local diversity could be predicted by which species were initially present in a local assemblage because certain species had facilitative or inhibitory effects on subsequent colonizers. Likewise, France and Duffy (2006) demonstrated that systematically varying starting inter-patch species composition can allow extinctions and colonization to be tracked directly, providing a clear understanding of how dispersal alters alpha, beta and gamma diversity through temporal turnover.

As the initial degree of difference in community composition between patches in an experimental metacommunity can alter experimental outcomes, a clearer justification for using patches with identical starting communities should be included by those researchers who choose this method. Better still, systematically varying starting patch composition, or even quantifying
initial inter-patch differences in species composition when patches are seeded from natural sources, would allow researchers to determine how local colonization and extinctions are driving changes in diversity, and provide a more direct link between theory and empirical measures.

Spatial network configuration and directional dispersal

In many natural metacommunities, dispersal follows paths constrained by landscape elements, which results in asymmetric or directional movement of individuals between local sites. Dendritic or riverine networks, where hydrological connections and topography shape dispersal, are one of the most widespread examples of this phenomenon (Benda et al. 2004). A growing body of theoretical and observational work suggests that the directional, hierarchical and branching nature of such systems, and the resulting asymmetry in colonization rates at local habitat patches, can strongly influence metacommunity diversity (Muneepeerakul et al. 2007; Muneepeerakul et al. 2008; Brown & Swan 2010; Salomon et al. 2010). For example, theory predicts that inter-patch differences in species composition and abundance that keep beta diversity high are more likely in riverine networks compared to conventional lattice networks (Muneepeerakul et al. 2007; Carrara et al. 2012). Likewise, models have shown that asymmetrical dispersal can result in higher extinction rates (Vuilleumier & Possingham 2006), that can cause declines in local diversity (Muneepeerakul et al. 2007).

Despite mounting evidence of the importance of dispersal asymmetry and network type for the dispersal-diversity relationship, few experimental studies have included dendritic or hierarchical network structure when testing the relationship between dispersal and metacommunity diversity (5 of the 50 studies reviewed here – Fig. 2.2). However, those that have used dispersal treatments that mimic riverine networks have demonstrated that dendritic connectivity can result in lower local diversity and higher beta diversity (Altermatt et al. 2011; Carrara et al. 2012), and that local diversity may vary predictably with a patch’s position within the network (e.g. central vs. peripheral, headwater vs. confluences) (Carrara et al. 2012; Carrara et al. 2014). These early results indicate that incorporating heterogeneity in network structure into metacommunity experiments may be a critical future direction for this field. Indeed, incorporating different
network structures would not only test emerging theory, but would also create experiments that better reflect the wide variety of dispersal mechanisms prevalent in natural metacommunities.

**Integrating approaches from related fields**

Determining which metacommunity processes are driving experimental outcomes presents a formidable challenge to researchers due to the multitude of interacting processes occurring at multiple spatial scales in most experimental systems. Here we outline three bodies of theory developed in related ecological fields that could help disentangle the mechanisms underlying observed dispersal-diversity relationships.

**Scaling from local interactions to regional dynamics: The invasion criterion**

Metacommunity models generate distinct predictions for the dispersal-diversity relationship that arise from differences in local interactions and how they ‘scale up’ to determine both local co-occurrence and regional coexistence. For example, a competition-colonization trade-off requires a competitive hierarchy that is consistent across patches (Tilman 1994). In contrast, source-sink dynamics require species to have negative growth rates caused by abiotic conditions or biotic interactions in some patches, and positive growth rates in other patches (Pulliam 1988).

Recent advances in coexistence theory provide a clear method for assessing the outcome of local processes within patches, and could thus be used to decouple the effects of local interactions from regional processes (Chesson 2000; Adler et al. 2007). Specifically, the invasion criterion is a simple test of species interactions that determines whether local coexistence is possible in the absence of dispersal by assessing whether a species has positive population growth rates when it is at low abundance and its competitors are at equilibrium (Siepielski & McPeek 2010). Mutual invasibility, where all species meet the invasion criterion, is necessary for competing species to stably coexist within a patch in the absence of immigration (Chesson 2000; Siepielski & McPeek 2010). In this framework, coexistence is differentiated from co-occurrence, in which species are slowly declining to extinction or are maintained by incoming colonists (Siepielski & McPeek 2010). Importantly, the invasion criterion allows researchers to determine the patches and species that a focal species can occur in or with, and by inference, when dispersal alters the outcomes of these local processes. While a number of studies have used the invasion criterion to
formally evaluate local coexistence in the absence of dispersal (Wilson et al. 1999; Stomp et al. 2004; Jiang & Morin 2007; Godoy & Levine 2014), this method has yet to be integrated into metacommunity ecology.

The invasion criterion is particularly relevant for testing metacommunity dynamics because different metacommunity paradigms make distinct predictions about the maintenance of local diversity in the absence of dispersal. For example, local (within-patch) tests of competitive dominance can be compared among patches to determine whether there is a competitive hierarchy that is consistent across patches; if pairwise tests of the invasion criterion reveal a consistent competitive hierarchy among patches, the local conditions required for a competition-colonization trade-off are met. Conversely, if competitive hierarchies differ among patches and respond to patch characteristics, species sorting or mass effects are more likely to be driving diversity patterns. In cases where the order of arrival determines the outcome of competition through priority effects (see section below), the invasion criterion can be used to identify the alternate stable states that result (Peay et al. 2012). Such tests can also help researchers move beyond testing single paradigms for entire metacommunities by elucidating species-specific interactions. For example, tests of the invasion criterion can identify when co-occurring species are competitors vs. mutualists, which in turn can explain why species show positively or negatively correlated responses to changes in connectivity, and could help to reveal underlying drivers of the dispersal-diversity relationship (Gilbert & O’Connor 2013).

To illustrate how the invasion criterion can distinguish among metacommunity processes, we consider a competitive metacommunity with heterogeneous patches (Fig. 2.3). In a heterogeneous metacommunity, increasing connectivity could increase alpha diversity either by allowing species to reach preferred patches (species sorting; middle of Fig. 2.3) or by allowing species to subsidize populations in sub-optimal patches with immigrants from optimal patches (mass effects; right side of Fig. 2.3). Quantifying the invasion criterion within patches would determine which of these processes is maintaining diversity. In this example, the invasion criterion allows for a clear determination of whether species are persisting in optimal patches or are maintained by immigration from source populations (Fig. 2.3). Although such tests may appear difficult for large numbers of species, recent work by Levine and colleagues has demonstrated that invasibility tests of multiple species can be undertaken simultaneously within
a community when species at very low abundances are only likely to interact with abundant species rather than each other, which greatly reduces the number of experimental treatments required (Levine & HilleRisLambers 2009; Godoy & Levine 2014).

Figure 2.3 Hypothetical results for an experiment using the invasion criterion to distinguish between species sorting and mass effects in a heterogeneous metacommunity. i) Species A and B are found only in habitat (patch type) 1, species C and D are found in both patch types and species E and F are found only in habitat 2. ii) If species sorting is driving occurrences, all species will be able to invade all patches in which they are found (i.e. population growth rate of each species when rare will be positive in the absence of immigration). iii) If mass effects increase local diversity, species that occur in both patch types (species D and C) will each only meet the invasion criterion in one (source) environment and fail to meet the invasion criterion in the other (sink) environment. Note that the rates of population decline in sink patches must be smaller than immigration rates to maintain these sink populations. In this example, other species (A, B, E, F) are still found in their optimal environments.

In addition to helping determine which paradigms best describe local processes in a metacommunity, tests of the invasion criterion could allow a researcher to partition the relative influence of each mechanism. For example, theory predicts that local diversity will be low when connectivity is insufficient to get all species to all appropriate patches, and high when connectivity is sufficient for mass effects to subsidize local diversity (Mouquet & Loreau 2003). By determining the proportion of species that are maintained by mass effects or species sorting using the invasion criterion methods described in Fig. 2.3, the relative role of each process could be quantified at any level of dispersal. Similarly, the invasion criterion can determine how frequently species are absent from patches where they could invade, as is predicted to occur when dispersal limitation is shaping species distributions. This type of partitioning approach that
facilitates the integration of multiple metacommunity processes could move metacommunity studies into a clearer, more mechanistic understanding of the link between dispersal and diversity.

From competitive metacommunities to food webs: Incorporating multiple trophic levels

Although much of metacommunity theory focuses on competitive interactions (Leibold et al. 2004), it is widely recognized that trophic interactions can play an important role in structuring diversity in patchy systems (Gouhier et al. 2010; Pillai et al. 2010; Haegeman & Loreau 2014). However, food webs are inherently complex – even simple webs often consist of several modules, or small groups of species that differ in the nature of their interactions (Holt 1997; McCann et al. 1998). When this complexity is coupled with differential dispersal among species, a broad suite of resulting effects is possible, which has made a general framework for food web metacommunities elusive. Despite this gap, 58% of the experiments reviewed here nonetheless used metacommunities with multiple trophic levels (Fig. 2.2). Several such studies have assessed the effect of trophic interactions on the dispersal-diversity relationship by including predators as a treatment (Shurin 2001; Kneitel & Miller 2003; Cadotte et al. 2006; Howeth & Leibold 2010a) or as a form of patch heterogeneity (Howeth & Leibold 2010b). Such experiments have demonstrated that trophic interactions can fundamentally alter dispersal-diversity relationships. For example, predation pressure that extirpates species locally can lead to a dampening of the predicted hump-shaped relationship between dispersal and local diversity (Kneitel & Miller 2003; Howeth & Leibold 2010b), which may explain why all six studies that reported a hump-shape found this result under no-predation conditions (Kneitel & Miller 2003; Matthiessen & Hillebrand 2006; Howeth & Leibold 2010b; Matthiessen et al. 2010b; Severin et al. 2013). These findings highlight the necessity of incorporating trophic complexity into metacommunity studies in order to fully understand the dispersal-diversity relationship. Fortunately, recent theory that integrates trophic interactions and metacommunity processes suggests several considerations that could guide empirical research, three of which we discuss here: isolating the effects of local interactions through food web modules, allowing prey and predator dispersal to vary independently, and quantifying how dispersal alters food web metrics.
As with the use of the invasion criterion to determine how dispersal alters local competitive dynamics, local tests of food web dynamics can be used to elucidate mechanisms through which dispersal affects the outcome of local trophic interactions. Locally, the removal of specific species to quantify interaction strengths and stability has been used to clarify trophic interactions within food web modules (Paine 1992; Gilbert et al. 2014). When these tests are performed in the presence and absence of dispersal, they allow ecologists to quantify exactly how local interactions are modified by dispersal, providing a clear link between theory and experimentation (Rip & McCann 2011). For example, when a predator drives the local extinction of a prey species that would persist in its absence, changes in this outcome when local patches are connected by dispersal would provide evidence of dispersal generating refugia for prey (Taylor 1990). Similarly, when a top predator stabilizes local dynamics by moving between patches, local communities will show less temporal variation as predator dispersal increases (Rooney et al. 2006). Although this approach of decoupling local trophic interactions from regional processes has yet to be adopted in metacommunity studies, many natural mesocosms have had their food webs characterized in previous research and are well suited to such tests (Srivastava et al. 2004). From the perspective of generating a broader framework for food web metacommunities, such separation of local interactions and dispersal could both inform the assumptions of theoretical models and test their predictions.

Understanding the effects of dispersal on even well-understood local food webs requires that dispersal differences among trophic levels be acknowledged and incorporated into theoretical and experimental work. The spatial and temporal scale at which organisms disperse can vary substantially by trophic level, and theoretical work has demonstrated that altering which trophic levels are allowed to disperse can dramatically alter impacts on metacommunity diversity (Shurin & Allen 2001; Amarasekare 2008; Haegeman & Loreau 2014). For example, simulations demonstrated that although a hump-shaped relationship between dispersal and local diversity is predicted when consumer and resource dispersal vary simultaneously, increasing consumer dispersal while keeping resource dispersal low leads to a positive relationship between dispersal and diversity (Haegeman & Loreau 2014). In contrast, theoretical work that
examines locally unstable predator-prey dynamics predicts that high predator dispersal can cause both species to go regionally extinct (Taylor 1990). When coupled with tests designed to clarify local interactions, the experimental separation of predator and prey dispersal to determine how dispersal of each trophic level affects diversity could greatly benefit studies of trophic metacommunities (Limberger & Wickham 2011). However, studies that integrate multiple trophic levels often impose dispersal treatments that homogenize dispersal rates across trophic levels (Verreydt et al. 2012; Declerck et al. 2013) or use predation as a treatment to assess how prey diversity varies with dispersal and predation (Kneitel & Miller 2003; Cadotte et al. 2006; Howeth & Leibold 2010a). Methods that allow predators and prey to disperse at more natural, and often vastly different, rates (Gilbert et al. 1998; Chase et al. 2010), or experimentally separate predator and prey dispersal (Limberger & Wickham 2011), provide a better match to natural systems and have great promise for testing and inspiring theory.

In complex food webs where simple modules are insufficient to describe the impacts of dispersal on trophic interactions, measures like stability (e.g. time to extinction) and complexity (e.g. chain length) can help characterize how food web structure is altered by dispersal (Amarasekare 2008; LeCraw et al. 2014). For example, food webs are predicted to be most stable at intermediate dispersal rates if low dispersal allows asynchrony between patches and enables depleted prey populations to be rescued from extinction and very high dispersal allows prey overexploitation by removing prey refugia (LeCraw et al. 2014). Likewise, chain length is predicted to increase at intermediate dispersal as lower trophic levels are able to get to more patches and build up food chains; however, at very high dispersal, complexity may be reduced if predators drive prey extinct in many patches and lead to their own extinction (reduced chain length) or specialist species can reach every patch and outcompete generalists (decreased chain branching) (Pillai et al. 2011; LeCraw et al. 2014). While there is a substantial body of work outlining theory that links spatial structure to food web properties (Holt & Hoopes 2005; Gravel et al. 2011) and testing it empirically (Huffaker 1958; Holyoak 2000; Bonsall et al. 2002; Vasseur & Fox 2009), these metrics have rarely been integrated into empirical investigations of dispersal-diversity relationships (but see Howeth and Leibold (2010b); Staddon et al. 2010)). Complementing species diversity metrics with an assessment of how dispersal alters food web
stability and/or complexity could provide valuable mechanistic insights into why and how diversity is affected by dispersal.

Using theoretical insights to inform experimental treatments (e.g. dispersal treatments that allow predators and prey to disperse separately) and responses (e.g. key food web properties) would enhance the realism of these experiments, make them stronger tests of existing theory, and may uncover emergent properties of metacommunities that as of yet remain unknown. Indeed, one of the challenges with the general framework for competitive metacommunities proposed by Leibold et al. (2004) is that it may oversimplify the dynamics in any given metacommunity; deconstructing trophic metacommunities from basic principles could provide the flexibility for researchers to more clearly link theory to empirical data generated from study systems characterized by a variety of competitive and consumptive interactions. Although such complexity makes simple predictions for the effects of dispersal on diversity difficult, the suggested approaches provide a strong foundation for understanding trophically structured metacommunities.

The legacy of colonization history: Priority effects

Priority effects are broadly defined as any change in the trajectory of community assembly that results from a change in the order in which species arrive at a local site. For example, priority effects can occur if early arrivers draw down a common resource or modify the environment in a way that prevents subsequent colonizers from establishing (Sutherland 1974; Fukami 2015). Likewise, for species with fast generation times or systems with infrequent dispersal, local adaptation of a species before its competitor arrives may increase the likelihood of the late arriver being excluded (Urban & De Meester 2009). Although the mechanisms through which priority effects alter local diversity have been well-described, their impact on metacommunity diversity remains a subject of active debate (Fukami 2015). In some cases, priority effects in metacommunities may cause positive feedbacks in which the local success of an early colonist hinders late arrivers and leads to the regional domination of that species in the metacommunity (Shurin et al. 2004; Fukami 2015; Vanoverbeke et al. 2015). In other cases, high regional diversity may be maintained in spite of priority effects if abiotic heterogeneity creates spatial refuges (Shurin et al. 2004), or variation in species interaction strength among local
communities produces alternative community states (Pu & Jiang 2015). In either case, priority effects can be important determinants of metacommunity diversity. However, the importance of colonization history is only just beginning to be considered in metacommunity experiments (Pu & Jiang 2015; Vanoverbeke et al. 2015).

In metacommunities, species-specific dispersal rates influence the order in which individuals arrive at a local patch, and, through priority effects, this order of arrival can alter coexistence and diversity. The relationship between dispersal rates and priority effects is therefore a potentially important, but largely unexplored, mechanism through which dispersal can alter metacommunity diversity. Recent work on priority effects has made progress in determining when dispersal and local conditions are likely to result in priority effects (Table 2.1). Three insights from this work could provide new pathways for incorporating priority effects into dispersal-diversity research and offer exciting future directions for metacommunity ecology.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Condition that favors priority effects</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Species’ dispersal rates are similar</td>
<td>Fukami (2015)†</td>
</tr>
<tr>
<td>Species traits</td>
<td>Species pairs are close relatives</td>
<td>Peay et al. (2012)<em>, Tan et al. (2012)</em></td>
</tr>
<tr>
<td></td>
<td>Species pairs have high niche overlap</td>
<td>Vannette and Fukami (2014)*</td>
</tr>
<tr>
<td></td>
<td>Species have rapid growth rates</td>
<td>Fukami (2015)†</td>
</tr>
<tr>
<td></td>
<td>Species strongly impact the environment</td>
<td>Vannette and Fukami (2014)*</td>
</tr>
<tr>
<td></td>
<td>Species can evolve rapidly</td>
<td>Loeuille and Leibold (2008)†, Urban and De Meester (2009)<em>, Vanoverbeke et al. (2015)</em></td>
</tr>
<tr>
<td>Local conditions</td>
<td>Productive environment</td>
<td>Chase (2010)<em>, Kardol et al. (2013)</em>, Vannette and Fukami (2014)*</td>
</tr>
<tr>
<td></td>
<td>No predators</td>
<td>Chase et al. (2009)*</td>
</tr>
<tr>
<td></td>
<td>Small habitat size</td>
<td>Fukami (2004)*</td>
</tr>
</tbody>
</table>

*Experiment, †Model, †Review
Theory on priority effects predicts that lower dispersal rates should increase the importance of colonization history, because longer time lags between species’ arrivals allow early arrivers more time to establish, grow, alter the environment, and evolve (Table 2.1; Chase (2003); Fukami (2015)). This hypothesis is only beginning to be tested empirically, and early experimental evidence is conflicting; while one recent study found that differences in colonization history in a protist microcosm produced alternate community states regardless of dispersal rate (Pu & Jiang 2015), an experiment that manipulated planting intervals in an old field system detected stronger priority effects at longer time intervals (Kardol et al. 2013). If lower dispersal rates can indeed increase the likelihood of competitive exclusion through priority effects, the resulting alternate stable or transient states in local communities could strongly influence alpha, beta and gamma diversity in dispersal-diversity studies. Researchers therefore need to be cognisant of whether priority effects may be occurring within their experimental systems in order to fully capture the spatial scaling of diversity.

Priority effects are also most likely to occur when species have similar dispersal rates, but individuals can arrive at local sites at different times (Fukami 2015). In metacommunity experiments, the method used to manipulate dispersal and the nature of starting communities together determine whether interspecific differences in arrival time, and thus priority effects, can occur. For example, bulk dispersal, in which species arrive at a patch together at each transfer event, eliminates much of the interspecific variation in arrival times that would occur in a natural metacommunity. Likewise, if all species are present in all patches at the start of an experiment, there can be no differences in arrival time and thus no priority effects. Researchers that start with homogenous communities or use methods that synchronize arrival times should consider the implications of eliminating priority effects, while those using methods that allow species to arrive sequentially should consider how priority effects might impact results (e.g. Cadotte (2006b); Berga et al. (2015)).

Finally, experimental conditions that result in high niche overlap between competitors, or allow early arrivers to rapidly monopolize a patch, are most likely to result in priority effects (Table 2.1; Peay et al. (2012); Vannette and Fukami (2014); Fukami (2015)). This includes systems that contain closely related species with fast growth rates living in small, productive habitats (Table 2.1). For example, Peay and colleagues used tests of the invasion criterion in nectar
yeasts to demonstrate that priority effects were strongest between close relatives (Peay et al. 2012). Notably, many of the conditions and species traits that promote priority effects match the characteristics of systems frequently used in experimental tests of the impact of dispersal on metacommunities. These insights on local conditions that promote priority effects could be used not only to help researchers determine when priority effects are more or less likely to occur in metacommunity experiments, but could also provide clear hypotheses that may be best tested within a metacommunity framework. A continued integration of metacommunity and priority effects research could provide new advances to both fields, and may be essential to fully understand how dispersal affects metacommunity diversity.

Conclusion

Empirical metacommunity studies have the potential to provide a mechanistic understanding of the effect of dispersal on diversity by clarifying how and when dispersal alters or reinforces local community dynamics. Our review illustrates how experimental methods that preserve heterogeneity in dispersal and community composition have led to novel insights, and can continue to create better experimental tests of theory. Likewise, the integration of rapidly developing theory and experimental approaches from recent work on the invasion criterion, trophic dynamics and priority effects could help researchers face the challenge of disentangling the role of local species interactions and dispersal in shaping diversity patterns. These advances promise to provide new insights from empirical studies, inform the development of theory, and enhance our understanding of metacommunity dynamics.

Acknowledgements

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References


CHAPTER 2: DISPERSAL AND METACOMMUNITY DIVERSITY


CHAPTER 2: DISPERSAL AND METACOMMUNITY DIVERSITY


CHAPTER 2: DISPERSAL AND METACOMMUNITY DIVERSITY


Appendix A: Supplementary information to Chapter 2

Details of literature review

In December 2014, we searched the Web of Science for articles with “diversity” AND “metacommunity” AND (“dispersal” OR “connectivity”) in the title, abstract or keywords; this returned 320 results, all of which were assessed for inclusion. We also searched (“metacommunity” AND “dispersal” AND “diversity”) in Google Scholar; this returned 6470 results, of which the top (ranked by relevance) 150 papers were assessed for inclusion. In November 2015, we repeated the Web of Science search using the terms “diversity” AND (“metacommunity” OR “patch”) AND (“dispersal” OR “connect*”) AND “experiment*”; this returned 107 results, all of which were assessed for inclusion. We supplemented these with experiments that met our criteria cited in a meta-analysis (Cadotte 2006) and a review (Logue et al. 2011) on similar topics. We also included any relevant studies that met our criteria cited in papers found in online searches.

We included only experiments; all reviews, frameworks, theoretical papers, simulations and observational studies were excluded. We restricted our review to experiments that manipulated the rate at which individuals move between habitat patches (either by directly altering the rate at which individuals move between patches or by manipulating patch connectivity) using two or more levels of dispersal (including any no-dispersal controls) and measured (any type of) diversity in two or more patches. Studies used various methods to quantify alpha and beta diversity. For beta diversity, we report whichever measure was included in the paper (e.g. Bray-Curtis, Jaccard’s, γ/α, γ-α). For alpha diversity, we report local species richness results for consistency, except in the two cases where only Shannon diversity was reported (France & Duffy 2006; Steiner et al. 2011); for these two studies, we report Shannon diversity results for alpha. In addition to testing the dispersal-diversity relationship, several of the experiments included here also tested how additional factors (ex: directional dispersal, metacommunity size, disturbance) affect diversity. In these cases, results comparing diversity across different dispersal levels (within a level of the additional factor) were extracted.
This resulted in the inclusion of 50 studies published between 1996 and 2015 (Fig. S2.1). A complete list of these 50 studies along with the relevant methods and results for each is available in the Dryad Digital Repository (Grainger & Gilbert 2016).

Supplementary tables and figures

Table S2.1 Four metacommunity paradigms and their underlying assumptions

<table>
<thead>
<tr>
<th>Paradigm</th>
<th>Description</th>
<th>Assumptions</th>
<th>Species differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species sorting</td>
<td>Patch heterogeneity causes spatial separation of species’ niches. Dispersal facilitates species (re)establishment in patches where they perform best</td>
<td>Frequent enough to enable species to reach suitable habitat patches following local extinction or shifting patch characteristics</td>
<td>Heterogeneous</td>
</tr>
<tr>
<td>Mass effects</td>
<td>Source patches in which a species performs well supplement sink patches in which it performs poorly</td>
<td>Frequent enough to maintain sink populations (immigration rate &gt; local extinction rate)</td>
<td>Heterogeneous</td>
</tr>
<tr>
<td>Patch dynamics</td>
<td>Spatial dynamics are driven by colonization and extinction rates, which are altered by species interactions within patches</td>
<td>Species have different dispersal abilities</td>
<td>Homogenous</td>
</tr>
<tr>
<td>Neutral</td>
<td>Species are equivalent in competitive and dispersal abilities and undergo stochastic changes in abundance over time</td>
<td>Species have equal dispersal abilities</td>
<td>Homogenous (or species do not respond differently to heterogeneity)</td>
</tr>
</tbody>
</table>

1Paradigms are summarized based on Leibold et al. (2004)
2For example weak competition and facilitation (Klausmeier 2001)
3For example competition-colonization trade-off (Tilman 1994) or unstable predator-prey dynamics (Taylor 1990)
Figure S2.1 Publications dates of studies included in our review.

References


Chapter 3: Predators modify biogeographic constraints on species distributions in an insect metacommunity


Abstract

Theory describing the positive effects of patch size and connectivity on diversity in fragmented systems has stimulated a large body of empirical work, yet predicting when and how local species interactions mediate these responses remains challenging. We used insects that specialize on milkweed plants as a model metacommunity to investigate how local predation alters the effects of biogeographic constraints on species distributions. Species-specific dispersal ability and susceptibility to predation were used to predict when patch size and connectivity should shape species distributions, and when these should be modified by local predator densities. We surveyed specialist herbivores and their predators in milkweed patches in two matrix types, a forest and an old field. Predator-resistant species showed the predicted direct positive effects of patch size and connectivity on occupancy rates. For predator-susceptible species, predators consistently altered the impact of biogeographic constraints, rather than acting independently. Finally, differences between matrix types in species’ responses and overall occupancy rates indicate a potential role of the inter-patch environment in mediating the joint effects of predators and spatial drivers. Together, these results highlight the importance of local top-down pressure in mediating classic biogeographic relationships, and demonstrate how species-specific responses to local and regional constraints can be used to predict these effects.

Introduction

In heterogeneous landscapes, the size and spatial isolation of habitat patches shape the populations and communities that inhabit them (MacArthur & Wilson 1967; Hanski 1994a; Jones et al. 2015). Island Biogeography and metapopulation theories predict that species are most likely to occur in large, well-connected habitat patches that receive new colonists at high frequencies and support large populations that are resistant to extinction (MacArthur & Wilson
Although these classic predictions have explained species distributions in a range of taxa (Hanski 1994a; van Noordwijk et al. 2015), in other cases their explanatory power has been limited or absent (Gilbert 1980; Prugh et al. 2008). Identifying when and why the biogeographical constraints of patch size and connectivity drive species distributions would bring us closer to understanding the mechanisms that underlie broad diversity patterns.

One explanation for why species distributions diverge from classic biogeographical predictions is that local biotic interactions can overshadow or modify the impact of regional processes (Gripenberg & Roslin 2007; Gravel et al. 2011). For example, predators can obscure relationships between connectivity and diversity by inhibiting species that are able to reach a patch from establishing or persisting (Shurin 2001; Kneitel & Miller 2003). Top-down pressure from predators may even reverse predicted spatial relationships if small or isolated patches act as refugia from predator-induced extinctions (Holyoak & Lawler 1996). While the links between resource heterogeneity and species distributions are well explored in the metacommunity literature, the effects of top-down constraints are less understood (Logue et al. 2011; Grainger & Gilbert 2016). In particular, predictions for when and how local trophic interactions will alter regional patterns of diversity have remained elusive (Resetarits et al. 2005; Grainger & Gilbert 2016).

A key to understanding the interplay between local trophic drivers and regional spatial drivers of species distributions are the characteristics of a species’ biology that govern its local persistence and inter-patch movements (Harvey & MacDougall 2014; van Noordwijk et al. 2015). Dispersal ability determines the rate at which species move between patches, and has been used to predict species’ responses to spatial patch characteristics (De Bie et al. 2012; Jones et al. 2015; van Noordwijk et al. 2015). While weak or passive dispersers are only likely to reach patches that are well-connected or of a large target size, strong, active dispersers may reach and select among a broader range of habitat patches (Kennedy & Gray 1993; Resetarits et al. 2005). An integration of biotic constraints, along with dispersal constraints, could provide a more mechanistic understanding of the forces that structure metacommunity diversity. For example, inedible or well-defended species should show little effect of top-down pressure, while readily consumed prey species are expected to have higher extinction rates or altered dispersal choices.
when predators are abundant (Shurin 2001; Resetarits et al. 2005). For such species, lower occupancy rates resulting from predator-induced mortality may dampen spatial relationships (Shurin 2001), or change relationships between spatial drivers and occupancy for species capable of actively dispersing away from predators (Kennedy & Gray 1993; Resetarits et al. 2005). The combined use of dispersal ability and susceptibility to predation could enable predictions of how local and regional factors independently and interactively shape species distributions.

In addition to the intrinsic characteristics of species, the inter-patch matrix can also structure species distributions by altering both dispersal rates among patches and the persistence of populations within patches (Ricketts 2001; Prevedello & Vieira 2010). For example, the physical characteristics of the matrix can aid or impede a species’ movement among patches, depending on the degree of physical barriers to dispersal and the fitness costs of traversing the matrix (Ricketts 2001). Likewise, patches within matrices preferred by predators could suffer higher predation rates due to spillover into local patches (Bayne & Hobson 1997).

We developed and tested predictions for when patch size, connectivity and predators constrain the distributions of nine specialist herbivores that live in milkweed patches. Common milkweed (Asclepias syriaca) is a perennial forb that produces toxic cardenolides and sticky latex to defend against herbivores. The small suite of insect herbivores that are adapted to eat milkweed have served as a model system in studies of dispersal and plant-herbivore interactions. As such, there is a wealth of natural history information for these species, including published data on dispersal distances and susceptibility to predation (Table 3.1; Zalucki and Kitching (1982a); Matter (1996); Smith et al. (2008)). We used these data to position the nine specialists into a framework that predicts whether the distribution of each species should be constrained by predators, patch spatial characteristics, or some combination thereof (Fig. 3.1). In this framework, the seven species with average dispersal distances of <100 m are predicted to show positive relationships with patch size and connectivity (right half of Fig. 3.1). In contrast, the two lepidopterans (tussock moth and monarch butterfly), which frequently disperse over 1 km, are predicted to be unconstrained by patch size and connectivity (left half of Fig. 3.1). Similarly, early instar monarch caterpillars and three aphid species are consumed by predators and should be negatively impacted by their presence (top half of Fig. 3.1), while the defensive coloring or
hard bodies of the remaining five species result in their having few known invertebrate predators (bottom half of Fig. 3.1).

We surveyed nine specialist milkweed herbivores and their general predators in milkweed patches imbedded in an old field and a deciduous forest to test two predictions: (1) the impact of local predators and biogeographical constraints (patch size and connectivity) on each species can be predicted by its dispersal ability and susceptibility to predation, and (2) local predators will modify the impacts of biogeographical constraints on the distributions of species susceptible to predation.

**Figure 3.1** Predictions for constraints caused by local predators and spatial drivers (patch size and connectivity) for nine focal specialist milkweed herbivores. See Table 3.1 for references used to derive predictions, and Appendix B for insect image sources.
Methods

Natural history

The nine specialist milkweed herbivores observed in this study include three aphid species, one seed bug, two beetles, two lepidopterans and one leaf-mining fly. The aphids are *Aphis nerii*, *Aphis asclepiadis* and *Myzocallis asclepiadis*; all three aphid species feed on milkweed phloem and are eaten by generalist invertebrate predators (Table 3.1). Monarch caterpillars consume milkweed leaves and, despite chemical defenses, are also readily consumed by generalist invertebrates, particularly at the early instar stages (Prysby (2004); Table 3.1). In contrast, the long-horned milkweed beetle (*Tetraopes tetrophthalmus*), milkweed stem weevil (*Rhyssomatus lineaticollis*), milkweed-leaf miner (*Liriomyza asclepiadis*), small milkweed bug (*Lygaeus kalmii*) and milkweed tussock moth (*Euchaetes egle*) are not vulnerable to predators due to their size, hard exoskeletons, aposematic coloration, cryptic lifestyle or toxicity (Table 3.1).

The dispersal abilities of our focal species range from 15m to over 1000km (Table 3.1). Because the mean distance between patches within a matrix type at our field site was <1000m in both the old field and forest, we predicted that species with low dispersal distances (≤ 100m) would be associated with large, well-connected patches, while the long-distance dispersers (>>1km; monarchs and tussock moths) would be unconstrained by these spatial drivers (Fig. 3.1). While specialist milkweed herbivores are largely confined to milkweed patches, generalist predators including spiders, assassin bugs and ladybugs inhabit both milkweed patches and the surrounding matrix.
CHAPTER 3: PREDATORS MODIFY BIOGEOGRAPHIC CONSTRAINTS

Table 3.1 References for dispersal estimates and predation susceptibility for specialist milkweed herbivores used to derive the predictions presented in Fig. 3.1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average dispersal</th>
<th>Species used for dispersal reference</th>
<th>Susceptible to predation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aphis asclepiadis</em></td>
<td>100m(^1)−7</td>
<td>Various aphid species (<em>Aphis</em> and other genera)</td>
<td>Yes(^{16,17})</td>
</tr>
<tr>
<td><em>Aphis nerii</em></td>
<td>100m(^1)−7</td>
<td>As above</td>
<td>Yes(^{16,17})</td>
</tr>
<tr>
<td><em>Myzocallis asclepiadis</em></td>
<td>100m(^1)−7</td>
<td>As above</td>
<td>Yes(^{16,17})</td>
</tr>
<tr>
<td>Milkweed weevil</td>
<td>15m(^8)</td>
<td>Milkweed weevil</td>
<td>No(^{4})</td>
</tr>
<tr>
<td>Milkweed leaf miner</td>
<td>20m(^9)</td>
<td>Congener of the milkweed miner</td>
<td>No(^{1})</td>
</tr>
<tr>
<td>Small milkweed bug</td>
<td>30m(^10,11)</td>
<td>Small milkweed bug</td>
<td>No(^{18,19})</td>
</tr>
<tr>
<td>Long-horned milkweed beetle</td>
<td>37m(^12-14)</td>
<td>Long-horned milkweed beetle</td>
<td>No(^{19})</td>
</tr>
<tr>
<td>Monarch butterfly</td>
<td>&gt;1000m(^15)</td>
<td>Monarch butterfly</td>
<td>Yes(^{20-22})</td>
</tr>
<tr>
<td>Milkweed tussock moth</td>
<td>&gt;1000m(^16)</td>
<td>Confamiliar of the milkweed tussock moth</td>
<td>No(^{22,23})</td>
</tr>
</tbody>
</table>


* Aphids are weak flyers capable of active dispersal on the scale of metres to tens of metres, but they can also be passively dispersed by wind currents for kilometers. In our system, where all patches are <2000m apart and many patches are less than 100m apart, active short-distance dispersal and short to medium distance blowing are likely to be more relevant than rare long-distance wind dispersal events for moving aphids between patches. We therefore estimated average aphid dispersal to be between the literature estimates for these two dispersal modes (100m), but with more weight given to short-distance dispersal.

† No references were available for weevils and miner predator susceptibility, so we classified these species as unsusceptible due to the cryptic lifestyle of leaf miners and the hard protected body form of weevils.

Study site and surveys

We conducted this study at the Koffler Scientific Reserve (KSR) in Southern Ontario, Canada (44°03’N, 79°53’W). At this site, milkweed grows in old fields and in forest clearings, in patches ranging from a few to thousands of plants. For our study, we selected one old field area and one forested area (Appendix B Fig. S3.1) in order to assess whether our results were consistent across different habitats; however, the lack of replication of matrix types precludes us from drawing conclusions about the effect of the matrix on species distributions. The old field area is bounded by trees (forest or forest fragments) and cultivated land, while the forest area is bounded by residential areas and roads. Within each of these areas, we selected 30 focal milkweed patches (out of 103 old field and 36 forest patches) for insect surveys. We selected patches to maximize the range of patch sizes and inter-patch distances. We calculated the area (hereafter patch size) and connectivity of all sampled and unsampled patches by mapping the
perimeter of each patch using a high precision Trimble GPS unit (GeoXH Geexplorer) and calculating the area of polygons in ArcGIS (v. 10.3). We calculated the edge-to-edge distances between each patch and all other patches within the same matrix type (forest or old field) for use in our connectivity function (Statistical methods). Patches had an average area of 131m² (± 345m² SD) in the old field and 93m² (± 345m² SD) in the forest, and a mean distance between pairs of patches (within the same matrix type) of 271m (± 160m SD) in the old field and 835m (± 584m SD) in the forest (Appendix B Fig. S3.2).

For surveys, we randomly selected 30 plants that were at least 30 cm tall within each milkweed patch, and in patches with fewer than 30 individuals, we sampled all plants. We surveyed focal plants for insects and arachnids every two weeks between early July and early September 2014, for a total of five surveys. Specialist milkweed herbivores were identified to species, while predators were identified to family; individuals that were difficult to identify were photographed or collected and keyed out at a later date. Twenty-five insect and arachnid families were classified as predatory, based on feeding guild classifications in published studies (Voigt et al. (2003); Harvey and MacDougall (2014); Appendix B Table S3.1). Ants (Hymenoptera, Formicidae) are a major predator of monarch caterpillars, and were included as predators in the monarch analysis (Zalucki & Kitching 1982b; Prysby 2004). As milkweed weevils and leaf miners occur primarily in the spring (May and June), before our surveys, their presence was determined post-hoc by counting leaf scars (miners) and stem scars (weevil) in late July (Van Zandt & Agrawal 2004a).

Statistical analysis

We analyzed the effect of patch size, patch connectivity and predator abundances (all predators summed) on the plant-level occupancy of each specialist milkweed herbivore in each matrix type. We used plant-level occupancy for two reasons: first, this measure allowed us to keep search effort constant across patches of different sizes that correspondingly had different numbers of plants surveyed (see Methods above). Second, this measure allowed us to test the basic Island Biogeography hypothesis that higher colonization rates and lower extinction rates in large and connected patches should result in a greater number of individuals per species per unit
area (Holt et al. 1995; Jones et al. 2015). Thus, we used plant-level occupancy to test whether insect densities, at the level of individual patches, differed.

To calculate inter-patch connectivity, we used the following metapopulation model (Hanski 1994b):

\[ C_i = \sum_{j \neq i}^n A_j e^{-d_{ij}/\alpha} \]

where \( C_i \) is the connectivity of patch \( i \), \( d \) is the Euclidean distance between any two patches, \( \alpha \) is the mean dispersal distance of the species or group of interest, and \( A \) is the area of all source (non \( i \)) patches (the summation incorporates distances from all other sites). This connectivity metric uses the standard assumption of an exponential dispersal curve with a mean dispersal distance of \( \alpha \). As a result, connectivity between site \( i \) and \( j \) decreases at greater distances (\( d_{ij} \)) and increases with greater dispersal ability (\( \alpha \)) and greater area (\( A \)) of source patches. This model has a similar functional form as Hanski’s incidence function (equation 4 in (Hanski 1994b)). We obtained estimates for the mean dispersal distance (\( \alpha \)) for each specialist species from published studies, where possible (Table 3.1). For monarchs and tussock moths, which are capable of dispersing long distances (many kilometres), we used an \( \alpha \) value of 1000m, which represents a case of low or no dispersal limitation in this system.

For all species except leaf miners and weevils, we ran binomial generalized linear mixed models with patch size, patch connectivity and predator abundance as predictor variables, presence-absence of the species on each plant as the response variable, and patch, survey date and plant as random factors. Including patch as a random factor in the analysis ensured that patch was the unit of measure for linking insect distributions to our patch-level explanatory variables. For weevils and miners, whose occupancy was estimated at a single time point, models did not include time or predators, as many predators emerge after these two species, and predator abundances were quantified later in the season. Three species with fewer than ten observations in either the forest or the old field could not be analyzed in that matrix type (Table 3.2). We also tested for effects of matrix type on predator abundances and the occurrence of each focal species using glms with matrix type as the predictor and patch as a random factor.
All statistical analyses were conducted in R (v. 3.2.4) using the glmmadmb function in the glmmADMB package. For all analyses, we started with the most complex model and dropped all non-significant higher order interactions (see Appendix B for additional statistical methods). We present the highest order significant interaction(s) or main effects from each model. In all models, all predictors were standardized prior to analysis (centered on zero with a standard deviation of one) to account for differences in scale between our predictor variables, and predator abundance and patch size were log transformed to meet model assumptions. Figures were created using the visreg package, and show back-transformed predictions from models that include only fixed effects, due to issues with estimating confidence intervals in complex models when random effects are included (Bates et al. 2014).

Results

Occupancy rates varied across our focal species; while some species were widespread, with occupancy rates of over 30% in both matrix types (e.g. *Myzocallis*, leaf miner), others were more rare overall, occupying fewer than 5% of plants per patch (e.g. *A. nerii*, long-horned milkweed beetle) (Table 3.2; Appendix B Fig. S3.3). Occupancy rates of seven of our focal species were driven directly by patch size and/or connectivity in at least one matrix type (see Fig. 3.2 for direct effects of spatial drivers). Specifically, occupancy rates of five species were positively associated with patch size (*Myzocallis*, weevil, long-horned milkweed beetle), connectivity (leaf miner), or both (small milkweed bug) in one or both matrix types (Fig. 3.2a-f; Table 3.2). The positive effect of patch size on *Myzocallis* occupancy in the forest was only apparent when patches were poorly connected (area x connectivity interaction; $P = 0.03$; Fig. 3.2g). In contrast, monarch occupancy was negatively associated with patch size in the forest ($P = 0.009$; Fig. 3.2h), and *A. asclepiadis* occupancy was negatively associated with patch connectivity in the old field ($P = 0.003$, Fig. 3.2i). Tussock moth occupancy was not related to any predictor in the forest, the only habitat where this species occurred (Table 3.2).
Table 3.2 Details of model results. Effect indicates the highest order interaction(s), or significant main effects. ***P<0.001, **P<0.01, *P<0.05. S = patch size, C = patch connectivity, P = predator abundance. ‘Total occurrences’ indicates total number of times each species was observed (presence, not abundance), while ‘occupancy’ indicates the mean percentage of plants per patch occupied by each species (± SE). For both total occurrences and occupancy rates, observations from five surveys were summed (except in the case of weevils and miners, which were surveyed at a single time point). “Not analyzed” indicates the three models that could not be run because a species’ occupancy in that matrix type was too low.

<table>
<thead>
<tr>
<th>Species</th>
<th>Matrix</th>
<th>Total Occurrences</th>
<th>Occupancy (%)</th>
<th>Effect</th>
<th>Sig.</th>
<th>Fig.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aphis asclepiadis</em></td>
<td>F</td>
<td>46</td>
<td>4.6 ± 1.9</td>
<td>S x P, C x P</td>
<td>***,**3.3a, 3.3b</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>82</td>
<td>15.0 ± 4.0</td>
<td>C</td>
<td>**</td>
<td>3.2i</td>
</tr>
<tr>
<td><em>Aphis nerii</em></td>
<td>F</td>
<td>15</td>
<td>3.3 ± 1.4</td>
<td>None</td>
<td></td>
<td>3.3c</td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>10</td>
<td>1.5 ± 0.6</td>
<td>S x P</td>
<td>*</td>
<td>3.2i</td>
</tr>
<tr>
<td><em>Myzocallis asclepiadis</em></td>
<td>F</td>
<td>546</td>
<td>43.4 ± 7.3</td>
<td>C x S</td>
<td>*</td>
<td>3.2g</td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>381</td>
<td>41.6 ± 5.6</td>
<td>S</td>
<td>**</td>
<td>3.2e</td>
</tr>
<tr>
<td>Weevil</td>
<td>F</td>
<td>70</td>
<td>8.9 ± 3.8</td>
<td>S</td>
<td>**</td>
<td>3.2a</td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>175</td>
<td>31.8 ± 5.6</td>
<td>None</td>
<td></td>
<td>3.2f</td>
</tr>
<tr>
<td><em>Miner</em></td>
<td>F</td>
<td>199</td>
<td>36.6 ± 5.0</td>
<td>C</td>
<td>*, *</td>
<td>3.2f</td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>410</td>
<td>81.0 ± 3.2</td>
<td>None</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Small milkweed bug</em></td>
<td>F</td>
<td>0</td>
<td>0</td>
<td>Not analyzed</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>27</td>
<td>3.3 ± 0.8</td>
<td>S, C</td>
<td>*, **</td>
<td>3.2b, 3.2c</td>
</tr>
<tr>
<td><em>Long-horned beetle</em></td>
<td>F</td>
<td>6</td>
<td>1.4 ± 0.8</td>
<td>Not analyzed</td>
<td></td>
<td>3.2d</td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>13</td>
<td>1.6 ± 0.6</td>
<td>S</td>
<td>*</td>
<td>3.2d</td>
</tr>
<tr>
<td><em>Monarch</em></td>
<td>F</td>
<td>33</td>
<td>6.7 ± 2.2</td>
<td>S</td>
<td>*</td>
<td>3.2h</td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>37</td>
<td>5.9 ± 1.5</td>
<td>C x P</td>
<td>**</td>
<td>3.3d</td>
</tr>
<tr>
<td><em>Tussock moth</em></td>
<td>F</td>
<td>103</td>
<td>25.6 ± 5.1</td>
<td>None</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>OF</td>
<td>4</td>
<td>0.5 ± 0.3</td>
<td>Not analyzed</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.2 Species with occupancy rates affected only by patch size (a,b,d,e,g,h) and/or connectivity (c,f,g,i), but not predators. Lines are best fits from the statistical model, and shading is a 95% confidence interval (see methods). In panel g, light and dark grey bands are 95% confidence intervals around fitted lines, with connectivity set at low (10th quantile) and high (90th quantile) levels, respectively. Note the difference in Y axes among panels.
Predators altered the effect of patch size and/or connectivity for three of four species that are susceptible to predation: *A. asclepiadis*, *A. nerii* and monarchs (see Fig. 3.3 for interactions between predators and spatial drivers). In the forest, *A. asclepiadis* had a positive relationship with patch size when predators were at low abundance that was diminished when predators were abundant (two-way interaction; $P = 0.001$; Fig. 3.3a). Likewise, *A. nerii* had a positive relationship with patch size in the old field that was reversed at high predator abundance (two-way interaction; $P = 0.01$; Fig. 3.3c). Finally, the negative relationships between connectivity and monarch (old field) and *A. asclepiadis* (forest) occupancy were only apparent when predators were abundant (two-way interaction; $P = 0.006$; Fig. 3.3b, d).

Occupancy rates of five out of nine species differed between the old field and forest site: whereas four species had significantly higher occurrence rates in the old field (miners, weevils, small milkweed bug and *A. asclepiadis*), only the tussock moth had significantly higher occupancy in the forest (all $P < 0.05$; Appendix B Fig. S3.3). The impact of predators, patch size and patch connectivity also varied between the old field and forest sites for most species (Table 3.2).

In summary, we detected positive associations with patch size and connectivity for four weak dispersers (small milkweed bug, long-horned milkweed beetle, weevil and miner), and no or negative associations with these spatial drivers for the two dispersive species (tussock moth and monarch) (Fig. 3.2; Table 3.2). Interactions between predators and spatial drivers drove the distributions of three predator-susceptible species (*A. nerii*, *A. asclepiadis* and monarchs; Fig. 3.3). One weak disperser, *A. asclepiadis*, showed an unexpected negative effect of patch connectivity (Fig. 3.2i), while one predator-susceptible species (*Myzocallis*) did not show the negative response to predators that we predicted (Table 3.2).
Figure 3.3 Species with occupancy rates affected by both predators and spatial drivers. Lines are best fits from the statistical model and shading is a 95% confidence interval, with light pink and dark red set at low (10th quantile) and high (90th quantile) predator abundances, respectively. Note the difference in Y axes among panels.

Discussion

While many studies have examined the effects of patch size and connectivity on species distributions, the influence of local biotic processes on these relationships remains poorly understood in most natural systems. Here we found that predators altered biogeographic
predictions for a third of our focal species, indicating the substantial role that local top-down pressure can play in moderating biogeographical constraints. More generally, our study demonstrates that the independent and interactive effects of predators and spatial drivers can be well-predicted by the \textit{a priori} positioning of species along axes of local and regional constraint.

Our simple framework was remarkably successful in predicting when biotic interactions or spatial drivers should impact the distributions of our focal species. The positive effect of patch size and connectivity on the distributions of the four well-defended species with limited dispersal (Figs. 3, 1, 3.2) supports the emerging use of dispersal ability to predict species’ responses to spatial structure in patchy landscapes (\textit{e.g.} De Bie \textit{et al.} (2012); Jones \textit{et al.} (2015)). Similarly, we predicted that predators would mediate the distributions of four readily-consumed species, and found supporting evidence for three of these species. In all cases, predators impacted distributions via interactions with spatial drivers, by dampening positive relationships or creating negative relationships with patch size or connectivity (Fig. 3). If not accounted for, predators could obscure the effects of spatial drivers, which might explain why biogeographic constraints do not emerge as important predictors in many taxa (Gilbert 1980; Prugh \textit{et al.} 2008).

While our study cannot definitively determine the mechanisms underlying the interactive effects of predators and spatial drivers, experimental work has demonstrated that predators can alter the impact of spatial structure by changing colonization and extinction dynamics (Shurin 2001; Kneitel & Miller 2003; Resetarits \textit{et al.} 2005). The negative impacts of predators can manifest both as direct consumptive effects, and as non-consumptive effects that include behavioural modifications and stress-induced mortality and reductions in fitness (Preisser \textit{et al.} 2005; McCauley \textit{et al.} 2011). Through these mechanisms, predators can weaken the positive effects of patch size and connectivity on occupancy by reducing establishment of arriving species, by increasing extinction rates of species that do establish, or by causing active dispersers to avoid certain patches (Kneitel & Miller 2003; Resetarits \textit{et al.} 2005; Howeth & Leibold 2010). These different predator effects are not mutually exclusive, and in this study, predators both dampened and reversed the effects of biogeographic constraints for poorly-defended species (Fig. 3), suggesting that more than one of these interactive effects may play a role in shaping species distributions (Kennedy & Gray 1993; Resetarits \textit{et al.} 2005).
The negative relationships with patch size and connectivity that emerged at high predator densities for three species are suggestive of active predator avoidance by these predator-sensitive species (Fig. 3b,c,d). For example, monarch butterflies are excellent dispersers and, rather than showing no association with patch size and connectivity, monarch caterpillars occurred most often in small and isolated patches, especially when predators were present (Fig. 3.2h; Fig. 3.3d). Previous research indicates that monarch butterflies may choose to lay their eggs on small milkweed patches as a behavioural adaptation to seek refuge from predators or competitors, which could explain this result (Zalucki & Kitching 1982b, a). In addition, monarch caterpillars are negatively impacted by the latex induced by early season weevil feeding (Van Zandt & Agrawal 2004a), which could be why monarchs were rare in large forest patches where weevils were common (Fig. 3.2a, h). Although aphids have more limited dispersal than monarchs, some develop winged morphs in response to predators, indicating the potential for dynamic feedbacks between patch selection and predator abundance (Dixon & Agarwala 1999; Mehrparvar et al. 2013). The exploitation of spatial constraints by active dispersers that manifest as negative patch size and connectivity relationships is a phenomenon that is not included in many models, but could be integrated into future research.

Although the distributions of most species were well-predicted by our framework, there were two interesting departures that generate hypotheses for future study. Contrary to our predictions, there was no effect of predators on the distribution of one aphid species, Myzocallis (Fig. 3.2e, g), which contrasts with previous research suggesting that predators readily consume all three of these specialist aphid species (Smith et al. 2008). However, unlike the other two aphid species, Myzocallis lives on undersides of milkweed leaves and is light green in color (Smith et al. 2008), and our results raise the possibility that this cryptic habit of Myzocallis may be an effective strategy against invertebrate predators (Denno et al. 2003). A second departure from our expectations was the direct negative effect of connectivity on A. asclepiadis occupancy in old field patches (Fig. 3.2i). This species is considered more vulnerable than other aphids to competition and predation (Mooney et al. 2008; Smith et al. 2008), which it may offset by selecting more remote habitats. Both departures from our expectations provide hypotheses about divergent strategies among functionally-similar aphid species that, if tested experimentally,
could help untangle the mechanisms underlying the coexistence of these close competitors (Mooney et al. 2008).

We contrasted two matrix types, forest and old field, to provide a broader scale look at how predators and spatial drivers shape the distributions of our focal species. Although our use of only one old field site and one forest site precludes general conclusions about the impact of different matrices on observed relationships, it is interesting to note that the factors driving species distributions differed between our two matrix types for most focal species (Table 3.2). As well, the matrix appeared to filter species at a broader scale, as five of our nine focal species were more common in one matrix type than the other (Table 3.2; Appendix B Fig. S3.3). These differences could have multiple underlying causes including the greater number of milkweed patches in the old field, unmeasured differences in avian predators or microclimate, or effects of the different landscapes surrounding each matrix. In either case, our results suggest that the inclusion of multiple replicated matrix types in future studies could reveal underappreciated landscape-scale patterns in metacommunities, and complements previous work demonstrating the importance of the matrix in shaping the distribution of species in fragmented habitats (Prevedello & Vieira 2010).

Although certain features of our study system should be considered carefully in extrapolating these results to other systems, the predictive framework used here has the potential to be applied more broadly to other types of metacommunities and local interactions. For example, local variation in bottom-up constraints such as resource quality could be used in place of, or in addition to, the top-down predator constraint we focused on here, particularly since responses to plant defenses are known to vary across herbivore species (Van Zandt & Agrawal 2004b; Gripenberg & Roslin 2007). The inclusion of resource quality as a local factor could be especially fruitful in systems such as ours where clonal plant growth has the potential to create substantial inter-patch differences in resource quality. Likewise, in aquatic systems in which habitat patches consist of ponds or lakes that vary in resource availability and quality, the inclusion of local bottom-up constraints could be particularly worthwhile (De Bie et al. 2012).

The lack of herbivore diversity in the milkweed system made it feasible for us research and classify each species along axes of spatial constraint and predator susceptibility; however, less
intensive methods could also be used to classify species in more diverse or less well-studied systems. For example, if dispersal ability or responses to certain plant defenses are known to be phylogenetically conserved, then in diverse communities, higher-order taxonomic groups such as families could be placed into a predictive framework like the one presented in Fig. 3.1 (Blomberg et al. 2003). While our inability to control for phylogeny due to our small number of focal species presents a limitation in that dispersal ability and susceptibility to predation may not be independent of evolutionary relationships, in more speciose communities, phylogenetic constraint on traits driving local and regional responses could serve as an efficient method for predicting species’ responses. Similarly, trait-based approaches could be used in speciose communities as a short-cut for generating predictions. For example, differences in dispersal can be characterized by dispersal mode and individual height for plants (Thomson et al. 2011; Jones et al. 2015), while in animals, body size has been used to predict dispersal distance, competitive hierarchies and trophic interactions (Woodward & Hildrew 2002; De Bie et al. 2012). Such traits could provide a key to predicting species’ local and regional constraints a priori in a broad array of metacommunities, just as they are increasingly used for understanding communities inhabiting continuous landscapes. If used more broadly, the approach presented here could reveal predictable impacts of local interactions on species’ responses to classic biogeographic constraints, and bring us closer to untangling the combined role of local and regional drivers in shaping ecological communities.

Acknowledgments

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References


CHAPTER 3: PREDATORS MODIFY BIOGEOGRAPHIC CONSTRAINTS


Appendix B: Supplementary information to Chapter 3

Supplementary statistical methods

In two patches in the old field, all plants died early in the study, and these two patches were excluded from all analyses. For models with a low number of observations (<50), we removed time from the model to avoid over-fitting and model failure; to do this we calculated presence-absence of each species on a plant over the five surveys and averaged predator abundances across all surveys. We tested for correlations between our predictor variables, and found none (R<0.1 for all). Because the inclusion of plant size as an offset caused over-fitting and model failure, we also tested for correlations between plant size and all predictors to ensure that there was no confounding effect of plant size on specialist occupancy. Plant size was weakly correlated with patch size for old field patches only (R=0.36), and we therefore consider our predictors to be independent of one another, and not driven by differences in plant size.

References for insect images used in figures

Long-horned milkweed beetle: photograph by Mike Quinn © TexasEnto.net
Small milkweed bug: photograph by Tom Murray © bugguide.net
Weevil: modified from photograph by Roland E. Barth © fnanaturesearch.org
Leaf miner: photograph by MJ Hatfield © bugguide.net
Tussock moth: modified from photograph by Ed Nisley © softsolder.com
Monarch: photograph by Marty Nevils Davis © martydavisphotos.com
Aphids: modified from images created by Dr. Kailen Mooney (UC Irvine)
**Supplementary tables and figures**

**Table S3.1** List of insect and arachnid families classified as predators.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araneae</td>
<td>Agelenidae</td>
</tr>
<tr>
<td></td>
<td>Nyphaenidae</td>
</tr>
<tr>
<td></td>
<td>Araneidae</td>
</tr>
<tr>
<td></td>
<td>Clubionidae</td>
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<tr>
<td></td>
<td>Dictynidae</td>
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<tr>
<td></td>
<td>Linyphiidae</td>
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<tr>
<td></td>
<td>Philodromidae</td>
</tr>
<tr>
<td></td>
<td>Salticidae</td>
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<tr>
<td></td>
<td>Tetragnathidae</td>
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<td>Coccinellidae</td>
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<td>Staphylinidae</td>
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<td>Cantharidae</td>
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<td>Opiliones</td>
<td>Phalangiidae</td>
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<td>Thysanoptera</td>
<td>Aeolothripidae</td>
</tr>
</tbody>
</table>

†Two additional families that contain both predatory and herbivorous species (Pentamonidae and Miridae) were observed in low abundances this study, but were not included as predators due to insufficient taxonomic resolution to positively determine feeding guild.
Figure S3.1 Maps of (a) old field and (b) forest study areas, with all milkweed patches (including both focal patches and non-focal patches) shown as yellow polygons. Note the difference in scale between the forest and old field areas – the forest area has a larger extent, and thus patches of a given size appear smaller in this map (b) than they would in the old field (a). Black arrows point to nine forest patches that are difficult to see due to their small size relative to the large scale of the forest site. Maps were created using ArcGIS (v. 10.3) and Google Earth (imagery and map data ©2015 Google; map accessed online January 22 2015; mapped area centered on 44.034145, -79.527321).
Figure S3.2 Patch sizes (areas) and inter-patch distances (distances between pairs of patches) of all milkweed patches (including both focal patches and non-focal patches) in the (a,c) old field, and (b,d) forest study areas. Note the log scale for patch sizes.
Figure S3.3 Mean occupancy rates (proportion of plants per patch occupied) of each specialist in the forest and old field. Data points are mean values ± one standard error. Note the difference in Y axes among panels.
Chapter 4: Temperature-dependent species interactions shape priority effects and the persistence of unequal competitors


Abstract

The order of species arrival at a site can determine the outcome of competitive interactions when early arrivers alter the environment or deplete shared resources. These priority effects are predicted to be stronger at high temperatures, as higher vital rates caused by warming allows early arrivers to more rapidly impact a shared environment. We tested this prediction using a pair of congeneric aphid species that specialize on milkweed plants. We manipulated temperature and arrival order of the two aphid species, and measured aphid population dynamics and milkweed survival and defensive traits. We found that warming increased the impact of aphids on the quantity and quality of milkweed, which amplified the importance of priority effects by increasing the competitive exclusion of the inferior competitor when it arrived late. Warming also enhanced interspecific differences in dispersal, which could alter relative arrival times at a regional scale. Our experiment provides a first link between temperature-dependent trophic interactions, priority effects and dispersal. This study suggests that the indirect and cascading effects of temperature observed here may be important determinants of diversity in the temporally and spatially complex landscapes that characterize ecological communities.

Introduction

The order in which species establish in a community can determine coexistence outcomes and the trajectory of community assembly, through a process known as priority effects (Alford & Wilbur 1985; Drake 1991; Fukami 2015). Priority effects occur when early arrivers draw down a common resource (“niche pre-emption”) or change the environment (“niche modification”) in a way that alters the success of late arrivers (Vannette & Fukami 2014). While priority effects have traditionally been considered mainly in the context of alternate stable states, recent research has demonstrated the important role that assembly history can play in structuring
transient communities including ephemeral ponds, plant patches and flower nectar microbes (Fukami & Nakajima 2011; Fukami 2015). The broad range of communities that can foster priority effects suggests that they are likely to have important and wide-reaching impacts on coexistence and diversity in a variety of ecological communities. As a result, emerging research seeks to understand the conditions that favour priority effects, and their impact on community assembly and coexistence (Fukami 2004; Kardol et al. 2013; Pu & Jiang 2015).

Any condition that increases the ability of early arrivers to quickly deplete resources, modify the environment, or both, should amplify the importance of arrival order for competitive outcomes (Kardol et al. 2013; Fukami 2015). Theoretical and empirical studies have demonstrated that priority effects are strongest when competing species have high growth rates, high niche overlap, and compete strongly for the same limited resource (Tilman 2004; Peay et al. 2012; Tucker & Fukami 2014; Vannette & Fukami 2014; Fukami 2015). As such, conditions that increase population growth rates of early arrivers or their per capita impact on the quantity or quality of a shared resource should strengthen priority effects (Chase 2003, 2010; Kardol et al. 2013; Rudolf & Singh 2013).

Temperature regulates population growth and feeding rates in ectothermic species (Brown et al. 2004; Dell et al. 2011), indicating that, below the threshold at which rising temperatures begin to reduce these rates, rising temperatures should result in stronger priority effects. Moreover, recent extensions of metabolic theory to species interactions predict that stronger temperature dependence of herbivore vital rates, compared to those of their plant resources, should cause temperature to systematically alter plant-herbivore interactions (O’Connor et al. 2011).

Specifically, the higher temperature sensitivity of respiration relative to photosynthesis, and the resulting higher activation energies of herbivores than autotrophs (Allen et al. 2005; López-Urrutia et al. 2006; Dell et al. 2011), causes herbivore feeding and population growth rates to outpace growth rates of primary producers as temperatures increase (O’Connor et al. 2009). This temperature asymmetry can cause herbivores to rapidly deplete their plant resource (Gilbert et al. 2014). Ultimately, faster resource depletion lowers herbivore abundances and fluctuations, reducing the maximum size that populations can reach (O’Connor et al. 2011; Dell et al. 2014; Gilbert et al. 2014).
This influence of temperature on plant-herbivore interactions should have a predictable two-pronged effect on how early arriving herbivores impact late arrivers, by changing both the quantity and quality of the plant resource. First, early arriving herbivores are predicted to reduce plant resources more rapidly at higher temperatures, increasing niche pre-emption. Second, when a stronger top-down pressure from herbivores prompts an increase in the induction of plant defenses (Underwood 2000), late arrivers will feel the negative impacts of stronger niche modification. Despite this potential for higher temperatures to strengthen priority effects in plant-herbivore systems by systematically altering trophic dynamics, this hypothesis has yet to be explored empirically.

Temperature can also impact priority effects on a broader metacommunity scale if dispersal dynamics are temperature-dependent, by altering the order in which species colonize resource patches or the length of time between colonization events by different species (O’Connor et al. 2007; Altermatt et al. 2008). Temperature-dependent dispersal emerges through a variety of mechanisms, from altered per capita dispersal success to shifts in local dispersal cues (Travis et al. 2013). In herbivorous insects, for example, crowding and low resource quality can induce higher dispersal rates, as individuals leave in search of better habitat (Zera & Denno 1997; Benard & McCauley 2008). As a result, the temperature dependence of plant-herbivore interactions is expected to increase dispersal at higher temperatures by precipitating a decline in resource quantity and quality. When these temperature-induced shifts in dispersal change species’ arrival order or increase the time between colonization by different species, they have the potential to alter priority effects at a regional scale. An integration of dispersal into research on priority effects could thus provide a more complete picture of how warming will change species interactions and coexistence in patchy landscapes.

We tested the effects of temperature on priority effects using two congeneric aphid species that specialize on milkweed: Aphis nerii and A. asclepiadis. The patchy distribution of milkweed plants causes the initiation of local aphid populations to be constrained by dispersal among plants, such that aphid species rarely arrive at a plant at the same time. These aphid species have high niche overlap (both feed exclusively on milkweed phloem), rapid population growth rates that are sensitive to temperature (Agrawal et al. 2004), and can reach large population sizes capable of depleting their ephemeral plant resource to the point of death. Milkweed also has physical defenses that can be affected by aphid feeding, making priority effects through niche
modification a potential determinant of competitive interactions (Agrawal 2004a; Woods et al. 2012). Finally, previous research has demonstrated that these two species are competitively unequal, and that priority effects may play a role in their ability to coexist. Compared to A. asclepiadis, A. nerii produces more offspring, has higher feeding rates, is more dispersive, is less affected by competition, and is preyed upon less (Mooney et al. 2008; Smith et al. 2008). However, A. asclepiadis can produce frost-tolerant eggs capable of overwintering in cold northern climates, whereas A. nerii is obligately parthenogenic and must disperse north from warmer overwintering sites each summer (Groeters 1989; Mooney et al. 2008). Although the arrival times of these species vary from year to year and across their shared range, earlier arrival could give A. asclepiadis, the putatively inferior competitor, an advantage that helps these two species coexist (Mooney et al. 2008).

In our experiment, we manipulated temperature and the order of arrival of aphid species to test hypotheses about four related processes that together shape the local and regional coexistence of two unequal competitors. We hypothesized that a stronger temperature dependence of insects relative to plants would result in several consequences of higher temperatures: (1) higher aphid population growth rates and lower aphid maximum population sizes, (2) a stronger, aphid-induced decline in both plant quantity (less growth and greater mortality) and quality (greater induction of defensive traits), (3) stronger priority effects, as early arrivers exert a stronger impact on milkweed, and (4) higher dispersal rates, as aphids leave to avoid low-resource conditions. We show that predictable consequences of temperature on herbivores and plants alter priority effects and dispersal rates to shape competitive outcomes. These results have broad implications for understanding the local and regional coexistence of competing species under climate change.

Methods

Natural history

Common milkweed Asclepias syriaca (hereafter milkweed) is a native perennial commonly found in old field habitats across eastern North America. Milkweed is chemically defended with neurotoxic cardenolides and physically defended with trichomes covering the leaf surface and latex that is expelled when leaves are damaged. Milkweed physical defenses (trichomes and latex) occur constitutively, and can be induced by herbivory (Van Zandt & Agrawal 2004; Ali &
Agrawal 2014). As a result of its defenses, milkweed hosts only a small group of specialist
herbivorous insects that includes two aphid congeneres (Aphis asclepiadis and Aphis nerii) that
feed on phloem and coexist on milkweed (Mooney et al. 2008; Smith et al. 2008). Both aphid
species reproduce through parthenogenesis, and produce both unwinged morphs that are largely
sedentary and winged morphs capable of actively dispersing between plants, with winged
morphs more readily produced in crowded conditions (Groeters 1989).

**Experimental set-up**

We grew milkweed plants from seed obtained from a commercial nursery (Prairie Moon
Nursery, Winona, MN, USA) (detailed methods in Appendix C). We started aphid colonies
from individuals collected from Koffler Scientific Reserve (44°03'N, 79°53'W) and maintained
colonies at room temperature (~ 21°C).

In two growth chambers, we conducted a five week experiment that crossed two temperatures
(20.1°C and 22.2°C mean daily temperature, described below) with five levels of competition
and a control: (1) A. nerii alone, (2) A. asclepiadis alone, (3) both species added simultaneously,
(4) both species with A. nerii added two weeks before A. asclepiadis, (5) both species with A.
asclepiadis added two weeks before A. nerii and (6) milkweed with no aphids as a control. This
resulted in a total of 12 treatments, each replicated between 8 and 11 times, for a total of 120
plants. We placed potted plants within cages to contain aphids (Appendix C Fig. S4.1), and
implemented our warming treatment at the individual plant level to avoid chamber effects. To
raise the temperature of our warmed cages, we used 50w light bulbs painted black (so that heat
but not light was emitted), and we left the light bulbs unplugged in our unwarmed treatment
(Appendix C Fig. S4.1). To quantify dispersal, we secured a 10cm X 12.5cm yellow sticky card
(Plant Products, Ancaster, Canada) at the opposite end of the cage as the plant (approximately
45cm away from the plant) to catch dispersing aphids. Throughout the experiment we monitored
the temperature and humidity inside cages, and soil moisture in potted plants (Appendix C).

Warming increased the temperature by an average of 2.1°C (from 20.1°C to 22.2°C mean daily
temperatures; Appendix C Fig. S4.2). These temperatures are well below the critical thresholds,
often called optimal temperatures (e.g. Dell et al. (2011)), for our species (El Din 1976;
Agrawal et al. 2004), and were selected because they approximate both inter-annual temperature
fluctuations at our field site and projected temperature increases under climate change (IPCC (2014); Appendix C).

In treatments with a single species, we added six adult individuals of that species on day one of the experiment. In treatments that had species arriving together, three individuals each of A. nerii and A. asclepiadis were added on day one of the experiment. For each of the priority treatments, we added three individuals of the early arriving species to the plant on day one of the experiment, and added three individuals of the late arriving species on day 14; this two week lag was selected to approximate typical lags in colonization of a given plant between these species, and corresponds to the amount of time required for these species to begin increasing the production of winged individuals in a population (see Results). All treatments (except no-aphid controls) therefore had six aphids added in total. One day after each aphid population was introduced to its experimental unit, we replaced any aphids that had died overnight or had become winged adults, and removed any nymphs produced overnight. We did this because the aphids we added were sometimes damaged by handling, were gravid, or were in the early undetectable stages of wing development, and we wanted to ensure that all added aphids were healthy unwinged adults.

Plant and aphid responses

We measured the impact of aphids and temperature on the following plant responses: growth, mortality, trichome density, and latex production (Appendix C). To quantify plant growth and latex production, we measured the change in plant height (Agrawal 2004b) or latex exudation by first measuring these responses one day before the experiment started, and repeating measurements three weeks into the experiment (on day 21), when 98% of the plants were still alive. We also measured trichome density on leaf tips three weeks into the experiment. We quantified plant mortality as whether or not plants died (>50% of leaves senesced) by the end of the experiment. Plant mortality was assumed to be herbivore-induced, as all but one of the control plants (no aphids added) remained healthy throughout the experiment and did not lose any leaves.

To quantify aphid population dynamics, we counted all aphids on each plant and recorded the number of winged and unwinged individuals twice a week, for a total of ten surveys. To get an indirect measure of long-distance dispersal potential, we counted the number of winged
individuals on each plant. To get a direct measure of short-distance dispersal, we photographed the sticky card in each cage at each survey, and later counted the number of individuals of each species that had landed on the card between each survey point. Because cards remained in the cages throughout the experiment and were not replaced, and aphids decayed and turned black within a few days of landing on the cards, the two species were indistinguishable when both occurred on the same card. We therefore restricted our measurement of dispersal to treatments in which each species was alone (detailed methods in Appendix C). We ran the experiment for five weeks, which is roughly to the length of time that our two aphid species interact during a growing season.

Statistical analysis

To determine the impact of temperature on aphids (Hypothesis 1), we analyzed the effect of temperature on the population growth rates and maximum population size of each species when grown alone (in the absence of interspecific competition). For these analyses, we used only single-species treatments, which all had starting densities of six aphids, as other treatments could be influenced by their lower starting conspecific density. Aphid “populations” in our analyses include all aphids of a single species on one plant (experimental unit), and do not include dispersed individuals (as these could not be quantified for interspecific competition treatments). To determine the effect of temperature on the population growth rates of each species, we constructed a four-parameter logistic model with a fixed lower asymptote (the other parameters were the upper asymptote, midpoint and scale), using the ‘nlme’ function, with replicate included as a random effect in a random slope, random intercept analysis. We fixed the lower asymptote of our models at the initial population size at 6 aphids (the number of aphids initially added to each plant), and truncated the data for each plant to include all sampling times up to and including the population maximum, to avoid modeling the subsequent population decline. We corrected for heteroscedasticity in the error term by using the weights function to scale the error with the sample date, and by allowing this scaling to differ between temperature treatments. The inverse of the scale parameter of the logistic model describes the steepness of the curve at the inflection point, and corresponds to the population growth rate in the absence of density dependence (Paine et al. 2012). For this analysis, parameter estimates for A. asclepiadis depended on the starting values for the parameters. We therefore used the starting values that led
to the closest match between the observed data (numbers through time and maximum population size), but note that varying the starting values did not qualitatively change our results.

We calculated maximum population size as the maximum number of aphids reached in each population, and determined the date at which each population peaked. We ran separate linear models for each species, with temperature as the predictor variable and log maximum population size or date of population peak as the response variable.

To test the impact of temperature and aphids on plants (Hypothesis 2), we analyzed the effect of temperature and aphid population size on two plant responses indicative of resource quantity (plant growth and death) and two responses indicative of plant quality (latex exudation and trichome density). For all plant analyses, ‘population size’ was the maximum number of aphids reached on a plant, with all individuals from both species summed. For this analysis, our goal was to test the impact of aphid abundances and warming on milkweed responses, as per our hypotheses, rather than focus on the effects of our competitive treatments (i.e. arrival order and aphid species identity) on plant responses. Additionally, because aphid abundances were also affected by competitive treatment, plants within competitive treatments were not independent for this measure. For these reasons, we analyzed plant responses using the mean values of aphid maximum population size for each of our 12 treatments as our aphid predictor, and the mean values of our plant responses for each treatment as our response. We used separate linear models to analyze plant growth, latex and log (trichomes), with temperature and aphid population size as the predictor variables. We used a binomial glm to analyze plant survival, with temperature and aphid population size as the predictor variables and mortality by the end of the experiment as a binary response variable. We also ran planned post-hoc comparisons on control plants (without aphids) to assess the effect of warming on plant responses in the absence of aphids, in order to determine whether observed warming effects on plant responses were direct effects, or were driven by aphid feeding.

To determine whether priority effects were present and whether they were influenced by warming (Hypothesis 3), we analyzed the effect of temperature and arrival order on the maximum population size and population persistence of each aphid species separately. For each species we included all six multi-species treatments: three levels of arrival order (arrived two weeks before its competitor [“early”], at the same time [“same time”], or 2 weeks after its
competitor [“late”]) crossed with two temperature levels (cool and warm). Although “early” and “late” treatments had lower initial densities (3 aphids of one species added on the first day and 3 aphids of the other species added two weeks later) than the “same time” treatment (3 aphids of each species added on the first day), our aphid responses (maximum population size and population persistence) were selected to be insensitive to small differences in starting densities. For maximum population size, we used linear models with temperature and arrival order as predictor variables, and the log of the maximum population size reached by that population as the response variable. For *A. asclepiadis* population persistence, we used a binomial glm with temperature and arrival order as predictors, and persistence (whether or not that population declined to zero by the end of the experiment) as a binary response (see Appendix C). We did not analyse *A. nerii* persistence, as all populations persisted until plant death or the end of the experiment.

To specifically test whether higher temperatures strengthen priority effects, we ran two additional analyses. We were interested in additive and interactive effects of temperature and arrival order; however, because persistence was analyzed with a logistic regression that estimates log odds ratios, and the maximum population size analysis was log transformed, interactive effects cannot be quantified using the linear model and binomial glm described above. We therefore performed a planned comparison of persistence in early and late arrival treatments across our two temperatures on a linear scale, testing solely for an interaction between temperature and arrival order. For this analysis we used a generalised least squares (gls function in nlme package), with a separate variance fitted for each treatment combination using the weights function for both analyses.

To test whether dispersal rates depend on temperature (Hypothesis 4), we analyzed the effect of temperature on the proportion of winged individuals and per capita dispersal to sticky cards in single-species treatments, over the course of the entire experiment. We used binomial glms, with temperature and time (survey date) as predictor variables, winged/unwinged or dispersed/not dispersed as binary response variables, and plant as a random factor. We included both time and time squared (with time centred at zero) in the models, to allow the model to capture non-linear trends in dispersal over time.
We included ‘chamber’ in all analyses, and as we found no significant effects of chamber, we do not report these results. For all analyses, we started with the most complex models and dropped all non-significant higher order interactions. All statistical analyses were performed in R (version 3.0.3).

Results

Hypothesis 1: the impact of temperature on aphids

In single-species treatments, *A. nerii* had higher growth rates and reached higher maximum population sizes than *A. asclepiadis* (Fig. 4.1), and warming advanced population peaks by ~6 days for *A. nerii* ($F_{1,18} = 13.40, P = 0.002$) and ~11 days for *A. asclepiadis* ($F_{1,18} = 11.26, P = 0.003$; Fig. 4.1a,b). Warming increased population growth rates for *A. nerii* ($F_{1,84} = 8.91, P = 0.0037$; Fig. 4.1c), but had no effect on *A. asclepiadis* growth rates ($F_{1,117} = 1.57, P = 0.21$; Fig. 4.1d). As predicted, maximum population sizes were lower under warmed conditions for both species (*A. nerii* $F_{1,17} = 11.37, P = 0.004$; *A. asclepiadis* $F_{1,18} = 7.66, P = 0.013$; Fig. 4.1e,f).

Although most aphid populations (87% for each species) peaked before the experiment ended (Fig. 4.1a,b; growth curves for all treatments in Appendix C Fig. S4.3), four out of ten *A. asclepiadis* populations in cool conditions were still increasing at the end of the experiment. Therefore, both the timing of these population peaks and the maximum population sizes would have been higher if the experiment had continued longer, and our results likely underestimate the impact of warming on these measures for *A. asclepiadis*. 
Figure 4.1 The impact of temperature on aphid populations. (a,b) Aphid abundances throughout the experiment when species were grown with no interspecific competition (circles with vertical error bars), and the mean date at which populations peaked within each treatment (squares with horizontal error bars), (c,d) population growth rates in the absence of density dependence, estimated as the slope at the inflection point in a four-parameter logistic model (see Methods) and (e,f) maximum population size reached in each treatment. Cool treatments are shown in light blue and warm treatments are in dark red. The black star on A. nerii indicates that this species is the superior competitor. Data points are mean values ± one standard error. Note the smaller scale for A. asclepiadis, and the log scale for maximum population sizes.
Hypothesis 2: the impact of temperature and aphids on milkweed plants

Across treatments, plant growth was negatively associated with aphid abundances ($F_{1.9} = 5.95, P = 0.037$), but was not affected by temperature ($F_{1.9} = 0.13, P = 0.72$; Fig. 4.2a). More than a third of plants (44/120) died, and plant mortality increased with aphid abundance ($F_{1.9} = 12.21, P = 0.007$) and warming ($F_{1.9} = 11.22, P = 0.008$). There was no effect of warming on mortality for control plants ($P > 0.05$), indicating that aphids killed plants, and that this effect was intensified at higher temperatures (Fig. 4.2b). Trichome density increased with aphid abundance ($F_{1.9} = 6.62, P = 0.030$) and warming ($F_{1.9} = 12.76, P = 0.006$), and there was no effect of warming on trichomes for control plants ($P > 0.05$), indicating that the increased trichome production with warming was contingent upon the presence of aphids (Fig. 4.2c). Although latex was unaffected by aphid abundances ($F_{1.9} = 1.07, P = 0.34$) or temperature ($F_{1.9} = 1.56, P = 0.24$), in no-aphid control plants the change in latex exudation was higher in warm (1.10mg ± 0.46 95%CI) than cool (0.12mg ± 0.39 95%CI) conditions, indicating that warming increased latex exudation in the absence of aphids (Fig. 4.2d).

Hypothesis 3: the impact of temperature on priority effects

In multi-species treatments, the maximum population size reached by $A. nerii$ depended on temperature ($F_{1.53} = 6.52, P = 0.013$) and arrival order ($F_{2.53} = 4.47, P = 0.016$), with the smallest populations occurring in warmed and in late arrival conditions (Fig. 4.3a; Appendix C Fig. S4.3). However, post-hoc contrasts showed that there was no interaction between temperature and arrival order for $A. nerii$ maximum population size ($P = 0.80$; Appendix C Table S4.1; Fig. 4.3a), indicating that temperature did not alter the impact of priority effects on maximum population size for this species. Arrival order ($F_{2.53} = 20.24, P < 0.001$), but not temperature ($F_{1.53} = 2.05, P = 0.16$), affected the maximum population size reached by $A. asclepiadis$; early arrival resulted in larger maximum population sizes (Fig. 4.3b), and there was a marginal interaction between temperature and arrival order for $A. asclepiadis$ ($P = 0.053$; Appendix C Table S4.1; Fig. 4.3b). Given the number of statistical comparisons performed, we do not further interpret this marginally-significant interaction.

Temperature did alter the impact of priority on population persistence. While all $A. nerii$ populations persisted when in competition (Fig. 4.3c), many $A. asclepiadis$ populations declined to extinction, with extinction rates impacted by both temperature ($\chi^2 = 17.65, df=1, P < 0.001$)
and arrival order ($\chi^2 = 17.84, \text{df} = 2, P < 0.001; \text{Fig. 4.3d}$). Planned post-hoc contrasts (see Methods) revealed an interactive effect of arrival order and temperature on *A. asclepiadis* extinction; in the warm treatment, persistence declined by 80% in late versus early arrival treatments, whereas in the cool treatment it declined by only 22% ($P = 0.003$; Appendix C Table S4.1; Fig. 4.3d).

**Figure 4.2** The impact of temperature and aphids on milkweed plants. (a) Plant growth (change in height between the first and 21st day of the experiment) (b) plant mortality (the proportion of plants that died before the end of the experiment), (c) trichome density at three weeks, and (d) change in latex production (difference in exudation between the first day and 21st day of the experiment). Cool treatments are shown in light blue and warm treatments are in dark red. Aphid abundance in all panels is the mean of the maximum number of aphids reached per plant in a treatment (both aphid species combined when both species were present). The grey line of best fit in panel (a) indicates that only aphid abundance had a significant effect on plant growth. Data points are mean values for each treatment ± one standard error. Note the log scale for trichomes (panel c).
Figure 4.3 The impact of temperature and arrival order on aphid populations. (a,b) Maximum population size, and (c,d) proportion of aphid populations that persisted until the plant died, for each species when grown in competition with the other species. Each species was added two weeks before its competitor (“early”), at the same time as its competitor (“same time”), or two weeks after its competitor (“late”). Model results shown represent P-values from linear models (for temperature and arrival order effects) or planned post-hoc comparisons (for the interaction between temperature and arrival order), with significance indicated as P<0.05 (*), P<0.01 (**), P<0.001 (***), or not significant (NS) (see Methods). Cool treatments are shown in light blue and warm treatments are in dark red. The black star on A. nerii indicates that this species is the superior competitor. Data points are mean values ± one standard error. Note the log scale for maximum population size (panels a and b).
Hypothesis 4: the impact of temperature on dispersal

For *A. nerii* grown alone, both the proportion of winged individuals and per capita dispersal had negative coefficients for the squared effect of time (both \( P < 0.001 \); all winged and dispersal df =1), indicating that both measures had non-linear responses, and that both reached maxima prior to the end of the experiment (Fig. 4.4a,c). There was also a time by temperature interaction for both responses (proportion of winged individuals \( P = 0.011 \); per capita dispersal \( P < 0.001 \)); in warmed conditions, both responses increased more rapidly and plateaued sooner, resulting in overall higher mean levels of dispersal in the second half of the experiment (Fig. 4.4a,c).

For *A. asclepiadis* grown alone, the proportion of winged individuals and dispersal increased over time (both \( P < 0.001 \); Fig. 4.4b,d). There was also a rapid rise in *A. asclepiadis* dispersal rate in the second half of the experiment, indicated by a positive coefficient for the squared effect of time (\( P < 0.001 \); Fig. 4.4d). Finally, temperature altered the trend for *A. asclepiadis* winged individuals, as towards the end of the experiment the proportion of winged individuals increased, but only in cool conditions (temperature x time squared \( P < 0.001 \); Fig. 4.4b).
Figure 4.4 The impact of temperature on aphid dispersal. (a,b) The proportion of aphids with wings at each survey, and (c,d) proportion of individuals of each species newly dispersed to sticky cards since the previous survey. Significance of temperature effect is indicated as $P<0.05$ (*), $P<0.01$ (**), $P<0.001$ (***) or not significant (NS). Cool treatments are shown in light blue and warm treatments are in dark red. The black star on A. nerii indicates that this species is the superior competitor. Data points are mean values ± one standard error.

Discussion

Our study demonstrates that temperature can strengthen priority effects among competing herbivores by changing how these herbivores impact their plant resource. We predicted that temperature would alter competitive dynamics in this system through four distinct pathways, and found support for all four of our hypotheses. Higher temperatures caused populations of both species to peak earlier and reach lower maximum sizes (Fig. 4.1), as predicted if warming causes herbivores to exert stronger top-down pressure that lowers their carrying capacities. Our
plant responses show a greater per capita impact of aphids at higher temperatures on both resource quantity (plant mortality) and quality (trichomes) (Fig. 4.2). This decline in resources at higher temperatures was associated with a stronger effect of arrival order on the population persistence of the weaker competitor \((A. asclepiadis)\), with early arrival increasing persistence much more at high temperatures than at low temperatures (80% versus 22%; Fig. 4.3d). Warming also increased the dispersal rate of \(A. nerii\) but not \(A. asclepiadis\), indicating that the temperature could alter the relative dispersal rates of these two species, and thus their arrival order at a local site (Fig. 4.4). Taken together, these results demonstrate that even in a simple, three species system, temperature can simultaneously disrupt multiple processes that span spatial and temporal scales and together determine local and regional coexistence.

The most pronounced effect of temperature and arrival timing on herbivore dynamics was the increased extinction rate of \(A. asclepiadis\) when it arrived late in warmer conditions (Fig. 4.3d). The greater disadvantage of late arrival for \(A. asclepiadis\) compared to \(A. nerii\) indicates that when competition is asymmetric, the inferior competitor may rely more on arriving first. This supports classic priority effects research showing that a competitively inferior species of fly was only able to persist when it arrived before its competitor (Shorrocks & Bingley 1994), and more recent work demonstrating how native plants can be suppressed to local extinction when exotic grasses germinate earlier in the growing season and deplete shared resources (Wainwright et al. 2012). These pronounced priority effects that shape community assembly are most likely to occur whenever ecologically similar species compete strongly for a shared and limited resource (Fukami 2015), as was the case in our study and in many documented cases of priority effects (Alford & Wilbur 1985; Peay et al. 2012; Vannette & Fukami 2014; Cleland et al. 2015). In addition, the stronger growth response of the dominant competitor to warming that we observed (Fig. 4.1c,d) may be common to other systems if fast-growing species tend to have higher optimal temperatures (Frazier et al. 2006) or are able to respond more rapidly to increased temperatures (Walker et al. 2006). Whenever warming intensifies competitive asymmetries, the weaker competitor could become increasingly dependent on priority effects to persist. A formal examination of the link between temperature responsiveness and competitive rank across ecosystems would provide valuable predictive insights into how these dynamics will play out as the climate warms.
CHAPTER 4: TEMPERATURE-DEPENDENT PRIORITY EFFECTS

Higher temperatures increase herbivore vital rates more than producer vital rates across a range of taxa (Dell et al. 2011), which has been shown both theoretically (Gilbert et al. 2014) and empirically (O'Connor et al. 2009) to result in increased top-down pressure on primary producers. We predicted that this different temperature response of plants and insects would exacerbate the impact of aphids on milkweed plants and result in more pronounced priority effects at higher temperatures (O'Connor et al. 2011; Fukami 2015). Indeed, we found that warming strengthened the impact of aphids on plant mortality and trichomes (Fig. 4.2). The high levels of mortality experienced by plants with aphids, but not control plants, demonstrates the strong top-down pressure that herbivores can exert on their plant resources (Fig. 4.2b). The compounding effect that warming had on aphid-induced declines in plant longevity was likely a major driver of the lower population sizes and increased intensity of priority effects that we observed in warmed treatments (Figs. 4.1, 4.3). Likewise, trichomes increased at higher temperatures for plants with aphids, but not control plants, indicating that warming can amplify the induction of defenses (Fig. 4.2c). This greater induction of defenses may be a general indirect response to warming that results from greater impacts of herbivores on their hosts (Underwood 2000). When considered together, the temperature dependence of plant-herbivore interactions and the well-known impact of early season herbivory on late season herbivore performance in a variety of systems, including maize (Erb et al. 2011) and Brassica (Li et al. 2014), suggest that the strengthening of priority effects at higher temperatures via stronger niche pre-emption and niche modification could be widespread. This could have broad implications for herbivore coexistence under climate change, if warming increases the ability of early season herbivores to impede the establishment and persistence of later season competitors (Jamieson et al. 2012).

Priority effects frequently occur in metacommunities where limited dispersal leads to species arriving at different times, yet most studies of priority effects do not explicitly consider dispersal dynamics. Temperature can have direct and indirect effects on dispersal rates that could alter arrival times and scale up to impact metacommunity dynamics (Gilbert & O'Connor 2013; Travis et al. 2013). Species likely to have temperature-dependent dispersal rates include those that disperse in a life stage whose timing or length is altered by warming (e.g. marine plankton; O'Connor et al. (2007)), that require a critical temperature threshold for flight (e.g. winged insects; Battisti et al. (2006)), that undergo shifts in body size as temperatures change (e.g.
reptiles Kingsolver and Huey (2008)) or that have physiological dispersal responses to changes in local environmental conditions (e.g. wing-dimorphic insects; Zera and Denno (1997)). We predicted that warming would increase aphid dispersal rates due to declining resources (Dixon 1977), and used a direct measure of short-distance dispersal, as well as the production of winged individuals as a proxy for long-distance dispersal potential, to test this prediction (Fig. 4.4). These two measures of dispersal responded nearly identically to temperature, with warming increasing the propensity for short-distance dispersal and the production of winged individuals in *A. nerii* only (Fig. 4.4). The dispersal responses of *A. nerii* were likely driven by declining resources (Dixon 1977) and not crowding, as warmed plants had higher dispersal but lower densities (Figs. 4.1, 4.4). The observation that *A. asclepiadis* dispersal rate did not increase with warming (Fig. 4.4), despite lower resource quantity and quality in warmed conditions (Fig. 4.2b,c) demonstrates the species-specific nature of dispersal responses to temperature (Travis *et al.* 2013), and indicates that warming that could shift relative arrival times on individual plants. Modeling or empirical work that tests how responses of local interactions and dispersal to warming scale up to determine regional coexistence across a landscape of habitat patches will be essential to fully understand the impact of temperature on coexistence across spatial scales.

At a broader spatial scale, increasing temperatures are likely to advance both the spring emergence date for *A. asclepiadis* and the date at which temperatures are high enough to allow *A. nerii* to disperse northward (Bale *et al.* 2002). Likewise, the range limits of all three species may advance northward as the climate warms (Parmesan & Yohe 2003). For example, a shift in the winter range of *A. nerii* could be particularly rapid if warmer winter temperatures permit overwintering further north within milkweed’s current range. In this and other systems, northward range shifts or advancing phenologies that allow a dominant competitor to arrive earlier in the growing season could reduce or eliminate seasonal priority effects that are essential for the persistence of weaker competitors (Wainwright *et al.* 2012). Indeed, because shifts in phenologies (emergence date, migration date) and winter and summer ranges are unlikely to be completely synchronized across competing species, seasonal arrival orders could be disrupted in many systems, with resulting breakdowns in the advantages associated with early arrival (Yang & Rudolf 2010; Cook *et al.* 2012).

While both our plant and aphid results are consistent with theory describing the temperature dependence of trophic interactions, two aspects of our study system should be considered
carefully when interpreting our results within this theoretical framework. First, temperature change may cause physiological plant responses not captured by our measured responses, and not addressed by theory focused primarily on temperature-induced changes to growth and feeding rates. For example, increased physiological stress on plants precipitated by aphid feeding at higher temperatures could have contributed to plant declines with warming, independent of any temperature-induced changes to aphid growth or feeding rates (Jamieson et al. 2012). Likewise, the mechanisms through which aphids induce and respond to trichomes remain unresolved, and increased trichome density in warm conditions may have also been impacting aphid performance (Levin 1973; Agrawal 2004a, 2005).

Second, even when the predicted asymmetries in plant and herbivore temperature sensitivities occur, the theory we consider can give rise to different outcomes when interactions with other trophic levels or greater numbers of species are considered. For example, differences in plant vs. herbivore growth rates may depend on the temperature sensitivity of plant nutrient resources, which can be driven by soil microbes and standing stocks of organic matter (O'Connor et al. 2011; Gilbert et al. 2014). In our experiment, we supplied a limited and controlled amount of soil nutrients to avoid confounding plant-herbivore dynamics, which may explain why plant growth did not respond to warming (Fig. 4.2a) (Walker et al. 2006). Field studies may benefit from explicit tracking of soil nutrient dynamics, as differences among biogeographical regions are expected (Melillo et al. 1993; Delgado-Baquerizo et al. 2013), and may lead to predictable differences in plant-herbivore responses to warming (O'Connor et al. 2011). Similarly, more complex communities could experience different outcomes than the responses to pairwise competition observed here, as a result of higher-order interactions for example (Levine et al. 2017; Mayfield & Stouffer 2017). Nonetheless, priority effects are predicted to be especially pronounced in diverse communities (Fukami 2015), and have been shown to be a key determinant of community assembly in a variety of more speciose systems, including terrestrial plants (Fargione et al. 2003; Cleland et al. 2015), mycorrhizal fungi (Kennedy et al. 2009), nectar microbes (Vannette & Fukami 2014) and marine invertebrates (Petraitis & Latham 1999). Even in these more complex systems, early arriving species can determine the success of late arrivals, suggesting that the simplified system we examined is broadly relevant to ecological dynamics. Our results therefore suggest that in the many systems in which priority effects shape
ecological communities, the negative outcomes associated with late arrival could be exacerbated by warming.

In this study, we demonstrated how even a few degrees change in temperature alters plant-herbivore interactions, the importance of arrival time, and dispersal, thus revealing novel links across space and time in the responses of ecological communities to climate change. Our study builds on the results of recent experiments demonstrating how temperature can alter the impact of arrival time on competitive outcomes in tadpoles (Rudolf & Singh 2013) and microbes (Clements et al. 2013; Tucker & Fukami 2014) by linking the known temperature dependencies of trophic interactions and dispersal to priority effects. In doing so, we show how predictable responses to warming across trophic levels and spatial scales can generate substantial shifts in competitive outcomes. Rudolf and Singh (2013) illustrated how higher temperatures alter size-mediated competitive interactions and strengthen the impact of hatching order in amphibians, which may be a general phenomenon because of the relationship between temperature and development time (Yang & Rudolf 2010). Our work likewise suggests that the impact of temperature on resource-mediated competitive interactions that results in stronger priority effects may be a general response caused by the asymmetrical response of plants and herbivores to temperature. Although it is well understood that simply assessing individual species’ responses to warming tells an incomplete story of how species will fare under climate change, these complex spatial and temporal dimensions of species interactions have yet to be well-incorporated into our understanding of climate change impacts (Gilbert & O’Connor 2013; Wolkovich et al. 2014). Our study provides a starting point for incorporating spatial and temporal shifts in species interactions that are influenced by temperature, and suggests a way forward for better understanding the impacts of climate change in patchy ecosystems.

Acknowledgments

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References


Appendix C: Supplementary information to Chapter 4

Supplementary methods

Experimental plants and aphids

To grow experimental plants, we sterilized seeds in a 5% bleach solution to kill any fungus, nicked them to remove a small portion of the pericarp and placed them between two damp pieces of filter paper in a petri dish that was then sealed with parafilm. We stratified seeds in a refrigerator (4°C) for six days to induce germination, and then moved them to a dark incubator (28°C) to allow germination for 4 days. We planted germinated seeds in potting mix in 1L pots, and placed pots in a growth chamber set to a 24°C:18°C on a 14L:10D cycle. We fertilized each plant after 10 days with 1 tsp of 14:14:14 N:P:K slow release fertilizer, watered plants as needed, and left them to grow for 40 days until the start of the experiment. At this point plants had 4-6 sets of true leaves and were 10-20 cm tall.

Prior to the experiment, aphid populations were maintained by serial transfer to new milkweed plants, with all plants kept at room temperature (~21°C).

Experimental cages

We conducted the experiment in two growth chambers, both set with temperature and light on a 14 hr day:10 hr night diurnal schedule, with a 4°C difference between day and night, and constant 85% humidity. To contain aphids, we placed each plant in a tunnel-shaped cage (50cm long, 20cm wide at the base, 40cm high; Fig. S4.1). The cage was composed of a metal wire frame with 5cm by 10cm rectangular holes, overlaid with superfine netting (625 holes/square inch, Skeeta, Bradenton, FL, USA). We covered mesh in plastic sheeting (6mm thick SuperSix polyethylene film, North York, ON, Canada) to aid in local temperature manipulation within each cage. Cool cages had plastic sheeting on four sides to control for the effects of the plastic on light penetration and air flow, but ends were left uncovered. To warm cages, we used strings of 50w light bulbs, (Canadian Tire string umbrella lights, Wellend, ON, Canada) with each bulb painted with black paint (Tremclad Rust-Oleum, Concord, ON, Canada) so that heat but not light was emitted from bulbs. Warm cages had plastic on all six sides to retain heat, with holes at both ends to allow gas exchange. Each warm cage had two bulbs (painted black) suspended at
the top of the cage, and bulbs were left on through the duration of the experiment (night and
day). Cool cages had a painted bulb (not turned on) as a control. This warming treatment creates
the type of heat gradient found in natural grassland and old field systems (Barton & Schmitz
2009). We arranged cool and warm cages throughout the chambers in an alternating pattern, and
competition treatments were randomized within this alternating structure.

We monitored the temperature within cages at three heights (10cm, 20cm and 30cm from the
base of the cage) and humidity at 10cm from the base of the cage using Hobo data loggers
(Onset, Bourne, MA, USA) set to log every half hour. We used a total of eight loggers that were
rotated between cages (and alternated between cool and warm cages) every 24 hours. This
resulted in a total of twenty 24 hour periods logged for each of the two temperature treatments
(i.e. twenty cages). We measured the soil moisture of each plant twice a week and watered
plants if moisture level fell below 35% relative moisture.

The 2.1°C increase in temperature in our warm treatments is consistent with inter-annual
temperature fluctuations at the local field site where we collected the aphids; at this site the
average mean summer (June-August) temperature from 2004-2014 was 20.5°C, with the
warmest year (2005) having a mean temperature of 22.4°C (Buttonville Airport). This two
degrees of warming is also within the range of predicted temperature increases under
conservative climate change projections (IPCC 2014). Humidity in warmed treatments was also
raised by an average of 9.8%, but soil moisture in the potted plants was unaffected (Fig. A2). As
increasing humidity can increase plant performance (Ford & Thorne 1974), and warming was
associated with reduced plant performance (see Results), possible humidity effects on plants
may have resulted in an under-estimation of the negative impact of our warming treatment on
plants. Additionally, because humidity was high for both treatments (85.4% ± 2.6 SE in cool
95.2% ± 0.33 SE in warm) and soil moisture was unaffected by warming, we consider the
effects of the warming treatment on plants and aphids to be caused primarily by the difference in
temperature.

Plant responses

We measured four plant responses: growth, mortality, trichome density, and latex production.
To quantify latex exudation, we cut off the tip of the youngest fully expanded leaf (i.e. tissue
produced since the beginning of the experiment) so that a length of 0.5 cm of cut leaf tissue was
exuding latex (Agrawal 2005). We absorbed the latex onto a pre-weighed, 1cm filter paper (latex stopped flowing within ~10 seconds) and then re-weighed the paper to determine the mass of exuded latex (Woods et al. 2012). We measured trichome density by counting trichomes on the underside of the tip of the second youngest fully expanded leaf (Woods et al. 2012) using the highest magnification of a dissecting microscope (a 2.54 mm² circular area).

**Dispersal responses**

We calculated the proportion of winged individuals at each survey as all live winged individuals of that species in the cage (i.e. winged aphids on the plant + winged aphids dispersed to card since the previous survey) divided by all live individuals of that species in the cage (i.e. all aphids on plant + all aphids dispersed to card since the previous survey). We calculated per capita dispersal at each survey as the number of aphids dispersed to the sticky card since the last survey, divided by all live individuals of that species in the cage.

**Statistical analysis**

All population sizes include only those aphids on the plant at each survey point, as dispersed aphids in interspecific competition treatments could not be identified to species, as described above. For our analysis of the impact of temperature and arrival order on population persistence, we did not include replicates in which plants died as cases of competitive exclusion since plant death impacts both species equally. One treatment for *A. asclepiadis* (early arrival in cool temperature) had 100% persistence, which causes issues with model convergence and the estimation of standard errors. We therefore reran these analyses with a single extinction added to that treatment alone, and again with an additional single extinction analysis added to all treatments. These changes did not qualitatively alter our results.
Supplementary tables and figures

**Table S4.1** Post-hoc comparisons of maximum population size and survival rate of early vs. late arrival treatments in cool and warm treatments (results from generalised least square shown, see Methods). A significant interaction indicates that the impact of early versus late arrival depended on the temperature treatment. Means associated with the interactions reported here are shown in Fig. 4.3.

<table>
<thead>
<tr>
<th></th>
<th><em>Aphis nerii</em></th>
<th><em>Aphis asclepiadis</em></th>
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<tbody>
<tr>
<td>Max pop size</td>
<td>P</td>
<td>P</td>
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<tr>
<td>Temperature * order</td>
<td>0.80</td>
<td>0.053</td>
</tr>
<tr>
<td>Persistence (%)</td>
<td>Temperature * order</td>
<td>NA</td>
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**Figure S4.1** Diagram of experimental cages used to warm milkweed plants and aphid populations. Not to scale.
Figure S4.2 Effect of the temperature treatment on (a) temperature and (b) humidity in experimental cages, and (c) soil moisture in potted milkweed plants. Data points are mean values ± one standard error.
Figure S4.3 Population growth curves for each species in all treatments: (a,b) each species alone, (c,d) added early, (e,f) added at the same time as its competitor and (g,h) added late. Cool treatments are shown in light blue and warm treatments are in dark red. Data points are (arithmetic) mean values for each treatment at each time point ± one standard error (note that figures in the main text show geometric means used in analysis). The black star on A. nerii indicates that this species is the superior competitor.
References


Chapter 5: Multi-scale responses to warming in an experimental insect metacommunity


Abstract

In metacommunities, diversity is the product of species interactions at the local scale and dispersal between habitat patches at the regional scale. Although warming can alter both species interactions and dispersal, the combined effects of warming on these two processes remains uncertain. To determine the independent and interactive effects of warming-induced changes to local species interactions and dispersal, we constructed experimental metacommunities consisting of enclosed milkweed patches seeded with five herbivorous milkweed specialist insect species. We treated metacommunities with two levels of warming (unwarmed and warmed) and three levels of connectivity (isolated, low connectivity, high connectivity). Based on metabolic theory, we predicted that if plant resources were limited, warming would accelerate resource drawdown, causing local insect declines and increasing both insect dispersal and the importance of connectivity to neighboring patches for insect persistence. Conversely, given abundant resources, warming could have positive local effects on insects, and the risk of traversing a corridor to reach a neighboring patch could outweigh the benefits of additional resources. We found support for the latter scenario. Neither resource drawdown nor the weak insect-insect associations in our system were affected by warming, and most insect species did better locally in warmed conditions and had dispersal responses that were unchanged or indirectly affected by warming. Dispersal across the matrix posed a species-specific risk that led to declines in two species in connected metacommunities. Combined, this scaled up to cause an interactive effect of warming and connectivity on diversity, with unwarmed metacommunities with low connectivity incurring the most rapid declines in diversity. Overall, this study demonstrates the importance of integrating the complex outcomes of species interactions and spatial structure in understanding community response to climate change.
Introduction

The ongoing rise in global temperatures is precipitating dramatic changes in the earth’s biota at a range of spatial scales (Walther et al. 2002). Locally, warming can accelerate species’ physiological processes and biological rates (Brown et al. 2004; Rall et al. 2012), with cascading impacts on population dynamics and species interactions (Savage et al. 2004; O’Connor et al. 2011; Dell et al. 2014). Globally, widespread range shifts and extinctions are being projected and documented through mapping and observational approaches (Thomas et al. 2006; Chen et al. 2011). However, there is a scarcity of climate change research focused at intermediate scales; despite the recognition that many species occupy networks of habitat patches, or metacommunities, only recently have ecologists begun investigating the effects of warming on the processes that govern the persistence and diversity of species living in patchy habitats (Thompson et al. 2015; Yvon-Durocher et al. 2015). Metacommunity diversity is a product of species’ interactions with their abiotic and biotic environments at the local scale, and movement between habitat patches at the regional scale (Leibold et al. 2004). Both of these processes have been shown to be sensitive to changes in temperature (O’Connor et al. 2011; Travis et al. 2013). Despite this, the combined impact of warming-induced changes to local community dynamics and inter-patch movement remains unknown. Integrating predictions for how warming alters local and regional metacommunity processes, and testing how these effects scale up to shape diversity in metacommunities, would provide a more complete understanding of the varied impacts of climate change on biological systems (Gilbert & O’Connor 2013).

Metabolic theory predicts that the vital rates of herbivores should be more strongly temperature-dependent than those of primary producers, causing warming to strengthen plant-herbivore interactions at the local scale (Allen et al. 2002; Savage et al. 2004; O’Connor 2009). This increased top-down pressure can hasten resource depletion (Jiang & Morin 2004; O’Connor et al. 2011), which for a single species of herbivore, can produce a large impact on host plants that precipitates herbivore population declines (Jiang & Morin 2004; O’Connor et al. 2011). In multi-species communities, rapid resource depletion induced by warming can strengthen competitive interactions between consumers that may manifest as declines in abundances of a poorer competitor (Jiang & Morin 2004) or reduced co-occurrence rates if species attempt to avoid or are excluded by one another (Gilpin & Diamond 1982; Gilbert & O’Connor 2013). In
the absence of resource limitation to primary producers, however, there may be little cost of warming to herbivores if temperatures remain below thermal thresholds (O’Connor et al. 2011). In this case, resource depletion and competitive interactions will be weak and unaffected by warming, and warming-induced increases in physiological rates should translate into shorter development times, higher population growth rates and larger population sizes (Ritchie 2000; Gilbert et al. 2014). The ultimate cost or benefit of warming for herbivore species is therefore likely to be context-dependent, and should rely critically on resource availability and competitive interactions.

The impact of warming on dispersal, and how this translates to a metacommunity-level response, also depends on a species’ physiological responses and interactions with its abiotic and biotic environments within habitat patches and the inter-patch matrix (Travis et al. 2013). Temperature can alter dispersal rates directly by changing body size and behaviour, or indirectly by prompting dispersal away from low-quality resources or antagonistic species interactions (Altermatt et al. 2008; Travis et al. 2013; Fronhofer et al. 2015). The ability for species to successfully move between patches, or functional connectivity, could therefore be altered by temperature changes that affect a species’ propensity or ability to move (Altermatt et al. 2008). Connectivity between patches allows poor dispersers to reach alternate habitat, allows species to reach patches containing their preferred habitat (species sorting), and allows individuals from high quality patches to supplement populations in poor quality patches (mass effects) (Tilman 1994; Leibold et al. 2004). As a result, temperature-induced increases in functional connectivity could increase diversity at both local and regional scales within metacommunities (Cadotte & Fukami 2005; Verreydt et al. 2012). Whereas previous experiments investigating the effect of warming on metacommunity dynamics have maintained tractability by warming local patches while manipulating dispersal rates (Limberger et al. 2014; Thompson et al. 2015), allowing warming to simultaneously alter both local species interactions and species’ movement between patches would provide a critical next step towards understanding the full impact of warming in spatially structured environments (Salt et al. 2016).

In contrast to the positive effects of dispersal, moving across an inhospitable matrix with less food and more predators often carries a substantial risk of mortality (Lucas et al. 1994). When increasing temperature causes individuals to be exposed to greater risk by increasing within-
generation dispersal propensity, for example, a positive effect of warming on dispersal could decrease metapopulation sizes of constituent species. Temperature could therefore lower the persistence of species in a metacommunity even when it increases dispersal rates. However, typical experimental manipulations of dispersal that manually transfer individuals between patches involve either no, very low, or uniform risk of movement, making it impossible to distinguish the positive and negative impacts of changing dispersal rates (Grainger & Gilbert 2016). Incorporating dispersal risk into experimental work could reveal a more realistic cost-benefit trade-off associated inter-patch movement, and a more accurate picture of how this will be impacted by warming.

The overall effect of warming on metacommunities is the product of costs and benefits of warming at the local scale, and how these feedback to dampen or amplify the costs and benefits associated with dispersal between patches (Gilbert & O'Connor 2013). For example, if warming induces local declines in limited resources and intensifies competition, connectivity to neighboring patches that contain additional resources could become more important for maintaining species diversity. Conversely, the risk of dispersing across the matrix could outweigh any benefits of additional food resources and competitor avoidance achieved by leaving a local patch, especially if resources are not limited locally.

We used an experimental approach to test how warming affects local dynamics, dispersal and feedbacks between these two responses. We manipulated the temperature and connectivity of experimental two-patch metacommunities housing milkweed plants and the specialist herbivores that eat them to determine how warming affects (1) the strength of local species interactions (plant-insect and insect-insect), (2) insect species’ performance within a patch, (3) insect movement within and between milkweed patches, and (4) the impact of connectivity on individual insect species performance and metacommunity diversity.

Methods

Natural history

Common milkweed (*Asclepias syriaca*) is a perennial forb found in old fields across eastern North America. Milweed is chemically defended with toxic cardenolides, and physically defended with trichomes covering the leaf surface and sticky latex expelled when leaves are
damaged. Milkweed defenses (trichomes and latex) occur constitutively, and can be induced by herbivory (Van Zandt & Agrawal 2004b; Woods et al. 2012; Ali & Agrawal 2014). Milkweed grows primarily in old fields, in patches ranging from a few to thousands of plants (Grainger et al. 2017).

As a result of its defenses, common milkweed hosts only eleven specialist insects capable of consuming it, five of which were included in this experiment: two species of aphid (*Aphis nerii* and *Aphis asclepiadis*), the long-horned milkweed beetle (*Tetraopes tetrophthalmus*; hereafter milkweed beetle), the small milkweed bug (*Lygaeus kalmii*; hereafter milkweed bug) and the monarch butterfly (*Danaus plexippus*). *A. nerii* and *A. asclepiadis* feed on milkweed phloem and can disperse short distances by crawling, or longer distances by producing winged morphs (Antolin & Addicott 1991). While *A. asclepiadis* is almost always tended by mutualistic ants offering protection from predators, *A. nerii* is only sometimes ant-tended (Mooney et al. 2008). The milkweed beetle consumes leaves, while the milkweed bug feeds primarily on milkweed seeds, and both species can fly short to moderate distances, up to tens of metres in a single flight (Caldwell 1974; McCauley et al. 1981; Matter 1996). Monarch caterpillars feed on milkweed leaves and crawl short distances between plants. All five species co-occur in our study area during the time period that our experiment was conducted (early July to late August), with some variation in the timing of their peak abundances: monarch caterpillars and *A. asclepiadis* abundances peak around late July, *A. nerii* abundances peak toward the end of August, while milkweed bugs and beetles have relatively low but stable abundances between June and September (Grainger, unpublished data). We selected these five species for their range of dispersal abilities (Grainger et al. 2017) and feeding guilds.

**Experimental set-up**

In the summer of 2014, we built an array of experimental metacommunities at Koffler Scientific Reserve, in Southern Ontario (44°03’N, 79°53’W). We selected a flat, grassy site with no naturally growing milkweed and built metacommunities consisting of a cleared circular 1m² plot covered with a cylindrical insect-proof cage (1.3m high X 1.1m diameter), and either connected to another cage by a mesh corridor (1m high X 0.5m wide and one of two lengths, described below) or left isolated (Appendix D Fig. S5.1). Cages were made of wire garden fencing lined with aluminum insect screen (C.R. Lawrence, Vaughn, ON) and topped with a fiberglass insect
screen lid (Barton and Schmitz (2009); Appendix D Fig. S5.1). Each metacommunity was randomly assigned one of three levels of connectivity: totally isolated (not connected to another cage), low connectivity (connected to neighboring cage with a long, 6m long corridor) or high connectivity (connected to neighboring cage with a short, 2m long corridor; Appendix D Fig. S5.1) and one of two levels of warming (unwarmed or warmed, described below) in a fully crossed design. We also had additional isolated unwarmed and warmed cages with plants only (no insects) as controls. This resulted in a total of eight treatments, each of which was replicated seven times in a blocked design. Two milkweed plants (see Methods below) were planted into each cage in July 2014 (hereafter, 1-year old plants), and an additional plant (approximately 15cm tall with eight mature leaves) was planted in June 2015. This resulted in a total of three milkweed plants per cage, arranged in an equilateral triangle and spaced 30cm apart.

Our warming treatment consisted of plastic sheeting (Home Hardware 3.3mm polyethylene plastic film) stapled to the sides of cages and corridors with the tops left open to allow rain to enter (Barton & Schmitz 2009). We selected the plastic type for its high transmittance of ultraviolet and visible light (Appendix D Fig. S5.2). We monitored the temperature and humidity in cages and corridors daily using Hobo data loggers (Onset, Bourne, MA, USA) attached to sticks and set to log every half hour. We measured cage temperature at three heights (30cm, 60cm and 90cm from the ground) and cage humidity at 60cm. We rotated loggers between cages (alternating between unwarmed and warmed cages) every 24 hours, for a total of 72 cages logged over the course of the experiment. We measured corridor temperatures in the centre of the corridor, at 30cm high. In cages, warming raised average cage temperatures by 2.7ºC during the daytime (9am to 9pm), and 1.1 ºC overall (Appendix D Fig. S5.3a,b). Our warming treatment also increased the average temperature variability observed daily (mean of the standard deviation of temperature measured from 9am to 9pm) by 1.0 ºC (Appendix D Fig. S5.3c). Our warming treatment had no effect on humidity (Appendix D Fig. S5.3f). In corridors, the warming treatment raised temperatures by 0.8 ºC on average (Appendix D Fig. S5.3d,e).

Experimental plants and insects

Milkweed plants were grown from seed obtained from a commercial nursery, and were planted into experimental metacommunities at eight weeks old (Appendix D; Prairie Moon Nursery, Winona, MN). *Aphis nerii, A. asclepiadis*, milkweed beetles, and milkweed bugs were collected
from milkweed plants growing on the reserve, while monarch caterpillars were reared from eggs imported from International Butterfly Breeders Association breeders. Insects were kept in indoor cages with potted milkweed (A. nerii, A. asclepiadis, monarch caterpillars) or milkweed leaves and seeds (milkweed bugs), or in outdoor cages with naturally growing milkweed plants (milkweed beetles) prior to being released into the experiment (Appendix D).

In early July, we placed one monarch caterpillar, two milkweed beetles, two milkweed bugs, and 15 each of A. nerii and A. asclepiadis on the largest 1-year old plant in one plot per metacommunity (hereafter the plant that was “seeded” with insects). Each two-plot metacommunity connected by a corridor (i.e. metacommunities in the low and high connectivity treatments) therefore had one plot into which all species were added, and one plot that had no insects at the beginning of the experiment. Monarchs and aphid populations that died within an initial five day acclimation period were replaced. To track dispersing individuals, we marked milkweed beetles (on elytra) and milkweed bugs (on pronotum) with unique identifiers (one or two small dots) using liquid correction fluid (Bic Quick-Dry Correctional Fluid). Marking did not interfere with wing expansion or flying.

Generalist arthropod predators (mainly spiders, but also ladybugs and stink bugs) were found throughout our study site. Because some milkweed specialists avoid or are vulnerable to predators, but were unable to disperse out of our isolated cages, we removed predators from cages at the beginning of the experiment. As removal of predators is rarely perfect, we consider this a predator reduction, and counted all predators in each cage halfway through the experiment to determine baseline predator abundances and to test for differences among treatments.

The experimental corridors contained plants and insects typical of old-field ‘matrix’ that occurs between milkweed patches at our field site. Corridor communities were primarily dominated by the grass Bromus inermis, which typically contains a diversity of herbivores and some predators, mainly spiders (Gilbert, unpublished data).

Insect and plant surveys

We ran the experiment for six weeks, from early July to late August, 2015. We measured plant height, trichomes and latex five days before the start of the experiment and one day after the end of the experiment in order to quantify plant growth, change in trichome density and change in
latex exudation rate over the course of the experiment (see Appendix D for detailed methods for trichomes and latex measurements). We considered plants to be dead when more than half the leaves had senesced.

We recorded the location of milkweed beetles and bugs and the location and body length of monarch caterpillars every day for the first five days of the experiment, and then three times a week thereafter, for a total of 22 insect surveys. We counted the number of aphids on each plant every three days starting after the initial replacement period, for a total of 17 aphid surveys. We also recorded the presence or absence of ants on each plant at each survey. All monarch caterpillars either died or pupated during the experiment, and we recorded the time to pupation and measured wing lengths of butterflies (a proxy for adult fitness) within one day of emergence from chrysalises.

Statistical analysis

All statistical analyses were performed in R (version 3.2.4). We included block as a random factor in all analyses, and used the package ‘lme4’ to run linear mixed effects models (LMEs) and generalized linear mixed effects models (GLMEs), except when noted. For all analyses, we started with the most complex model, tested for interactions using a likelihood ratio test (‘drop1’ function), dropped all non-significant higher order interactions, and re-tested the simplified model. We present the highest order significant interaction or significant main effects from each model. Except where noted (two analyses for which connectivity treatments were grouped), there were N=7 independent replicates (cages) of each treatment in all analyses.

We analyzed the effects of warming and the presence of insects on plants by comparing plants seeded with insects (the tallest plant in each isolated insect plot) to comparable plants never exposed to milkweed specialists (the tallest plant in each isolated control plot). We focused on four plant responses: growth (change in height), death, change in trichome density and change in latex exudation. We used LMEs for continuous responses (growth, trichomes, latex) and a binomial GLME for the binary responses (death), with warming and insects (presence or absence) as predictors, one of the four plant responses as the response, and the ‘weights’ function (nlme library) to account for heteroscedasticity of variance among treatments in the LMEs.
We analyzed the effect of warming on two types of insect-insect interactions: the probability of each species pair co-occurring on the same plant (a measure general competitive exclusion or avoidance) and the relationship between abundances of our two aphid species (a measure of competitive interactions between our two most closely related species). To determine whether warming affected the likelihood of two species occurring on the same plant within isolated plots seeded with insects, we summed the total number of surveys on which two species were found on the same plant and divided this by the total number of surveys on which both species were observed on milkweed (i.e. we removed surveys for which one species was found on the ground, the cage wall, or not located). This gave us the rate of plant-level co-occurrence for each species pair. We compared this to a null expected co-occurrence rate, calculated as the likelihood of any two individuals of different species occurring on the same plant within a cage. The null expected co-occurrence took into account the observed plant mortality throughout the experiment and the frequency at which each aphid species, milkweed bugs and milkweed beetles occupied one, two or three plants within a cage at each time step (calculations in Appendix D). The null expectation was 0.41 for species pairs that did not include aphids, 0.6 for species pairs that included A. nerii and 0.47 for species pairs that included A. asclepiadis (Appendix D).

To determine whether warming affected the relative abundances of our two aphid species on shared plants, we ran an LME with A. nerii maximum population size and warming as predictors and A. asclepiadis maximum population size as the response. Because A. nerii and A. asclepiadis population sizes were unexpectedly positively correlated (see Results), and we suspected an underlying effect of ant mutualists, we also analyzed the effect of ants on aphids by running separate LMEs for each aphid species with ant occurrence (number of surveys in which ants occurred on a plant, out of a total of 17 aphid surveys) and warming as predictors, and maximum aphid population size as the response. Given the sedentary and colony-forming habit of aphids, for these analyses we only included data from plants in isolated plots that had aphids introduced. Ant occurrence and aphid population sizes were strongly positively correlated (see Results), so we included the number of ants observed in plots as a covariate to account for the variation across our replicates in all tests of warming effects on aphids (local-scale performance, metacommunity-scale performance and dispersal) (see Methods below).
We analyzed the impact of warming on the local-scale performance of each of our five insect species in isolated plots, with performance quantified according to the life history and demography of each species. For monarchs, we used survival rate as our primary metric of local performance, as all monarchs either died as caterpillars or survived to become butterflies. We also analyzed the effect of warming on monarch caterpillar growth rates, time to pupation, and butterfly wing length. For milkweed beetles and bugs, 80 out of 84 individuals died before the experiment ended, and so we defined local performance for these two species as the number of days that an individual survived. Each individual was considered alive until the last day it was observed, and for each experimental replicate we took the average number of days surviving for the two milkweed beetles and two milkweed bugs. For aphids, we defined local performance as the maximum population size reached by each aphid species in each isolated treatment replicate. To account for the effects of ants on aphid abundances, we first ran a separate LME with ant occurrence as the predictor and the maximum population size reached by each species as the response. We then ran LMEs with warming as the predictor and residuals from this model as the response. In order to visualize species’ responses on a common scale, we used model results to calculate standardized effect sizes (Cohen’s $d$) with the package ‘compute.es.’

We analyzed the effect of warming on dispersal, with dispersal quantified using species-specific measures that best represent each species. Because monarchs and aphids moved across corridors too infrequently to allow statistical analysis of cross-corridor dispersal (Appendix D Table S5.1), we analyzed within-cage movements between plants (0.3 m) for these species. For each monarch caterpillar, we counted the total number of movements recorded from one survey to the next (off of a plant, onto a plant, or from one plant to another) and divided this by the number of days that caterpillar was alive to obtain a standardized dispersal metric. Because this analysis focused on within-cage movement, we grouped all connectivity treatments together (N=21 for each of unwarmed and warmed treatments), and for the six caterpillars that moved across corridors (Appendix D Table S5.1), we truncated the data at the date at which they left the seeded cage. We ran an LME with warming as the predictor and standardized dispersal as the response. Because we noticed a much higher variance within the unwarmed cages that was driven by differences in dispersal rate between caterpillars that died and those that survived to pupation, we ran an additional LME with warming and survival (died or survived to become a butterfly) as the predictors, and standardized dispersal as the response.
Milkweed beetles and bugs moved between plants too frequently to capture within-cage movements in our thrice-weekly surveys, so we focused on cross-corridor dispersal for these two species. For each species, we counted the total number of moves across a corridor (total moves for both individuals) and standardized this by the average number of days that the two individuals survived. We ran LMEs with warming and connectivity (low and high connectivity only, as isolated plots did not permit cross-corridor dispersal) as predictors, and standardized dispersal as the response.

For each aphid species, we quantified dispersal as a binary response (whether or not aphids from seeded plants colonized any other plants within the same cage). For each aphid species, we considered whether warming or the population size on the seeded plant influenced dispersal. Warming and population sizes were correlated (see Results), so we tested these two effects separately using GLMEs with either warming and ants or the number of aphids (of that species) on the seeded plant as the predictors, and binary colonization as the response. We selected the best model (lowest AIC value) for each species. Because this analysis was focused on within-cage movement, we grouped all connectivity treatments together (N=21 for each of unwarmed and warmed treatments).

We analyzed the combined effects of connectivity and warming on each species’ performance at the metacommunity scale. We used the same metrics of performance for each species as in the local analysis (survival rates for monarchs, days surviving for milkweed beetles and bugs, and maximum population sizes for aphids), but included data from entire metacommunities (e.g. maximum number of aphids totalled across cages seeded with insects and cages initially without insects) and included all three levels of connectivity in the analysis. We ran separate LMEs with warming and connectivity as predictors and the performance metric as the response. As with the local analysis, to account for the effects of ants on aphid abundances, we first ran separate LMEs with ant occurrence as the predictor and the maximum population size reached by each aphid species as the response. We then used the residuals from these models to run our final LMEs that had connectivity and warming as predictors, and the residuals of the initial ant model as the response.

To determine the effect of warming and connectivity on diversity, we calculated species richness (out of a maximum of 5 species) within each metacommunity at each of the 19 thrice-
weekly insect surveys. We first performed a linear regression for each metacommunity (experimental replicate) with intercepts forced through five (the initial richness of all metacommunities) to calculate the slope of the decline in richness over time and the standard error of that slope. We then ran a weighted LME that had warming and connectivity as the predictors, the slopes from the above model as the response, and that weighted the slopes by the inverse of their standard errors.

Finally, to ensure that our results were not impacted by inadvertent differences in predators among treatments, we tested the effect of our treatments on predator abundances using an LME with warming and connectivity as predictors and predator abundance as the response.

**Results**

The presence of insects had a negative effect on milkweed growth ($\chi^2 = 4.4, P = 0.036$; Fig. 5.1a), while warming had a positive effect ($\chi^2 = 4.3, P = 0.039$). Insects increased milkweed mortality ($\chi^2 = 6.60, P = 0.01$; Fig. 5.1b) and limited the increase in trichome density observed in control plants over the course of the experiment ($\chi^2 = 5.9, P = 0.01$; Fig. 5.1c), whereas warming had no effect on either measure (both $P > 0.1$). Neither warming nor insects impacted latex exudation (both $P > 0.4$; Fig. 5.1d). There were no interactions between insects and warming for any plant response (all $P > 0.2$), indicating that warming did not alter the impact of insects on any of these four milkweed responses (Fig. 5.1).

Species co-occurrence rates were higher than expected by chance for all species pairs except for the milkweed bug-milkweed beetle pair (Fig. 5.2a-c), and warming did not affect co-occurrence rates for any species pair (all $P > 0.05$). Likewise, there was a positive relationship between the maximum population sizes reached by *A. nerii* and *A. asclepiadis* ($\chi^2 = 28.6, P < 0.001$; Fig. 5.2d), both aphid species were also positively associated with ants (both $P < 0.001$, Appendix D Fig. S5.4), and neither relationship was affected by warming ($P > 0.7$).
Figure 5.10: Plant responses. The effect of warming and the presence of insects on (a) plant growth, (b) plant mortality (the proportion of plants that died before the end of the experiment), (c) change in trichome density and (d) change in latex exudation. Panels a, c and d show the change in height, trichome density or latex exudation over the course of the six week experiment. Data are from the largest plant in each isolated plot; these plots were either kept free of milkweed specialists (“no insects”) or were seeded with five milkweed specialists (“insects”). Unwarmed treatments are in light blue, and warmed treatments are in dark red. Data points are mean values ± one standard error.
Figure 5.2 Associations between species pairs. Rates of co-occurrence on the same plant for (a) species pairs that do not include aphids, (b) species pairs that include *A. asclepiadis* and (c) species pairs that include *A. nerii*. Panel (d) shows the positive correlations between the maximum population sizes of the two aphid species (*A. nerii* and *A. asclepiadis*). Horizontal dashed lines in panels a-c show the null expectation for each group, calculated to account for plant death over the course of the experiment, and for aphids occupying multiple plants at a single time point (see Methods). Error bars are 95% confidence intervals, so error bars not crossing the horizontal dashed line represent co-occurrence rates that are significantly different from the null expectation. Data for all panels are from plants in isolated plots that were seeded with five milkweed specialists. In all panels, warmed and unwarmed treatments are grouped because warming had no effect on associations between any species pair.
Warming improved the local-scale performance of three focal species and negatively impacted one species (Fig. 5.3). For monarchs, warming increased survival rates ($\chi^2 = 4.5, P = 0.03$; Fig. 5.3), increased growth rates ($\chi^2 = 8.13, P = 0.004$), decreased the time it took to pupate ($\chi^2 = 6.1, P = 0.01$) and had no effect on butterfly wing length ($\chi^2 = 0.005, P = 0.95$). Warming decreased the number of days that milkweed bugs survived ($\chi^2 = 4.7, P = 0.03$; Fig. 5.3), and did not affect the number of days that milkweed beetles survived ($\chi^2 = 1.7, P = 0.19$; Fig. 5.3). Warming increased the maximum population sizes reached by both *A. nerii* (warming $\chi^2 = 10.9, P < 0.001$; Fig. 5.3) and *A. asclepiadis* (warming $\chi^2 = 6.5, P = 0.01$; Fig. 5.3).

There was no effect of warming on monarch caterpillar within-cage movement ($P > 0.3$). Monarchs did however show an interactive effect of warming and survival status (whether or not an individual died during experiment or survived to pupation) on movement ($\chi^2 = 6.04, P = 0.014$); in unwarmed conditions, monarchs that died dispersed less (per day) than those that survived (Appendix D Fig. S5.5). Neither warming nor connectivity affected daily cross-corridor movement by milkweed bugs or milkweed beetles (all $P > 0.1$). For *A. nerii*, the best dispersal model included warming and ants, and there was a positive effect of both on dispersal (AIC = 40.9; warming $\chi^2 = 4.5, P = 0.03$, ants $\chi^2 = 18.8, P < 0.001$). Population size was also a significant predictor of dispersal for this species (AIC = 46.0, $\chi^2 = 13.5, P < 0.001$), indicating that for *A. nerii*, warming effects on dispersal likely occurred via increased population size (Fig. 5.4a). For *A. asclepiadis* dispersal, the model with population size (AIC = 46.2, $\chi^2 = 15.7, P < 0.001$) performed equally well as the model with warming and ants, although in the latter, only ants affected dispersal (AIC = 49.5; warming $\chi^2 = 0.6, P = 0.43$, ants $\chi^2 = 14.3, P < 0.001$). This indicates that for *A. asclepiadis*, population size but not warming impacted dispersal (Fig. 5.4b).
Figure 5.3 Local-scale performance of each species. Standardized effect of warming on the local-scale performance of each insect species. Positive values of Cohen’s d represent positive effects of warming, and negative Cohen’s d represent negative effect of warming. Performance is quantified according to each species’ life history: survival rate for monarchs, the number of days that milkweed bugs and beetles survived (averaged over two individuals per plot) and the maximum population size reached by *A. nerii* and *A. asclepiadis* (the total number of aphids on all three plants in a plot) after accounting for the effect as ants as a covariate. Data are from isolated plots that were seeded with five milkweed specialists. Error bars are 95% confidence intervals, so black error bars not crossing zero (horizontal dashed line) are significant effects, while the grey bar crossing zero is a non-significant effects. *P* values are from LMEs and GLMEs.
Figure 5.4 Aphid dispersal. (a) *A. nerii* and (b) *A. asclepiadis* dispersal as a function of the population size (of that species) on plants seeded with insects at the start of the experiment. Dispersal was quantified according to whether aphids colonized an unseeded plant within each cage (score =1), or did not colonize any neighboring plants (score = 0). Unwarmed plots are as light blue dots, and warmed treatments are dark red dots.
At the scale of the entire metacommunity, the performance of three out of five insect species was affected by warming, connectivity or both (Fig. 5.5). For monarchs, survival was higher in warmed conditions ($\chi^2 = 6.45, P = 0.01$), and lowest in low connectivity metacommunities ($\chi^2 = 10.13, P = 0.006$; Fig. 5.5a). For milkweed bugs, there was an interactive effect of warming and connectivity on the number of days surviving ($\chi^2 = 11.4, P = 0.0034$; Fig. 5.5b); in isolated plots, milkweed bugs survived for longer in unwarmed conditions, while in low and high connectivity plots, they survived for longer in warmed conditions. For milkweed beetles, there was no effect of warming or connectivity on the number of days surviving (both $P > 0.6$, Fig. 5.5c). For aphid maximum population size, *A. nerii* showed a positive effect of warming ($\chi^2 = 3.9, P = 0.048$; Fig. 5.5d) and no effect of connectivity ($\chi^2 = 3.5, P = 0.17$), while *A. asclepiadis* showed no effect of either warming or connectivity (both $P > 0.2$; Fig. 5.5e).

Species richness at the metacommunity scale declined from the initial five species as species died off throughout the experiment (Fig. 5.6a,b). There was an interactive effect of warming and connectivity on the rate of this decline; in unwarmed conditions, richness declined most rapidly in low connectivity metacommunities (i.e. those connected by 6m corridors), whereas connectivity did not alter rates of decline in warmed treatments (Warming x Connectivity interaction, $\chi^2 = 5.3, P = 0.02$; Fig. 5.6c). Predator abundances were unaffected by warming or connectivity (both $P > 0.2$).
Figure 5.5 Metacommunity-scale performance of each species. The effect of warming and connectivity on the metacommunity-scale performance of each insect species. Performance is quantified according to each species’ life history: (a) survival rate for monarchs, the number of days that (b) milkweed bugs and (c) milkweed beetles survived (averaged over two individuals per plot), and the maximum population size (the total number of aphids on all plants in a metacommunity) reached by (d) *A. nerii* and (e) *A. asclepiadis*. Connectivity levels are: “isolated” (cages not connected to another cage by a corridor), “low” connectivity (cages connected by a 6m corridor) and “high” (cages connected by a 2m corridor). Unwarmed treatments are in light blue and warmed treatments are in dark red. Data points are mean values ± one standard error. Panel d and e show back-transformed aphid population sizes after accounting for the effect of ant occurrence rates, and reported aphid results account for the effect of ants (see Methods).
Figure 5.6 Metacommunity diversity. The effect of warming and connectivity on the decline in metacommunity-scale species richness over the course of the experiment (19 surveys between July 7th and August 18th) in metacommunities initially seeded with five milkweed specialists. Panel (a) shows unwarmed treatments and panel (b) shows warmed treatments. Panel (c) shows the slopes of the lines in panels a and b (with intercepts forced through five, which was the initial richness of all metacommunities). Connectivity levels are: “isolated” (cages not connected to another cage by a corridor), “low” connectivity (cages connected by a 6m corridor) and “high” connectivity (cages connected by a 2m corridor). Unwarmed treatments are in light blue and warmed treatments are in dark red. Error bars show ± one standard error.
Discussion

Our experiment integrated warming effects across multiple metacommunity scales by allowing both local processes and dispersal to be simultaneously impacted by warming. We hypothesized that the effects of warming on metacommunities would depend on the interplay between the local costs and benefits of warming and the larger-scale risks and advantages of inter-patch movement. In our plant-insect system, competition for resources appeared to be weak, and warming mostly benefited insects locally. When local communities were connected into a larger metacommunity, inter-patch movement posed a species-specific mortality risk that increased mortality for two species when connectivity was low. These species-specific responses to warming at the local and metacommunity scales were shaped by life history and dispersal traits, and drove an interactive effect of warming and connectivity on metacommunity diversity. The net effect was a more rapid decline in diversity within this specialist insect guild in unwarmed, low connectivity metacommunities. Overall, this study illustrates how the impact of warming on species living in patchy habitats reflects complex responses at the species, community and metacommunity scales that can only be understood by integrating responses to warming across spatial scales.

We predicted that our focal insect species would respond negatively to warming if higher temperatures accelerated resource drawdown or intensified competitive interactions, but that they could benefit from warming if increased temperatures did not induce declines in the quantity or quality of the plant resource (Ritchie 2000; O’Connor et al. 2011; Gilbert et al. 2014). We found support for the latter scenario: while insects caused ~30% plant mortality and decreased plant growth, warming did not intensify these negative effects. Rather, warming increased plant growth, which appeared to offset any indirect negative impacts on plants that could have resulted from warming-induced changes in insect survival and population sizes (Fig. 5.1a,b). Likewise, despite relying on a common resource, we found no indication that any of our focal insect species were actively avoiding competition, nor that our two aphid species were negatively affecting one another (Fig. 5.2). On the contrary, almost all species pairs were more likely to co-occur on the same plant than expected by chance, and abundances of our two aphid species were positively correlated (Fig. 5.2). While the insect-induced plant mortality we observed is indicative of some degree of resource limitation in this system, the patterns of insect
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co-occurrence and correlated abundances suggest that here, competition for resources was not a major driver of insect behavior or population growth (Fig. 5.2). Indeed, this lack of resource competition occurred despite the fact that the size and number of experimental plants within each of our plots created smaller patches than what is often found in the wild, and our patches were stocked with relatively high densities of milkweed specialists (Van Zandt & Agrawal 2004a; Grainger et al. 2017). Explicitly testing the role of resource availability and resulting strength of competitive interaction strength in driving warming responses would require comparisons across multiple resource levels, which would be a worthwhile avenue for future research (O'Connor et al. 2009). In this study, other factors may have been more important determinants of insect location than the presence of competitors; for example, bottom-up differences in microhabitat quantity and quality, such as plant size and genotype, are known to be important drivers of preference and performance of milkweed specialists (Van Zandt & Agrawal 2004a; Mooney & Agrawal 2008). Likewise, for aphids that engage in mutualistic interactions with ants by providing a honeydew reward, the benefits of protection against predators can be substantial, and may be a stronger driver of aphid abundances than negative aphid-aphid interactions (Appendix D Fig. S5.4; Mooney and Agrawal (2008); Smith et al. (2008)).

Locally, warming increased monarch survival and population sizes of both aphid species, but decreased the longevity of milkweed bugs (Fig. 5.3). Warming experiments have reported both positive and negative effects of warming on species performance, with the direction of these effects depending on species identity, the ranges of temperatures used, the individual or population response of interest, and the nature and strength of species interactions (Bale et al. 2002; Jiang & Morin 2004; Walker et al. 2006; Barton & Schmitz 2009; O'Connor 2009; Gruner et al. 2017). When resource limitation or temperature stress do not limit population growth, warming can accelerate reproductive rates and induce larger populations of species with rapid reproduction and overlapping generations such as aphids (Barton & Ives 2014; Ju et al. 2015). Indeed, we saw a positive effect of warming on aphid abundances (Fig. 5.3). Likewise, the accelerated growth and development we observed for monarchs is a common response to warming that, when scaled up to the community level, can have implications for species interactions such as herbivory and predation (Gillooly et al. 2002; Yang & Rudolf 2010). For example, the decreased time to monarch pupation in warmed conditions may have helped
caterpillars avoid the high mortality rates incurred at early larval stages from predation and desiccation (Bale et al. 2002; Prysby 2004). In contrast to the positive warming effects on aphids and monarchs, milkweed bugs suffered shorter longevity at higher temperatures. While it is possible that increased competitive pressure from aphids and monarchs with warming precipitated the more rapid death of milkweed bugs via indirect competitive effects, the lack of avoidance or exclusion between these species makes this unlikely (Fig. 5.2). Rather, this negative response may reflect accelerated ectotherm development with warming that can hasten death (Amarasekare & Savage 2012). Overall, the local effects of warming observed here support the growing recognition that predicting the impact of climate change on ecological communities will necessitate integrating responses that span multiple levels of organization, including developmental rates, population growth rates and species interactions (Brown et al. 2004; Gilman et al. 2010; Amarasekare & Savage 2012).

Warming altered dispersal indirectly for two species, but did not result in the large increases in dispersal predicted if warming-induced resource declines prompt species to leave the host patch en masse (Zera & Denno 1997; Benard & McCauley 2008). For A. nerii, the warming-induced increase in dispersal (Fig. 5.4) was likely the result of larger population sizes in warmed conditions (Fig. 5.3), as crowding is a well-documented cue for aphid dispersal (Müller et al. 2001). For monarch caterpillars, warming altered the relationship between survival and movement (Appendix D Fig. S5.5). This could either indicate that in unwarmed conditions, higher quality individuals are more likely to both move and survive, or that moving between plants is advantageous because it facilitates the selection of superior resources or predator-free areas. While our study does not have the power to determine the directionality of this relationship or its underlying mechanism, this result raises the intriguing possibility that the benefits of movement can be temperature-dependant, and suggests an avenue of future research.

On a broader spatial scale, climatic changes in wind currents or weather events could alter long-distance dispersal patterns of these species in ways not captured here, for example by shifting the arrival times of species that overwinter further south and disperse northward to our site each spring (monarchs and A. nerii) (Travis et al. 2013). On a broader temporal scale, shifts in the emergence times of the species that overwinter in our region (milkweed bug, milkweed beetle and A. asclepiadis) could also alter the performance and competitive dynamics of these species (Williams et al. 2015). Despite limitations inherent in the spatial and temporal scale of our
study, our results support a growing body of evidence that dispersal responses to warming are often context and condition-dependent (Müller et al. 2001; Benard & McCauley 2008; McCauley & Mabry 2011; Fronhofer et al. 2015).

There was a substantial species-specific mortality risk in metacommunities connected by corridors, that, when combined with positive local effects of warming, scaled up to shape species-specific responses to warming and connectivity. Both monarch caterpillars and milkweed bugs had lower survival in connected metacommunities (Fig. 5.5). For these two species, attempts to move across corridors to a neighboring milkweed patch may have been thwarted by generalist predators that occur within the grass matrix at this site, or individuals may have simply died before reaching their destination. In contrast, large aphid populations incur little cost from each departing individual that are unsuccessful in crossing the matrix, and milkweed beetles may have been better able to reach neighboring patches or return to their original patch as a result of their superior dispersal ability (Lawrence 1988; Matter 1996). Although connectivity is widely viewed as beneficial for metacommunity diversity because neighboring patches provide refuge from resource limitation, predators or competitors (Leibold et al. 2004; Cadotte 2006), our results demonstrate that in cases where local conditions are favorable, the risk of dispersing can outweigh the benefits. This risk associated with moving between habitat patches is widely recognized in dispersal ecology (Bonte et al. 2012), yet methods used to manipulate dispersal in metacommunity experiments often eliminate dispersal risk or homogenize risk across species (Grainger & Gilbert 2016). The effects of this important feature of spatially structured environments on species and community-level responses are therefore likely to be under-reported. Continuing to incorporate dispersal risk into experimental work will provide a more complete picture of how inter-patch movement affects local and regional diversity.

The combined effects of local warming responses and inter-patch connectivity scaled up to shape diversity in our metacommunities (Fig. 5.6). Specifically, we saw more rapid declines in species richness in unwarmed metacommunities with low connectivity, compared to isolated or well-connected communities (Fig. 5.6). Higher temperatures offset the disadvantage of low connectivity; warming increased the survival of monarchs and milkweed bugs in metacommunities connected by corridors, while in unwarmed connected metacommunities,
these species were lost early in the experiment (Fig. 5.5). Taken separately, warming experiments that usually report declines in diversity at higher temperatures (Gruner et al. 2017), and metacommunity experiments that typically find increases in diversity at higher dispersal rates (Cadotte 2006; Grainger & Gilbert 2016), suggest that warming could induce declines in diversity that could be offset by connectivity. However, we found the opposite, indicating an interesting and surprising interaction between warming and connectivity at intermediate scales. Compared to isolated communities, low connectivity treatments that allow for dispersal experienced more rapid declines in diversity at ambient temperatures, and these losses were offset by warming. Recent experiments testing the combined influence of warming and connectivity on metacommunity diversity have likewise hypothesized that connectivity could mitigate negative impacts of warming, and have also failed to find support for this hypothesis; instead, these studies report declines in diversity at higher temperatures that were not mitigated by higher inter-patch dispersal rates (Limberger et al. 2014), or positive effects of dispersal at ambient but not warm temperatures (Thompson et al. 2015). Although these experiments differ from ours in their methodology and study organisms, when considered together these experiments demonstrate that responses to warming at the metacommunity scale can produce surprising outcomes. Although testing responses to warming across multiple spatial scales while capturing the range of local warming effects and the costs and benefits of dispersal remains a challenge, this study suggests a way forward for better integrating spatial structure into climate change research.

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References


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Appendix D: Supplementary information to Chapter 5

Supplementary methods

Rearing experimental plants and insects

We grew and planted our first batch of milkweed plants in the summer of 2014 (2 plants per cage), and due to the small size of these plants, a second batch was grown and planted in the summer of 2015 (1 plant per cage). To grow all plants, seeds were first nicked to remove a portion of the pericarp, bleached with a 5% bleach solution to kill fungus and placed between two sheets of moist filter paper in sealed petri dishes. Seeds were then refrigerated (3°C) for one week and then placed in a dark incubator (27°C) for three days to induce germination. Germinated seeds were planted into 1L pots in potting soil (Sungro Sunshine Mix #1), kept in a greenhouse set at a 10:14 hour light/dark cycle and 17:25 degree day/night temperatures, and watered as needed. Plants were fertilized 10 days after planting with 1 tsp 14:14:14 N:P:K slow release fertilizer. Seedlings were moved to an outdoor greenhouse at four weeks old and planted into the experiment at eight weeks old.

_A. nerii_ and _A. asclepiadis_ came from colonies started from individual aphids collected off of milkweed plants growing naturally at Koffler Scientific Reserve. Aphid colonies were maintained by serial transfer on potted milkweed plants kept indoors at room temperature. Milkweed bugs were collected from wild milkweed plants and kept in indoor cages with milkweed seeds and water for <1 week prior to the experiment. Monarch caterpillars were purchased from a commercial supplier (Lucy’s Butterfly Farm, Apsley, Ontario). Caterpillars were reared on tropical milkweed (Asclepias curassavica) from eggs imported from International Butterfly Breeders Association breeders. Caterpillars were kept indoors in cages at room temperature, and were at the 2\textsuperscript{nd} instar stage at the start of the experiment. Milkweed beetles were collected from wild milkweed plants and kept in outdoor cages containing naturally growing milkweed plants for <1 week prior to the experiment; this species was kept in outdoor cages containing larger wild milkweed plants because many adult milkweed beetles require a larger amount of milkweed than was feasible to grow in indoor cages.
Measuring milkweed defensive traits

To quantify latex exudation, we cut off the tip of the youngest fully expanded leaf (i.e. tissue produced since the beginning of the experiment) such that a length of 0.5 cm of cut leaf tissue was exuding latex (Agrawal 2005). We absorbed latex onto a pre-weighed, 1cm filter paper (latex stopped flowing within ~10 seconds) and then re-weighed the paper to determine the mass of exuded latex. Previous research on milkweed has found that wet latex weight provides a good estimate of latex production, and can be predictive of herbivore growth rates (Woods et al. 2012). We measured trichome density by counting trichomes on the underside of the tip of the second youngest fully expanded leaf using a dissecting microscope (Woods et al. 2012).

Calculating co-occurrence null expectations

To calculate null expectations for species co-occurrences, we started with the baseline null expectation that two species will occupy the same plant 33% of the time if cages contain three plants each, and that each species can only occur on one plant per time at each survey. However, this null expectation had to be adjusted upward because plants died during the experiment and aphids regularly occurred on multiple plants at each survey. We first adjusted null expectations of co-occurrence to account for the 30% milkweed mortality we observed in cages seeded with insects (Fig. 5.1), which is roughly the equivalent of going from an average of three to an average of two available plants in each cage over the course of the experiment. The average date at which plants died was in early August (halfway through the experiment), so we calculated baseline co-occurrence as the mean of 0.33 (probability of co-occuring with another species if there are three plants in the cage) and 0.50 (probability of co-occuring with another species in the cage if there are two plants in the cage). This works out to a null expectation of 0.41. We further adjusted null expectations of co-occurrence rates for species pairs containing either aphid species, as these species colonized plants over the course of the experiment and could thus occupy more than one plant at a single time step. A. nerii was observed 57% of the time on a single plant (a 0.41 probability of co-occuring with another species, as described above), 36% of the time on two plants within the same cage (a 0.83 probability of co-occuring with another species) and 7% of the time on three plants within the same cage (a 100 percent chance of co-occuring with another species). The weighted means of these three values gives a null co-occurrence rate of 0.60 for A. nerii with any other non-aphid species. Likewise, A. asclepiadis
was observed 85% of the time on a single plant (0.41 probability of co-occurrence) and 15% of the time on two plants (0.83 probability of co-occurrence). This works out to a null co-occurrence rate of 0.47 for *A. asclepiadis* with any other non-aphid species. Because each metacommunity was seeded with two milkweed bugs and two milkweed beetles, these species could also occur on multiple plants within the same metacommunity. However, both milkweed bug or milkweed beetle individuals within a pair were rarely observed on two different plants within the same metacommunity at the same survey. This was because these species were frequently found on cage walls, the ground, other vegetation within the cage, or were not located at a survey. Therefore incorporating these species’ presence on multiple plants did not raise expected co-occurrence rates above 0.33.

**References for insect images used in figures**

Long-horned milkweed beetle: photograph by Mike Quinn © TexasEnto.net

Small milkweed bug: photograph by Tom Murray © bugguide.net

Weevil: modified from photograph by Roland E. Barth © fnanaturesearch.org

Leaf miner: photograph by MJ Hatfield © bugguide.net

Tussock moth: modified from photograph by Ed Nisley © softsolder.com

Monarch: photograph by Marty Nevils Davis © martydavisphotos.com

Aphids: modified from images created by Kailen Mooney (UC Irvine)

**Supplementary tables and figures**

**Table S5.1** Cross-corridor moves for monarch caterpillars, *Aphis nerii* and *Aphis asclepiadis*.

<table>
<thead>
<tr>
<th></th>
<th>2m corridor</th>
<th>6m corridor</th>
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<tbody>
<tr>
<td></td>
<td>Unwarmed</td>
<td>Warmed</td>
</tr>
<tr>
<td>Monarch</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td><em>Aphis nerii</em></td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td><em>Aphis asclepiadis</em></td>
<td>3</td>
<td>0</td>
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</tbody>
</table>
Figure S5.1 Photograph of a warmed metacommunity with cages connected by a 2m long corridor.
**Figure S5.2** Light absorbance of four plastic types over a range of visible, ultraviolet and infrared wavelengths. The black line indicates the plastic that had the lowest absorbance (i.e. highest transmittance) over the broadest range of wavelengths, and was used in the experiment to increase the temperature of warmed cages (Home Hardware 3.3mm polyethylene plastic film). Plastics 1-3 are plastic drop cloths sold commercially for house painting. Absorbance was measured using a Thermo Scientific Multiskan Go Microplate Spectrophotometer.
Figure S5.3 Effect of the temperature treatment on (a) mean daily cage temperatures during the daytime (9am-9pm) (b) mean daily cage temperatures overall (both day and night), (c) cage temperature variability (standard deviation) during the daytime (9am-9pm), (d) mean daily corridor temperatures during the daytime (9am-9pm), (e) mean daily corridor temperatures overall (both day and night) and (f) cage humidity during the daytime (9am-9pm). Data points are means values ± one standard error.
**Figure S5.4** The maximum population size of (a) *A. nerii* and (b) *A. asclepiadis* increased with ant occurrence and with warming. Ant occurrence is the number of surveys on which ants were observed, out of a total of 17 surveys. Data are from plants in isolated plots that were seeded with five milkweed specialists. Unwarmed treatments are in light blue, warmed treatments are in dark red.
Figure S5.5 The effect of warming and survival status (whether or not an individual survived to pupation) on within-cage caterpillar movement. Standardized within-cage dispersal is the total number of moves within the same cage (off of a plant, onto a plant, or between plants), divided by the number of days surviving. Solid lines and filled dots represent monarchs that survived to pupation, and dashed lines and open circles represent monarchs that died during the experiment. Unwarmed treatments are in light blue, warmed treatments are in dark red. Data points are mean values ± one standard error.

References


Chapter 6: General conclusions

Ecologists are increasingly being tasked with aiming at a moving target, as the systems we study change in real time, and undisturbed communities become a thing of the past. The multitude of interacting global changes, from temperature change to drought, habitat destruction, and nitrogen deposition, present major challenges for those interested in keeping pace with understanding how natural systems are structured and function in the real world. Our best hope will be to stand on the shoulders of giants and use the knowledge gained over centuries of ecological research to untangle the impacts of anthropogenic change on ecological communities.

In this thesis, I used theory describing coexistence in patchy landscapes and the temperature-dependence of biological processes to achieve this goal. Below, I describe some of the main insights gained from this work, and the next steps needed to close remaining gaps.

Stronger links between the local and the regional

This thesis makes several novel contributions to ongoing efforts to link the processes that drive ecological dynamics within local habitat patches with patterns that emerge from the movement of individuals between patches. In Chapter 2, I describe a new method for using local invasion tests to distinguish between species’ occurrences that are the product of local competitive dynamics promoting stable coexistence from occurrences that rely on incoming colonists to support locally declining populations (Fig. 2.3). I also highlight the utility of food web metrics such as stability and chain length, both developed to describe processes at the local scale, to determine how and why dispersal alters patterns of diversity in trophic metacommunities. If integrated into metacommunity experiments, these approaches could help elucidate when and how dispersal counteracts or reinforces local dynamics in competitive and consumptive metacommunities.

In Chapters 2 and 4, I highlight priority effects as an understudied link between local dynamics and dispersal. While interest in priority effects has grown in recent years (Fukami 2015; De Meester et al. 2016), insights from this field have been slow to be adopted by empirical ecologists studying metacommunities. This is despite the fact that dispersal rates between patches determine if, and how frequently, individuals arrive at a local site, and thus play a major role in driving local priority effects (Vannette & Fukami 2017). I highlight this link first in
Chapter 2, by outlining how priority effects are a missing component of metacommunity experiments testing the relationship between dispersal and diversity, and emphasizing how and when priority effects are likely to be important. Despite the demonstrated importance of arrival order for community assembly (Chase 2010; Fukami 2015), experimental manipulations of dispersal often overlook or even prevent differences in arrival time and order at a local site. In Chapter 4, I then demonstrate how priority effects can link the impacts of warming on local dynamics and dispersal, by showing that warming simultaneously increases the importance of arrival time for local competitive outcomes and alters the very dispersal rates that determine arrival order. These results indicate that a better integration of priority effects into metacommunity ecology could uncover novel bridges between the local and the regional.

**Future directions**

While results from Chapter 4 indicate that the local competitive dynamics and dispersal responses of two competing species could create positive feedbacks that accelerate the extinction of the inferior competitor, confirming this will require further modeling work. Since the completion of this project, additional temperature-dependent feeding and fecundity responses have been measured in subsequent growth chamber experiments (Zachary Moore, unpublished data), and modeling of feedbacks at the metacommunity scale is in progress (Benjamin Gilbert, unpublished data). With this fuller dataset that describes the warming responses of *A. nerii* and *A. asclepiadis* feeding, fecundity, population growth, and dispersal, we will be able to create multi-scale theoretical predictions for metacommunity responses to warming.

More broadly, a more thorough integration of regional dispersal dynamics, including arrival order and timing, into a now widely accepted framework for describing local coexistence (Chesson 2000) would help square this approach with natural systems that rarely, if ever, exist in isolation. Contemporary coexistence theory describes the balance between niche differences that promote coexistence by causing species to be more limited by conspecifics than heterospecifics, and fitness differences that preclude coexistence by favoring the dominance of one species (Chesson 2000; Adler *et al.* 2007). Tests of this theory have focused on lab or field-based manipulations of pairwise competitive interactions to determine when species coexist versus when one excludes the other (Godoy *et al.* 2014; Kraft *et al.* 2015; Germain *et al.* 2016).
CHAPTER 6: GENERAL CONCLUSIONS

However, whether or not such tests describe patterns of co-occurrence in nature remains an open question. Preliminary evidence indicates that competitive outcomes predicted from contemporary coexistence theory and lab experiments can, in some cases, be representative of natural patterns of field-based patterns of occurrence (Grainger, unpublished data) and co-occurrence (Narwani et al. 2013). However, interspecific differences in dispersal could cause local competitive outcomes to be obscured whenever dispersal limitation prevents competitive species from reaching suitable patches (Germain et al. 2017) or high dispersal maintains species in locales from which they would otherwise be driven locally extinct. Indeed, pairwise competitive trials may be most likely to mirror natural patterns when dispersal between local patches is intermediate, such that species can reach all sites, but high dispersal rates don’t overwhelm local dynamics. Comparing lab-based competitive outcomes to co-occurrence rates from field experiments in which dispersal rates between local patches are manipulated would broaden the scope of what is becoming the dominant framework for studying local coexistence.

The importance of dispersal heterogeneity

A major takeaway from this thesis is the importance of interspecific differences in dispersal for metacommunity dynamics. In Chapter 2, I outlined how experimental designs that allow species to move at different rates are under-utilized, but are necessary to enable processes such as a competition-colonization trade-off arising from differences in dispersal ability between competitors, consumptive dynamics arising from differential dispersal ability of predators and prey, and priority effects arising from species’ differential arrival times at a local site. Consequently, a strength of my three empirical chapters was the use of designs that allowed, quantified, and highlighted species’ differential ability to move between patches. In Chapter 3, I demonstrated how interspecific differences in dispersal rates can be used to predict species’ responses to patch size and connectivity, and found that species with low dispersal ability were most constrained by the spatial arrangement of patches (Table 3.2). In Chapter 4, I showed that dispersal rates, and dispersal responses to warming, varied greatly across my two aphid competitors (Fig. 4.4). It was these differential dispersal responses that could create positive feedback loops in which the inferior competitor suffers more from arriving at a patch late under warming, and also becomes less dispersive and therefore more likely to arrive late. Finally, the use of semi-natural corridors as a dispersal manipulation in Chapter 5 allowed species to incur differential risk when moving across corridors between local patches. The high mortality risk
experienced by two species (Fig. 5.5) helped drive the surprising interactive effect of warming and connectivity that I detected (Fig. 5.6). Although experimental methods that allow species to disperse naturally between local habitat patches (rather than experimentally manipulating movement) are difficult to implement, these and other studies demonstrate the benefits of using creative experimental approaches that permit natural dispersal dynamics (Gonzalez et al. 1998; Chase 2010; Matthiessen et al. 2010).

**Future directions**

Incorporating dispersal into experiments in an ecologically relevant way is challenging, as any ecologist attempting to track or manipulate movement between local habitat patches knows. There will always be an inherent trade-off between the tractability of methods that move a desired number of individuals or a portion of the community, and the realism of methods that allow individuals to move themselves. Fortunately, there is now a suite of established and emerging methods for manipulating how many individuals are able to move between patches, while maintaining natural or semi-natural movement patterns. These methods can, and should, be applied across a variety of systems. As described in Chapter 2, empiricists have successfully used tubes connecting local habitats to control movement between patches in both aquatic (France & Duffy 2006; Guelzow et al. 2014) and terrestrial (Davis et al. 1998) mesocosms. Likewise, distances between aquatic mesocosms (Shulman & Chase 2007; Chase et al. 2010) and terrestrial habitat fragments (Harvey & MacDougall 2014) can be manipulated, as described in Chapter 2 and demonstrated in Chapter 4. Excitingly, new and creative approaches for manipulating dispersal continue to emerge, and have demonstrated the importance of heterogeneous dispersal in driving ecological dynamics. For example, a recent study that used different barriers covering flowers to manipulate the number of incoming microbe colonists detected the surprising result of increased beta-diversity at higher dispersal rates, which was attributed to priority effects caused by species’ differential arrival times (Vannette & Fukami 2017). Similarly, the use of experimental animal vectors to transport seeds with a range of animal-aided dispersal mechanisms is being pioneered for use in grassland systems (Rachel Germain, personal communication). Broader use of these established and emerging methods for manipulating dispersal in an ecologically relevant way would enable the detection of responses that only emerge when species’ differential ability to move themselves is taken into account.
CHAPTER 6: GENERAL CONCLUSIONS

This thesis presents strong evidence that dispersal heterogeneity can be a major driving force for metacommunity dynamics (Chapters 2, 3 and 5), and that dispersal responses to warming can vary across competing species (Chapters 4 and 5). Such interspecific variation in dispersal responses to warming will not only shape ecological dynamics at the mesoscale as the climate warms, but will also be instrumental in determining the extent of range shifts under warming (Davis et al. 1998). Yet little is known about the mechanisms that underlie organisms’ distinct dispersal responses to warming, and so dispersal remains a missing link in climate change research. This is due in part to a lack of empirical research investigating dispersal responses to warming, in part to the organism-specific mechanisms through which dispersal occurs, and in part to the complexity that emerges from the myriad interacting direct and indirect pathways through which temperature can affect dispersal (Travis et al. 2013). Thus far, evidence for the effects of warming on dispersal has been species and context-dependent (O’Connor et al. 2007; Altermatt et al. 2008; Massot et al. 2008). This presents a challenge for applying the results from one system more broadly. Functional approaches for classifying and predicting dispersal responses to warming could help generate a more general understanding of how warming affects dispersal. For example, passive and active dispersers are likely to have vastly different responses to warming, with responses for the former emerging from changes in body size and weather patterns, and responses for the latter derived from a combination of behavioral and physiological changes (Travis et al. 2013). Likewise, widely recognized impacts of warming on phenotypes, such as decreased body size (Gardner et al. 2011) could produce a common dispersal inhibition response across systems because smaller-bodied individuals are likely to be less dispersive (McCauley & Mabry 2011; De Bie et al. 2012). Parallel links between warming, plant height, and seed dispersal could also be investigated in plant systems (Thomson et al. 2011). Generating and testing broadly applicable predictions for the relationship between temperature and dispersal will be an essential next step in global change research.

Community responses to warming

In chapters 4 and 5, I used metabolic theory to generate predictions for my empirical tests of the effects of temperature on the strength of competitive and trophic interactions (Gilbert et al. 2014). As the range of models for population and community responses to temperature expands, empirical tests must keep pace with theoretical advances. Such empirical tests have thus far been conducted mainly in aquatic systems (O’Connor 2009; O’Connor et al. 2011), and my work
therefore breaks new ground by demonstrating their applicability in terrestrial systems. My work, and previous experiments that draw from metabolic theory, can serve as models for investigating community responses to warming (O’Connor 2009; O’Connor et al. 2011).

A potential take-away from comparing results from Chapters 4 and 5 is the importance of resource (primary producer and nutrient) availability for understanding consumer-resource dynamics under climate change. In the growth chamber, warming caused the predicted decline in resource quality and quantity, and consequently had negative impacts on consumer populations (Chapter 4). However a very different dynamic played out in the field experiment in Chapter 5. In the field experiment, warming did not precipitate the high levels of herbivore-induced plant mortality that I observed in the growth chamber. Consequently, consumer species had enough plant resources to accommodate their increased metabolic needs, and most benefited from warmed conditions (Fig. 5.3). There were many differences between the experimental set-up used in the growth chamber and field experiments, but one obvious and potentially important difference that could underlie these results was the size of the milkweed plants. In the growth chamber, milkweed plants were small (~15cm tall) and their growth was constrained to 1L pots supplied with a limited amount of nutrients. In the field experiment, by contrast, plants were larger (~40 cm tall), were planted directly into the ground so their growth throughout the experiment was not constrained, and nutrient availability in the soil was likely higher and more consistent throughout the experiment. The greater initial plant resource availability and the greater ability of plants to expand underground growth throughout the field experiment likely contributed to the faster (vertical) plant growth I saw with warming in the field experiment. This greater availability of plant resources to competing insects may have also prevented the high levels of insect-induced plant mortality observed in warmed conditions in the growth chamber, and facilitated the higher insect performance with warming observed in the field experiment.

Future directions

The discrepancy between the negative effects of warming on insect performance in Chapters 4, where plants were small and suffered herbivore-induced mortality in warmed conditions, and the positive effects of warming in Chapter 5, where plants were large and suffered low levels of herbivore mortality, points to the obvious next step of testing the effect of plant size on the outcome of temperature-dependent trophic interactions. This could involve testing plant-
herbivore dynamics with fully-crossed temperature and a plant size treatments to determine whether crashes in the plant resource with warming are dependent on plant size. From the work presented here, I would predict that larger plants will be better able to withstand the increased metabolic demands of insect herbivores under warmed conditions, and will be associated with positive effects on consumers. In contrast, smaller plants should be more vulnerable to rapid resource-drawdown that ultimately accelerates in herbivore population crashes.

More broadly, a general lesson from the growing body of empirical work investigating the effect of experimental warming on ecological communities is that rising temperatures often improve performance of some species at the expense of others, resulting in so-called “winners and losers” of climate change (Walker et al. 2006; Somero 2010). Or more subtly, as was the case in Chapters 4 and 5, warming can enhance the growth or performance of one species more than its competitors (Fig. 4.1). Unfortunately, system and organism-specific results have limited applicability, and we currently lack robust general rules for predicting these winners and losers. Drawing again from metabolic theory, thermal responses that vary predictably across geographic regions or taxonomic groups could be used to generate predictions about species’ and community responses to temperature change (Frazier et al. 2006; Vasseur et al. 2014). Thermal response curves describe the range of temperatures through which a species’ performance increases with rising temperatures, and the optimal temperature after which performance begins to decline (Brown et al. 2004). These rates of increase and temperature optima have been shown vary with trophic level (Dell et al. 2011) and with latitude (Frazier et al. 2006); this could provide a way to broadly predict the outcome of temperature change across communities a priori. For example, a species’ change in performance with warming, as determined by the location of current and future temperatures along its thermal response curve, depend on its adapted thermal tolerance. Because this thermal tolerance is related to a species’ current geographical range (Frazier et al. 2006), widely available range information could be used to predict how warming will differentially impact species in a community. This approach could be extended to investigate the links between competing species’ ranges, their temperature optima, and competitive outcomes under warming. Although species’ thermal tolerances are often used to predict their ranges and future range shifts (Pearson & Dawson 2003), current ranges are rarely used to predict the outcome of competition. The use of estimates of range-
derived temperature responses could be one step towards generating general rules for understanding community responses to warming.

**Conclusion**

In the first half of my thesis, I outlined and tested the importance of integrating complexities such as heterogeneity in dispersal ability and trophic interactions into empirical metacommunity research that has been largely focused on competitive dynamics and neutral dispersal. In the second half of my thesis, I brought dispersal dynamics into the field of climate change research that has focused mainly on local responses or continental-scale range dynamics. Overall, these contributions demonstrate the effectiveness of using basic ecological principles to understand patterns of coexistence and diversity in a rapidly changing world.

**References**


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