The Dissertation Committee for Robert Andrew Deans Certifies that this is the approved version of the following Dissertation

The Effect of Dispersal Behavior on Stability in Populations, Communities, and Ecosystems

Committee:

Larry Gilbert, Supervisor

Mathew Leibold, Co-Supervisor

Tim Keitt

Shalene Jha

William Resetarits

The Effect of Dispersal Behavior on Stability in Populations, Communities, and Ecosystems

by

Robert Andrew Deans

Dissertation

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Doctor of Philosophy

The University of Texas at Austin

May 2019

Acknowledgements

To my advisors Mathew Leibold and Larry Gilbert: thanks for your guidance and inspiration. My theoretical ecology and natural history knowledge were developed and refined in large part thanks to y’all. The other members of my thesis committee, Shalene Jha, Tim Keitt, and Bill Resetarits, were also very helpful and understanding during the progress of my work. I consider myself lucky to be advised by such a great set of scientists. Thanks to Dave Chalcraft and everyone back at ECU for supporting my decision to pursue a PhD. I was also able to develop my love of teaching and field research while working as a TA and RA for some great researchers and instructors, including Travis LaDuc, Alex Wild, Larry Gilbert, Rob Plowes, and Yoel Stuart. I received funding from the department of Ecology, Evolution, and Behavior at UT-Austin and from the Texas Ecological Laboratories Program, without which this work would not be possible.

I also owe thanks to the members of the Leibold lab group (Décio Correa, Catalina Cuellar Gempeler, George Livingston, Jacob Malcom, Emma Moran, Diogo Borges Provete, Chase Rakowski, Emlyn Resetarits, Genevieve Smith, and Shankari Subramaniam), all of whom helped me with support and advice both on these projects and in life in general. Thanks to Will Shim, George Livingston, Juan Palacio, Ian Wright, Roger Shaw, and Matthew Moskwik for being excellent friends, camping buddies, and fellow bug/bird chasers. I am also thankful for the love and support of my family Hal, Donna, Meredith, and Melanie and my girlfriend Alison Northup, who also provided invaluable help, advice, and support in the final stretches of my writing.

Abstract

The Effect of Dispersal Behavior on Stability in Populations, Communities, and Ecosystems

Robert Andrew Deans, Ph.D.

The University of Texas at Austin, 2019

Supervisors: Larry Gilbert and Mathew Leibold

Habitat choice, when organisms move among habitat patches in a directed fashion based on environmental cues, is an underappreciated force in Ecology. Theoretical work suggests that such choice behavior might be a potent source of stability in populations, communities, and ecosystems. I tested the effects of dispersal behavior on stability with a series of mesocosm experiments at each of these scales.

In populations of snails with stochastic disturbance, I found that movement among patches was density-dependent: snails tended to move away from high density and toward low density. These movements had dampening effect on oscillations in abundance, and they contributed to longer population persistence times relative to populations that were not connected by dispersal.

A second experiment manipulated the colonization behavior of aquatic insects in order to see how this dispersal behavior affects the community response to a pulse of fish predation on the insect communities. While choice behavior exacerbated the effects of fish predation, reducing species richness beyond what was observed in communities with randomized colonization, choice resulted in faster recovery of communities relative to random colonization.

A third experiment explored the effects of pulses of nutrient additions in mesocosms with developing aquatic insect communities. Presence of sediment had weak effects on stability, with small pulses of nutrients supporting more stable abundance values than ecosystems with no sediment. This stabilization effect was likely driven by habitat choice behavior, since the sediment input treatments affected organisms with active dispersal more than those with passive dispersal.

Collectively, these experiments show that dispersal behavior is an important factor to consider when attempting to explain the spatial and temporal variation in ecosystems. Habitat choice behavior can have particularly significant effects on stability. Predicting how species respond to environmental change therefore requires knowledge of how they move.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction to dispersal, habitat selection behavior, and stability

DISPERSAL AS A DRIVER OF COMMUNITY STRUCTURE

Dispersal, or the exchange of organisms among local habitats, is a major force driving community composition (Holt, 1993; Leibold et al., 2004; Urban et al., 2008; Vellend, 2010; Leibold and Chase, 2017). The process of colonization after dispersal is a necessary step during community assembly, and it provides the link between the local community of species and the regional species pool. Exchange of organisms among different patches of similar habitat can also directly affect local demography, gene flow, colonization/extinction dynamics, and species interactions within those habitats (Ricklefs and Schluter, 1993; Holyoak et al., 2005; Benton and Bowler, 2012a). The effects of dispersal on community structure can also be more indirect. For example, a tradeoff between competitive ability and dispersal ability might allow regional coexistence of strongly competing species. In addition, two species that don't directly compete for the same resources or even occupy the same habitat might nevertheless experience mutually reduced growth rates at high densities thanks to larger populations of dispersive predators that consume both species (Holt, 1993; Abrams and Ruokolainen, 2011).

While dispersal has long been recognized as an important influence on community structure (e.g. MacArthur and Wilson, 1967), it is often very simplified even in current theoretical models. For example, in systems of communities connected by dispersal, i.e. metacommunities, differences in rates of dispersal among local habitat patches can drastically change predictions about the structure and dynamics of the communities within each patch (Leibold et al., 2004; Haegeman and Loreau, 2014; Leibold and Chase, 2017). However, even in these modern models, dispersal is often assumed to be characterized by random, undirected movements in which the probability of colonization depends only on spatial factors, such as patch size and isolation (Binckley and Resetarits, 2005; e.g. Haegeman and Loreau, 2014). While simplification is usually necessary in any theoretical model, one might predict very different dynamics in cases in which organisms show non-random dispersal.

HABITAT SELECTION BEHAVIOR

Some organisms that are capable of active dispersal can make choices about when to emigrate and colonize new habitats. In addition, when multiple alternative habitat patches are available, organisms can select which patch to colonize. This habitat selection behavior likely evolved because individuals that were better able to sense and respond to cues related to survival and reproduction, such as resource availability or predator density, had a fitness advantage (Fretwell and Lucas, 1969; Holt, 1987; Morris, 1987; Morris, 2003). The resulting behavior tends to allow individual organisms to avoid low-fitness patches, such as patches with fewer resources or more predators, and prefer habitats in which their fitness would tend to be higher (Rosenzweig, 1991; Resetarits, 2001; Morris, 2003; Resetarits et al., 2005; Cantrell et al., 2010).

Hereafter, I will refer to the variation among patches in the fitness of colonizing individuals as "habitat quality". This definition is constrained to the perspective of individual organisms interested only in their own fitness, as opposed to population-level fitness. These perspectives may differ if, for example, an individual chooses habitats with low amounts of high-quality resources, which maximizes their own reproductive output, rather than habitats with very large amounts of low-quality resources, which would support a larger population (Johnson 2007). Assessing this type of habitat quality directly would involve detailed measurement of habitat-specific demographic parameters, but in general, habitat quality can be estimated by the preferences of individuals when given a choice among alternative patches. Focusing on habitat preference greatly reduces the complexity of measuring habitat quality, since there are countless factors that interact to determine an individual's fitness in a habitat (Johnson 2007). While the sensory mechanisms that contribute to habitat choice are still often conjectural, perhaps numerous, and difficult to measure, focusing on preference also ensures that the observed behavior is a natural phenomenon resulting from a species' sensory and behavioral traits, and isn't imposed by human assumptions (Resetarits et al. 2005).

Many factors have been demonstrated to affect habitat preference empirically. Preferences for specific resources, microhabitats, and microclimates have been demonstrated in various taxa, such as insects and birds, and these preferences are often linked to higher survival or fecundity (Hawkins, 1984; Martin, 2001; Gripenberg et al., 2010). Another common preference pattern is density-dependent dispersal, which often takes the form of competition avoidance (negative density dependence). This type of preference has been shown for both intraspecific competition (e.g. breeding birds, Fretwell and Lucas, 1969); and interspecific competition (e.g. sessile marine invertebrates, Grossberg, 1981). Positive density-dependent dispersal is also possible, especially when densities approach zero. These "Allee effect" scenarios where conspecific individuals may disperse toward areas of higher density could be caused by decreased efficiency foraging or finding oviposition sites (Kuussaari et al. 1998), decreased defense against predators, or difficulty finding mates at low densities (Parrish and Edelstein-Keshet, 1999). Perhaps for these reasons, some taxa, such as butterflies, seem to be attracted to areas of high density and repelled by areas of low density (Smith and Peacock, 1990; Roland et al., 2000).

Preference for habitats with fewer predators is also common, and while multiple effects can interact, predator presence often supersedes the effects of resources on habitat preference (Gilliam and Fraser, 1987; Savino and Stein, 1989; Rosenzweig, 1991; Resetarits, 2001; Resetarits et al., 2005; Binkley and Resetarits, 2008). In taxa that use different habitats for juvenile and adult stages, dispersing/ovipositing adults can respond to predation risk and resource levels for both themselves and their offspring. Preferences might be particularly strong when juvenile and adult selection pressures are aligned, or weaker when selection pressures oppose or are unrelated. For example, in an experiment manipulating nutrient levels and predation risk in pond mesocosms, ovipositing adult water beetles (which feed in ponds as larvae and adults) respond to both nutrients and fish predator cues, while ovipositing treefrogs (which are terrestrial as adults) avoid predators but seemly ignore nutrient levels in water (Binkley and Resetarits, 2008). In addition, a study exploring oviposition by butterflies showed that some butterflies prefer laying eggs on host plants in sunny habitats, despite higher larval survival in shady habitats, possibly due to increased predation risk (e.g. by spiders) of adults in shady habitats (Rausher, 1979).

THE EFFECTS OF HABITAT SELECTION BEHAVIOR ON POPULATIONS, COMMUNITIES, AND ECOSYSTEMS

Habitat selection by individuals can scale up to dramatically affect population regulation, successional assembly, community structure, species interactions, and ecosystem dynamics (Rosenzweig, 1991; Resetarits, 2001; Morris, 2003; Resetarits et al., 2005; Schmidt et al., 2000; Amarasekare, 2010). In general, habitat selection is expected to reduce spatial variation in fitness across space in stable environments. Theoretically, colonizing individuals will prefer a high-quality patch only until the density within the patch reduces its quality (i.e. available resources) to the level of alternative patches. Thus, while differences in density among patches might reflect initial patch quality, patches that have had enough time to develop populations of an organism might show little variation in quality for the perspective of a colonizing individual (Fretwell and Lucas 1969). In environments that vary over time, organisms may be able to track changes in resource availability or predation risk and thus have populations that are less prone to extinction (Diamond, 1975). While habitat choice may promote regional coexistence as a result of more persistent segregated populations, it is hypothesized to decrease local diversity due to less coexistence at local scales. This pattern of segregation could occur due to preferences for slightly different resources or due to variation among prey species for predator avoidance ability in different habitats (Rosenzweig 1991; Holt 1993).

One aspect of ecosystems that may be particularly sensitive to dispersal behavior is stability and change over time. Habitat selection behavior is predicted to be an important stabilizing factor under scenarios of environmental change, for it can prevent regional extinction by allowing organisms to distribute themselves into habitats of the highest quality despite changes in where high-quality patches occur, and it may allow populations to rebound more quickly after disturbances reduce intraspecific density (Diamond, 1975; Rozenzweig, 1981; Holt, 1987; Rosenzweig, 1991; Holt, 1993, Resetarits, 2001; Resetarits et al., 2005). In addition, density-dependent dispersal should result in decreased population growth rates in high-density patches, and increased population growth rates in low-density patches (Holt, 1993; Amarasekare, 2010). Thus, habitat selection should dampen oscillations in population sizes among linked patches and contribute to the rescue of populations in low-density patches. Despite strong predictions about the importance of habitat selection for stability, these hypotheses have not often been tested with controlled experiments in natural communities.

Several factors complicate the process of habitat selection and its effects. One such factor is individual variation in dispersal behavior. There are costs associated with dispersal, including energy used to move and the risk moving through or into less favorable areas. These costs, along with individual differences in preference, might affect many aspects of dispersal including overall dispersal rates, which individuals (phenotype, condition, life stage, etc.) are more likely to move, and the specific habitats dispersing individuals choose (Hanski and Singer, 2001; Matthysen, 2012). Another complication when predicting the effects of habitat selection is information: habitat selection requires some level of information about the quality of alternative patches. This scale-dependent information-gathering step has received little attention, and analysis of movement paths and the mechanisms of choice are a fruitful area for future research (Matthysen, 2012). Conditional dispersal and lack of information both have the potential to change the predictions of how habitat selection affects populations, communities, and ecosystems. While preference and fitness are usually linked, “ecological traps” involving preference for low-fitness habitats are also possible (Pulliam, 1988; Battin, 2004). This maladaptive behavior might arise when the link between the cue that an organism uses as a surrogate for habitat quality is no longer a good indicator of quality. For example, tree frogs often lay eggs in shallow, warm puddles. These conditions are likely linked with high resource/algae production, but these types of puddles are also prone to drying before the tadpoles have time to develop (Resetarits et al. 2005).

EXPERIMENTAL STUDY SYSTEM

I conduct experiments in artificial outdoor mesocosms that mimic small, ephemeral freshwater ponds or rock pools. Pond-dwelling organisms with active dispersal, such as aquatic insects and amphibians, can often colonize or oviposit in new areas very efficiently; indeed, many of these taxa are obligate dispersers with aquatic larvae and terrestrial or semi-terrestrial adults (Resetarits et al. 2005). Dispersal in this ephemeral system is comparable to foraging or oviposition-site-selection behavior, but it is functionally dispersal as it results in movement of individuals and gene flow among patches (Benton and Bowler 2012b). Mesocosms (such as above-ground plastic aquaria) can be used to recreate communities that approach the complexity of natural systems (Wilbur, 1997; De Meester et al., 2005). Mesocosms are ideal for experimental studies; they allow for increased replication and treatment combinations relative to field studies without the problem of confounding variables like differences in hydrology and other sources of variability in natural systems (Chalcraft et al., 2005).

Mesocosms have been used extensively to study species interactions, colonization, and habitat selection in pond taxa (Wilbur, 1997; Binckley and Resetarits, 2007; Resetarits, 2005). Aquatic insects have been shown to respond to a variety of biotic and abiotic factors, such as competitor and predator density, canopy cover, nutrient levels, and pesticides, during natural colonization from the surrounding environment (Resetarits, 2001; Holyoak et al., 2005; Binckley and Resetarits, 2007; Binckley and Resetarits, 2009; Vonesh and Kraus, 2009; Yee et al., 2009). Thus, pond mesocosms likely provide a very tractable system in which to test the role of habitat selection on stability in changing environments.

CONCLUSION AND RESEARCH GOALS:

A fundamental goal in ecology is to understand the causes of spatial and temporal variation in communities. This understanding has many practical applications: human society depends on ecosystem functions, which in turn depend on community structure (Holyoak et al. 2005, Cardinale et al. 2012). Ecosystem stability is expected to be particularly important in many applications, including the design of reserves, prediction of species responses to disturbance, and the control of pests (Kendall et al., 2000).

Habitat selection is a common, yet underappreciated dispersal strategy that may have far-reaching effects on stability (Morris, 2003; Edelaar and Bolnick, 2012). Thus, studying the effects of habitat selection will increase our basic understanding of ecosystems. In addition, all ecosystems on earth experience changes in physical, chemical, or biological characteristics over time. These changes can have important effects on populations and communities (Row et al. 2014). However, in order to make predictions about how ecosystems will respond in changing environments, it is critical to understand the role of habitat selection in species' responses to change, and how this can alter the stability of ecosystems over time.

While the role of habitat selection on stability has been explored theoretically (Rozenzweig, 1981; Rosenzweig, 1991; Heithaus, 2001; Abrams, 2007; Amarasekare, 2010), there are relatively few empirical studies using natural habitat preference that address this question. The goal of my research is to work towards empirically testing these theoretical predictions about how habitat selection behavior affects stability of communities and ecosystems over time. Specifically, I intend to answer the following questions:

1. Does habitat selection behavior affect spatial asynchrony and population persistence in metapopulations?

2. How does habitat selection affect resistance and resilience of community and ecosystem properties after a disturbance?
3. How does altered resource input timing affect stability in naturally assembling ephemeral pool communities?

Chapter 2: Metapopulations--negative density-dependent dispersal stabilizes snail populations in the face of disturbance

INTRODUCTION

Population sizes are often variable over time, and there is increasing interest in understanding population fluctuations and factors that stabilize these fluctuations (Row et al. 2014). Many factors can cause populations to fluctuate or increase the amplitude of fluctuations, including disturbance and other environmental changes, dispersal dynamics, variation in demographic parameters, and trophic interactions (Berthier et al., 2014). Theoretical work has shown that increasing amplitude of fluctuations is, in general, destabilizing, resulting in increased risk of population extinction (Holling, 1973; Hanksi and Simberloff, 1997). However, empirical studies relating population fluctuations to extinction risk do not always show a relationship (e.g. Schoener and Spiller, 1992), likely due to factors such as starting population size and interconnectivity with other populations (Hanski, 1998; Green, 2003).

Local populations that are interconnected by dispersal (metapopulations) have long been recognized as being demographically linked, with changes in one patch affecting other patches (Levins, 1969; Hanski, 1998). Local populations can go extinct, but subsequent recolonization from surrounding patches can occur. This extinction-colonization balance maintains the stability of the metapopulation if patches vary asynchronously (i.e. they do not all experience low density at the same time; Hanski, 1998). One factor that promotes asynchrony among populations is dispersal behavior.

Theoretical work has often suggested that dispersal behavior, especially density-dependent dispersal, can contribute to asynchrony of fluctuations in population sizes among different patches (Holt, 1987; Holt, 1993; Heithaus, 2001; Morris, 2003b; Abrams, 2007). Density-dependent movement usually results in decreased population growth rates in high-density patches, and increased population growth rates in low-density patches (Holt, 1993; Amarasekare, 2010). In other words, density-dependent dispersal tends to be negative, presumably as a strategy for avoiding intraspecific competition, and the per capita dispersal rate from one patch to another is expected to depend on the density of individuals in each population relative to resource levels in each patch (Fretwell and Lucas, 1969). At a metapopulation scale, this type of dispersal will contribute to dampening large oscillations and preventing local extinctions via rescuing populations in low-density patches. Therefore, asynchrony in populations can stabilize the dynamics of individual patches in addition to the entire metapopulation.

Density-dependent dispersal can arise via different mechanisms that vary with assumptions about the ability of organisms to gather information about their environment. Organisms might be able to sense their resources and their competitors, distributing themselves in a way that tends to maximize resource capture. This “cognitive navigation” or “interactive habitat selection” has received considerable attention (Fretwell and Lucas, 1969; Farnsworth and Beecham, 1999; Resetarits et al., 2005). Alternatively, organisms might simply move randomly, with movement away from high density resulting from these random walks in a process analogous to diffusion (Farnsworth and Beecham, 1999; Cantrell et al., 2008).

One way to possibly distinguish these different mechanisms involves isolating different aspects of dispersal. Dispersal is a multi-step process that includes emigration, transit, and immigration (Matthysen, 2012). If organisms are moving through a random diffusion process, one would expect emigration to be density-dependent: there would be more dispersal out of high-density patches and less dispersal out of low-density patches, resulting in a net movement from high density to low density driven by differences in emigration. However, if organisms are moving as a result of a cognitive choice based on their resources or competitors, then both the emigration and immigration stages can be density-dependent: the organisms both avoid high density and prefer low density when they move (Cantrell et al., 2006). Density-dependent dispersal via either of these mechanisms is likely to be stabilizing, but habitat selection (i.e. choosing to move away from high density and toward low density) is expected to be a faster, more efficient stabilizing force than diffusion (Cantrell et al., 2008).

Here, we report the results of a controlled mesocosm experiment in which the dispersal behavior of the aquatic snail *Physa acuta* (syn. *Physella acuta*) was manipulated in the presence of stochastic disturbance events. *P. acuta* is very active; measurements of movement rates of this species indicate that an individual can travel 20-40 m per day (Kappes and Haase, 2012). Like most pulmonate snails, *Physa* are simultaneous hermaphrodites, and thus do not show sexual dimorphism in dispersal rates. These snails are grazers of periphyton, detritus, and bacteria on surfaces (Pyron and Brown, 2015). *Physa* have been shown to respond to higher resource densities by increasing activity levels (Wojdak, 2009), and so they must have the ability to sense the amount of resources available to them. They also change microhabitats based on olfactory predator cues, with different responses for different predators (Turner et al. 1999). While snail populations are impaired by food limitation (e.g. Eisenberg, 1970), it is unclear whether *Physa* can detect conspecific density (Henry et al., 2006), or whether freshwater snails simply have directed movement toward greater densities of resources (e.g. Bovbjerg, 1968; Cameron and Carter, 1979).

Our dispersal manipulations were applied at the scale of replicate metapopulations, each with four patches. Three dispersal treatments were employed: no dispersal, choice, and diffusion. We predicted that landscapes with no dispersal would show the least stability, that choice landscapes (snails choose dispersal direction) would show the most stability, and that diffusion treatments (emigrating snails randomly assigned to destination patch) would show intermediate levels of stability. While the role of dispersal behavior on community structure has received considerable empirical attention (e.g., Resetarits et al. 2005), the effects of dispersal rates and behavior on temporal dynamics and stability of populations have been addressed with controlled experiments much more rarely (Ohgushi, 1995; Howeth and Leibold, 2010; Steiner et al., 2011).

METHODS

We conducted an experiment in systems of aquatic mesocosms that allow manipulation of dispersal of the aquatic snail *Physa acuta*. Each system of mesocosms (landscape) consisted of four artificial pools that were either connected by corridors or not (Figure 2.1). The mesocosms were made from plastic boxes that were 28 x 15 x 11.5 cm, with a total volume of approximately 4.8 L. In connected landscapes, corridors were built connecting all four patches using square vinyl pipes that were 40 x 8 x 6 cm. Hot glue was used to create a water-tight seal between the pipes and the mesocosms. Each corridor also received a piece of window screen with 2 mm mesh glued in the center, which prevented movement of snails among patches, but allowed water and chemical cues to diffuse from one patch to another. All landscapes were constructed in an evaporation-cooled greenhouse at UT's Brackenridge Field Laboratory (BFL) in Austin, TX.

Mesocosms were established on 3 June 2018. Each landscape was filled with rainwater collected from the roof of BFL buildings. To control for differences in total volume caused by corridors, patches in unconnected landscapes were filled to different depths to ensure that each patch had an approximate total volume of 3.4 L in all treatments. To control for differences in surface area and materials caused by corridors, pieces of vinyl pipe with hot glue were added to unconnected mesocosms, adding approximately 320 cm^2 of substrate surface area to these patches (the amount of underwater surface area in the corridors of a connected patch). To provide a food source for the snails, each patch received a 400 mL aliquot of pond water with its associated algae collected and mixed from four different *Physa*-containing ponds at BFL. In addition, *Quercus fusiformis* leaf litter and its associated periphyton were collected from one *Physa*-containing pond, and 5 g ± 0.2 g wet weight of this litter was added to each patch.

On 7 June 2018, a population of 10 individuals of *Physa acuta* was introduced into each patch. The density of snails in each patch falls within the range of observed densities in the field (pers. obs.). These snails were obtained from a single source pond at BFL, and ranged in size from about 5-8 mm. Environmental change was introduced to all landscapes via disturbance. Every 3 days, one of the four patches in each landscape picked with a random-number generator was subjected to a disturbance in which half of the snails were removed. To achieve this, all the snails in the patch were counted, and half of the individuals were removed haphazardly. If there was an odd number of snails in a patch, a coin flip was used to decide whether to round down (heads) or up (tails) when removing half of the individuals. Snails that died or were found aestivating above the water line were replaced with active individuals.

Three different experimental treatments were imposed based on snail dispersal behavior: no dispersal, diffusion, and habitat choice. In the “no dispersal” treatment, patches were not connected by corridors, and were spatially independent. In both diffusion and choice landscapes, the four patches were connected with corridors forming a square landscape with no diagonal connections (Figures 2.1 and 2.2). In connected landscapes, snails were free to move into the corridor connecting one patch to another, but they were prevented from entering the neighboring patch by the window screen in the center of the corridor. We assumed that if snails could actively sense and respond to higher resource levels in a neighboring patch, they would spend more time in the corridor connecting their patch to the one with higher resource levels. In the “habitat choice” treatment, snails that were found in the corridor connecting their patch with a neighboring patch at the time of sampling were moved to their chosen patch. In the “diffusion” treatment, snails leaving their patch in either corridor were collected, and a coin toss was used for each individual to determine which of the two connected patches it would be moved to (Figure 2.2). Dispersal events took place 3 days after the previous disturbance event. After dispersal events, the snails in each patch were counted, and then the next disturbance event was applied later the same day.

In order to explore population stability, snail population size in each patch was measured 3 days after the previous disturbance event and immediately after colonization manipulation. Two aspects of stability were explored: spatial asynchrony among patches and local population persistence. Spatial asynchrony was estimated via measurement of the variation in population size (N) among patches in a landscape in each treatment. This among-patch variation was estimated using both the range in population size (N Range = highest N minus lowest N in each landscape) and coefficient of variation (N CV = variance in N divided by mean N in each landscape). Local population persistence was measured by calculating the mean amount of time until the first local extinction for each treatment. We predicted that landscapes with no dispersal would be the most unstable, with more variation among patches and faster time to local extinction, since this treatment had no mechanism to dampen population fluctuations caused by disturbance or rescue patches with low density. We predicted that choice landscapes would show less variation among patches in population size relative to landscapes with diffusive dispersal, due to density-dependent immigration dampening variation in population size. We also predicted that landscapes with choice would show longer population persistence times than diffusion, since diffusive dispersal may, by chance, result in more clumped distributions across the landscape that are more susceptible to stochastic extinctions.

Attempts were made to measure periphyton abundance during the experiment, but these attempts failed. These efforts included measuring the weight of periphyton growing on flagging tape introduced at the beginning of the experiment and photographing the corridors connecting the patches at the end of the experiment to analyze the amount of green in the image. The weight of periphyton on flagging tape was outside the range of measurements of the balances available at the time. In the image analysis, variability in the amount of light affected the exposure of the photos, affecting the intensity of greenness. The algae in the corridors clearly varied with snail density during the experiment (Figure 2.3) but varied much less by the end of the experiment when the snail populations were dwindling.

The effects of time and treatment on N Range and N CV were explored using repeated-measures ANOVA. Time to first local extinction in each treatment was compared using ANOVA. Significant overall effects were further explored with pairwise comparisons, using the Benjamini and Hochberg (1995) false discovery rate (fdr) correction for multiple comparisons. All analyses were performed in R version 3.5.1.

RESULTS

The average range of population sizes in each landscape (N Range, Figure 2.4) varied significantly with both time and treatment (overall time*treatment effect: $F_{34,153}$=3.847, p = $5.57*10^{-9}$). Pairwise comparisons indicate that “no dispersal” treatments had significantly higher N Ranges than both “choice” and “diffusion” treatments on days 11 and 17-30 (fdr-adjusted $p < 0.04$). The choice and diffusion treatments only differed on day 3 and day 11, with diffusion treatments showing a higher N Range than choice treatments (fdr-adjusted $p = 0.010$ and 0.014 respectively, all other times $p > 0.09$).

The average coefficient of variation in population size (N CV, Figure 2.5) also varied with both time and treatment (overall time*treatment effect: $F_{34,153}=3.168$, $p = 6.84*10^{-7}$). Pairwise comparisons indicate that “no dispersal” treatments had significantly higher N Ranges than both “choice” and “diffusion” treatments on days 17-36 (fdr-adjusted $p < 0.05$). The choice and diffusion treatments only differed on day 3, day 11, and day 42, with diffusion treatments showing a higher CV than choice treatments (fdr-adjusted $p = 0.012$, 0.017, and 0.025 respectively, all other times $p > 0.08$).

The time to the first local extinction (Figure 2.6) varied significantly among treatment ($F_{2,9}=22.96$, $p=0.0003$). The no dispersal treatment had significantly shorter time to first local extinction than the choice treatment (fdr-adjusted $p=0.032$), and the diffusion treatment showed an intermediate time to first local extinction (diffusion vs. choice—fdr-adjusted $p = 0.103$, diffusion vs. no dispersal—fdr-adjusted $p = 0.060$).

DISCUSSION

The results indicate that independent populations of snails were much less stable than metapopulations with dispersal in the face of disturbance: landscapes with no dispersal had more variability in population size among patches and experienced local extinction faster. This result highlights the importance of density-dependent dispersal for stability. Because snails tended to move away from high density, dispersal stabilized fluctuations in population size and contributed to increasing the persistence of local populations. This result corroborates the predictions of various arguments (Hansson, 1991; Hanski, 1998; Bowler and Benton, 2005), mathematical models (Rohani et al., 1996; Saether et al., 1999; Amarasekare, 2010; Hauzy et al., 2010; Abbott, 2011), and other experiments (den Boer, 1970; Otronen and Hanski, 1983; Gonzalez et al., 1998; Gundersen et al., 2002) showing the effects of dispersal on stability in metapopulations. It is important to note that the effect of dispersal *per se* on population stability may depend on the rate of dispersal or the degree of connectivity among patches: if patches are so highly connected that their populations vary synchronously, dispersal may be destabilizing (Hanski and Woiwood, 1993; Kendall et al., 2000; Bowler and Benton, 2005; but see Abbott, 2011). However, negative density-dependent dispersal per capita will tend to promote asynchronous dynamics in population size across patches, and thus should be stabilizing in most circumstances (Saether et al., 1999; Bowler and Benton, 2005; Amarasekare, 2010). Therefore, in order to predict the effects of connectedness on population viability (e.g. for conservation applications), it is important to consider whether dispersal is density-dependent (Morris, 2003a).

The differences between choice treatments (where directed immigration was allowed) and diffusion treatments (where immigration was undirected) were more subtle. As predicted, snail populations in choice treatments tended to be slightly more stable (less variable and experiencing local extinction more slowly). However, the small magnitude of the difference as well as the limited extent of difference over time suggest that snails may not strongly direct their immigration toward lower conspecific density. Freshwater snails can sense and respond to chemical cues (e.g. Turner et al., 1999; Pyron and Brown, 2015). Bovbjerg (1968) showed that freshwater snails can detect and move toward some particularly nutritious resources at scales like the scale of our experiment. *Physa* has been shown to delay self-fertilization in favor of outcrossing at low density, and so it is possible that they could sense conspecific density in that context. However, experiments placing snails in water collected from rearing tanks at different densities have suggested that *Physa* does not seem to use chemical cues alone for this purpose (Henry et al., 2006). The minor difference between the choice and diffusion landscapes in our experiment may not represent preferential immigration at all; the difference could be explained by an increase in activity (Wojdak, 2009), or slightly higher residence times in corridors connected to patches with more resources/lower density (Farnsworth and Beecham, 1999; Bartumeus et al., 2005).

The cues used for directed dispersal and the perceptual range for these cues is an open question for most taxa (Lima and Zollner, 1996; Bowler and Benton, 2005). Many vertebrates are expected to have sophisticated responses to conspecific density, social factors, and resource levels, but invertebrates might vary more in their responses to these cues (Hansson, 1991; Bowler and Benton, 2005). Some invertebrates are able to sense and respond to resources at relatively large scales (e.g. detection of host plants 85m away in a butterfly; Conradt et al., 2001), but other taxa seem to have limited ability to sense resources at large scales, and may respond more strongly to density-independent cues such as weather (Fahrig and Paloheimo, 1987; Hansson, 1991; Bowler and Benton; 2005). Still, our results suggest that even in scenarios where immigration is undirected or only slightly directed, dispersal can still show negative density-dependence and be a stabilizing force relative to landscapes with no dispersal.

In environments that vary over both space and time, models predict the evolution of conditional dispersal strategies, where organisms move in a directed fashion toward higher density of resources (McPeek and Holt, 1992; Belgacem and Cosner, 1995; Cosner and Lou, 2003; Cantrell et al., 2006). This strategy might evolve because individuals who can detect and move toward resources would likely have a competitive advantage, and therefore a selective advantage, over individuals that cannot. However, dispersal is not only about food resources. The evolution of dispersal (rate, movement patterns, etc.) likely represents a balance of various interacting selective forces including inbreeding avoidance, social interactions, kin interactions, and habitat variability (Bowler and Benton, 2005; Matthysen et al., 2012). Therefore, taxa are likely to vary in their responses to density. Some taxa even show positive density-dependent dispersal.

Positive density-dependent dispersal, aka conspecific attraction, can be common, especially when population sizes are very small (Smith and Peacock, 1990; Roland et al., 2000). Scenarios where conspecific individuals may disperse toward areas of higher density could be caused by decreased efficiency foraging or finding oviposition sites, decreased defense against predators, or difficulty finding mates at low densities (Kuussaari et al. 1998; Parrish and Edelstein-Keshet, 1999), analogous to an “Allee effect". Positive density-dependent dispersal might contribute to large shifts in population sizes and reduced viability of metapopulations since it promotes extinction in low-density patches and synchronous population increases in high-density patches (Saether et al., 1999; Bowler and Benton, 2005), but it may also contribute to spatial coexistence when species interactions have strong effects on population demography (Huxel and McCann, 1998). Therefore, knowledge of whether and how species move in relation to density can help predict whether dispersal is expected to be stabilizing. In general, when dispersal tends to result in more even distributions of abundance relative to carrying capacity among patches (as in negative density-dependent dispersal), then dispersal is expected to be stabilizing (Kindvall and Petersson, 2000).

It is unclear whether the results of this population-level experiment might extend to metacommunities of interacting species. Negative density-dependent dispersal in response to density of competing species has been shown in some taxa (e.g. Grosberg, 1981; Denno and Roderick, 1992). This type of dispersal may lead to asynchrony and compensatory dynamics between multiple species (Cottingham et al., 2001; Loreau and Mazancourt, 2013). Given that dispersal behavior may have important implications for species coexistence (e.g. Schmidt et al., 2000; Grand, 2002; Křivan and Sirot, 2002; Amarasekare, 2010), there may thus be an interaction between habitat selection, coexistence, and stability (Tessier and Leibold, 1997; Haegeman and Loreau, 2014). Inclusion of multiple trophic levels adds further complications. If a predator was used in our experiment to remove individuals rather than a manual disturbance, dynamics may be much different. Choice behavior may result in more clumped distributions relative to random dispersal, due to the combined effects of consumptive removal and non-consumptive avoidance on population sizes within each patch (positive density-dependent dispersal as a result of predator avoidance). This may leave patches even more sensitive to disturbance, and if a predator is highly mobile relative to the prey, choice behavior may actually be de-stabilizing (Abrams, 1999; Abrams and Ruokolainen, 2011; see Chapter 3).

Habitat fragmentation as a result of human activities has caused dramatic changes in regional landscapes across the globe, and this fragmentation is a major conservation concern (Kindlmann and Burel 2008). Because fragmentation results in smaller patch sizes, it is expected to lead to smaller population sizes within the patches, resulting in higher extinction rates, lower dispersal rates, lower diversity, increased sensitivity to environmental and demographic stochasticity, and increased inbreeding depression (MacArthur and Wilson 1967, Simberloff 1988). Connectivity among patches by dispersing individuals can help overcome these problems (MacArthur and Wilson 1967, Kindlmann and Burel 2008), but connectivity might not always be stabilizing (Hanski and Woiwood, 1993; Kendall et al., 2000). Our experiment suggests that negative density-dependent dispersal is a strong stabilizing force even in the absence of strongly directed immigration. While this type of dispersal is common across a wide variety of taxa (Bowler and Benton, 2005), it is not universal (e.g. Kuussaari et al. 1998). In order to predict whether connectivity is important for the stability of populations, it is important to consider how species move relative to population density.

Figures and Tables

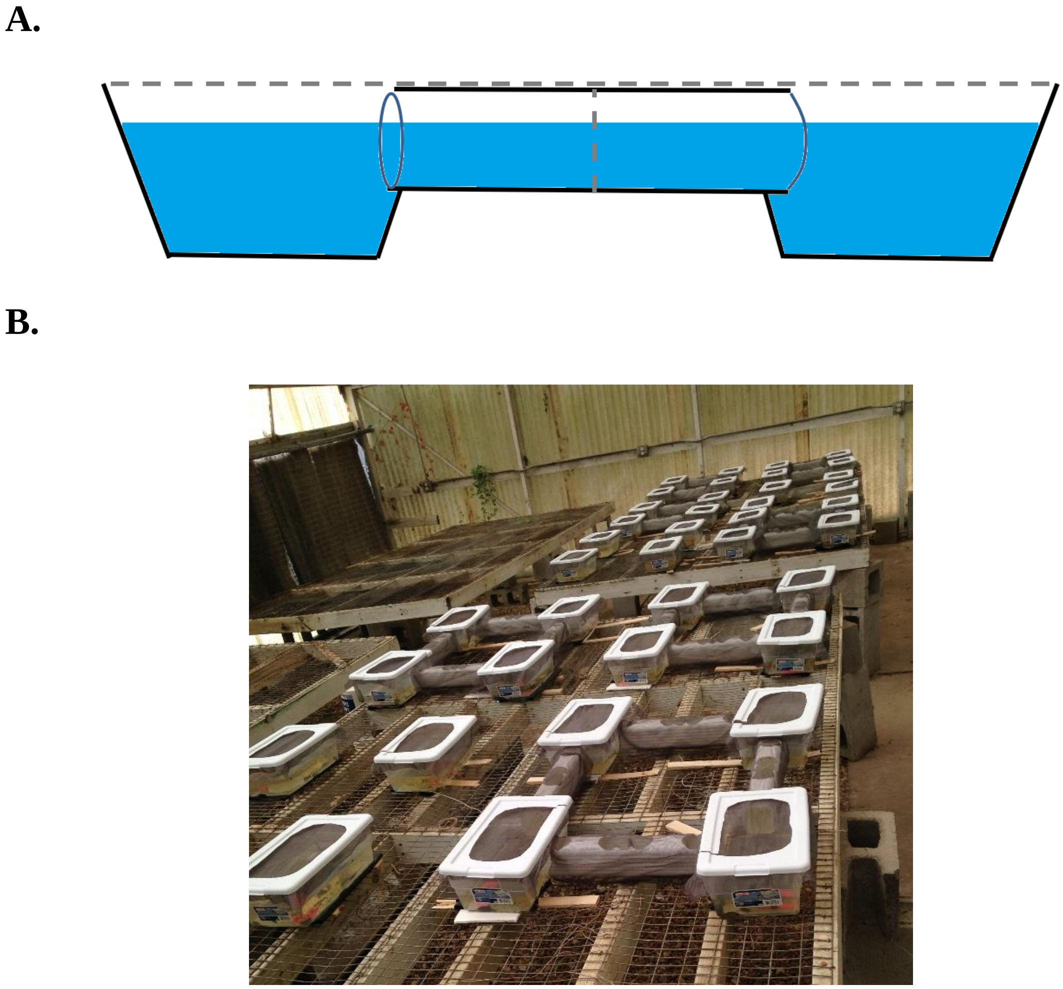
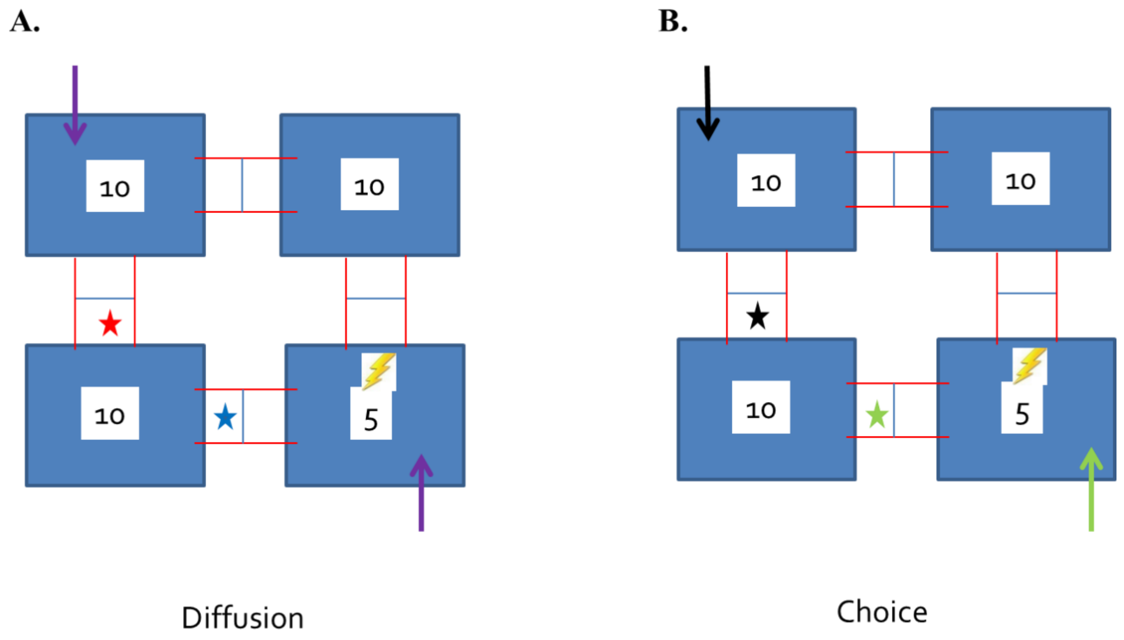


Figure 2.1: Mesocosm design. Panel A is a diagram showing the connections between two of the four patches in a connected landscape. Panel B is a photo of the experimental array, showing both connected and unconnected landscapes.



Diffusion

Choice

Figure 2.2: Diagram showing the different methods for the "diffusion" and "choice" treatments (Panel A. and B. respectively). Abundance of snails in each patch is represented by the number in the center of the patch. In this example, the lower right patch in both landscapes was disturbed, and the diagram shows the movement of snails from the lower left patch. In the diffusion treatment (A.), the snails moving out of the lower left patch in both directions (blue and red stars) are collected, and each individual is randomly assigned to one neighboring patch or the other (purple arrows indicating mixture of colonists from both emigrant pools). In the choice treatment (B.), the snails moving toward a neighboring patch are moved into that patch (immigrants match each different emigrant pool).

Figure 2.3: Photograph showing the variation in periphyton (algae growing on surfaces) in a corridor connecting a patch with low snail density (top) to a patch with higher snail density (bottom).

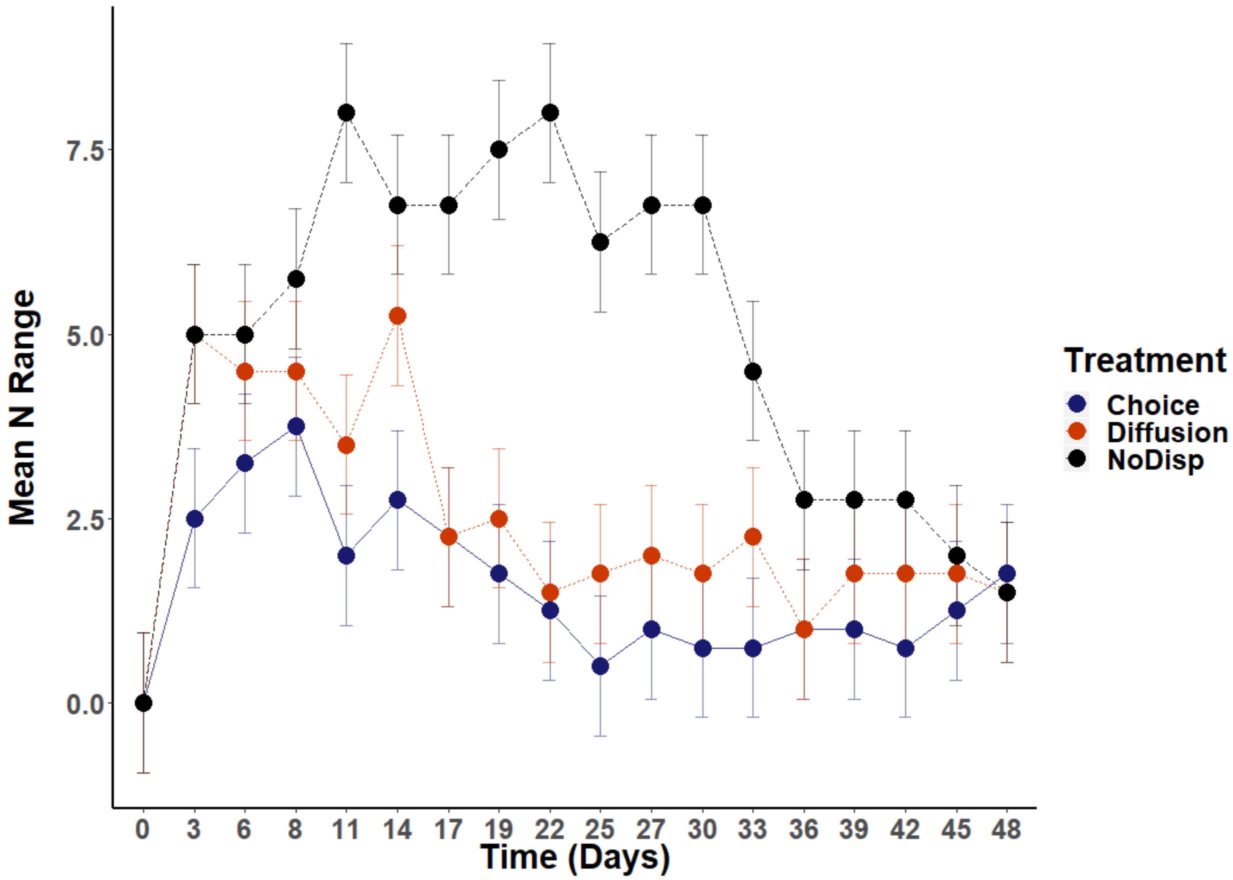


Figure 2.4: Average range in patch population size (mean ± Fisher's LSD) within each type of landscape over time. Landscapes with no dispersal showed greater range in population size during the middle of the experiment relative to landscapes with dispersal, indicating uneven distributions of abundance. Choice landscapes had lower N ranges than diffusion landscapes, but only at a few sampling points.

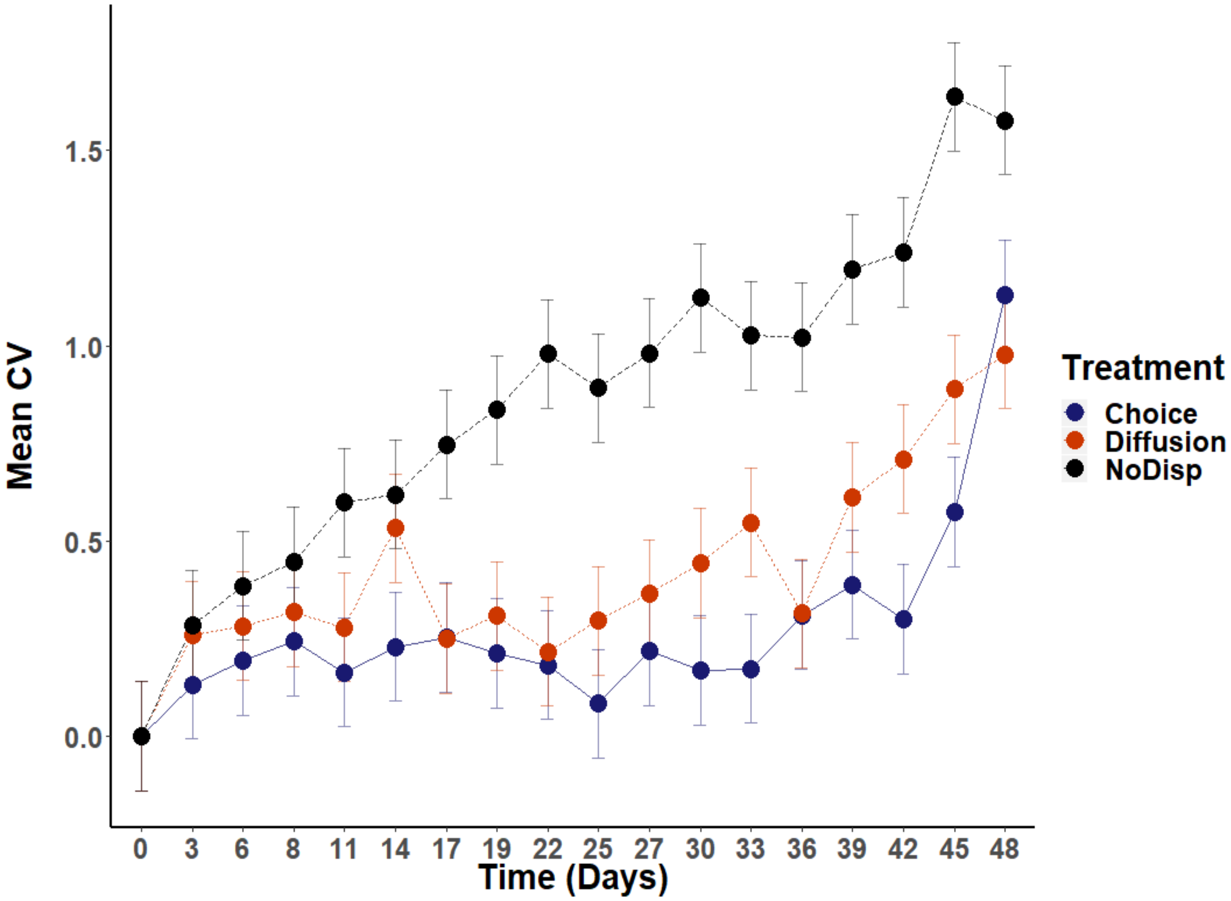


Figure 2.5: Average CV in patch population size (mean ± Fisher's LSD) within each type of landscape over time. Landscapes with no dispersal showed greater CV in population size during the middle of the experiment relative to landscapes with dispersal, indicating uneven distributions of abundance. Choice landscapes had lower CV than diffusion landscapes, but only at a few sampling points.

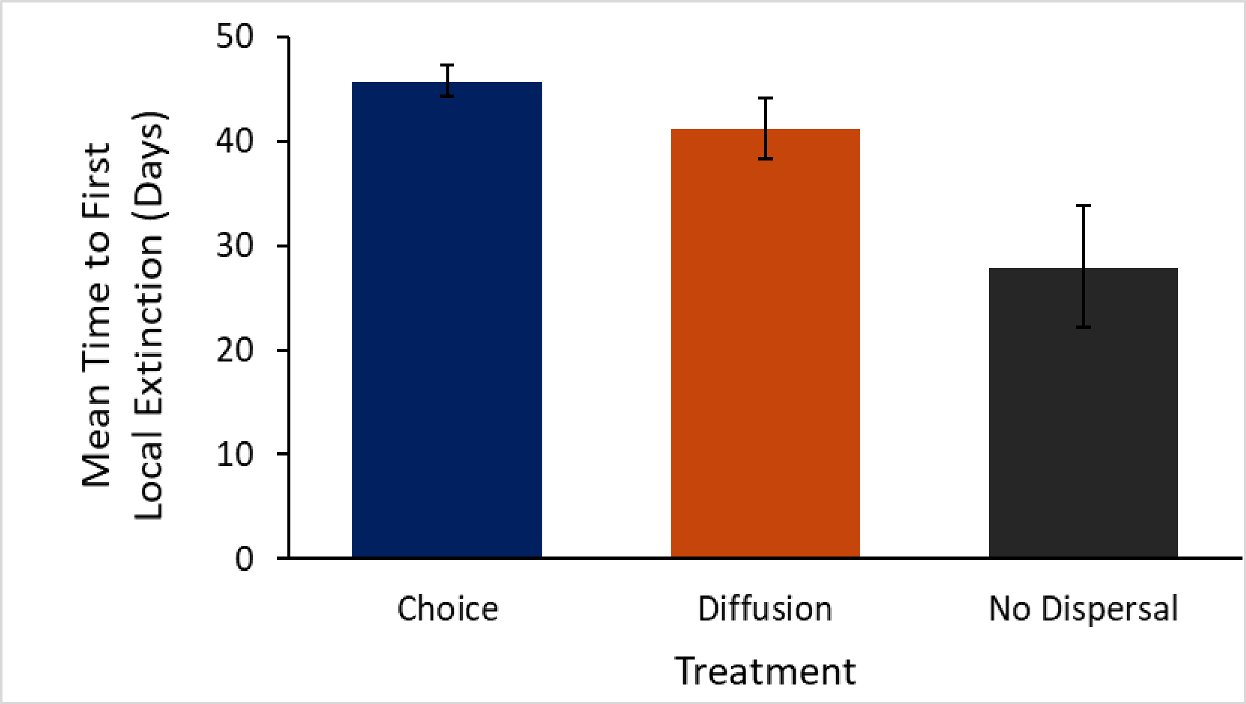


Figure 2.6: Average time to first local extinction in each type of landscape. Landscapes with no dispersal had significantly shorter time to first local extinction than choice landscapes. The diffusion landscapes had intermediate values for time to local extinction: they did not differ statistically from either the no dispersal landscapes or the choice landscapes.

Chapter 3: Metacommunities--Non-random colonization affects resistance and resilience

INTRODUCTION

Habitat choice behavior is predicted to be an important stabilizing factor under scenarios of environmental change. It can prevent regional extinction by allowing organisms to distribute themselves into habitats of the highest quality despite changes in where high-quality patches occur, and it may allow populations to rebound more quickly after disturbances reduce intraspecific density (Diamond, 1975; Rozenzweig, 1981; Holt, 1987; Rosenzweig, 1991; Holt, 1993, Resetarits, 2001; Resetarits et al., 2005). In addition, density-dependent dispersal should result in decreased population growth rates in high-density patches, and increased population growth rates in low-density patches (Holt, 1993; Amarasekare, 2010). Thus, habitat choice should dampen oscillations in population sizes among linked patches and contribute to the rescue of populations in low-density patches.

The effect of habitat choice on populations might scale up to influence community and ecosystem stability as well. If species experience more intraspecific competition than interspecific competition or interact weakly with their resources, more stable individual populations might promote stable coexistence and higher species diversity (McCann et al., 1998; Kokkoris et al. 1999; Chesson, 2000). Biodiversity itself has been shown to affect the stability of ecosystem attributes such as resilience and resistance to disturbance as well, linking community and ecosystem dynamics (e.g. Downing and Leibold, 2010).

One aspect of stability in communities and ecosystems is resilience, or the ability of the system to recover after a disturbance (Downing and Leibold, 2010). The resilience of an ecosystem, in part, depends on how quickly organisms recolonize the disturbed habitat, which in turn depends on connectivity among patches in a metacommunity. If organisms prefer to colonize disturbed communities, then their behavior might increase the resilience of community and ecosystem processes: communities may recover faster than expected compared to a system in which organisms move randomly. Individuals may display this preference for previously disturbed, low-density communities due to less competition and/or more resource availability. This type of negative density-dependent dispersal has been shown for both avoidance of intraspecific competition (e.g. breeding birds, Fretwell and Lucas, 1969); and interspecific competition (e.g. sessile marine invertebrates, Grossberg, 1981).

Resistance is defined as the ability of the ecosystem to remain unchanged by a disturbance. The effects of dispersal behavior on resistance may depend on the nature of the disturbance. Any event that results in the removal of biomass can be considered an ecological disturbance, but the cause of this removal (e.g. predation versus physical stress) may result in different outcomes (Rykiel, 1985). If the disturbance is caused by something that the colonizing individuals can detect and avoid, habitat choice may lower resistance, compounding the effects of disturbance. This might happen because the disturbance reduces density by removing individuals from patches (i.e. consumptive effects), but also reduces density via reducing immigration (i.e. nonconsumptive effects).

However, if the cause of the disturbance cannot be detected by dispersing individuals, habitat choice should not affect resistance.

Measurements of community and ecosystem properties in disturbed versus undisturbed communities can be used to explore resistance and resilience. Resistance can be viewed as the amount of initial displacement away from undisturbed conditions when a community is disturbed, with more displacement corresponding to less resistance. Resilience can then be measured as the rate at which disturbed communities converge back toward the properties of undisturbed communities (Downing and Leibold 2010). It is useful to calculate the proportional difference (PD) between undisturbed and disturbed measurements in order to standardize these measurements across multiple replicates in an experiment. Here, we report the results of a controlled experiment in artificial ponds testing whether manipulated differences in dispersal behavior of aquatic insects affect resistance and resilience of various community and ecosystem properties. Following Downing and Leibold (2010), we used linear regressions on the PD data to explore both the degree of displacement after the disturbance and the rate of convergence back toward control values for response variables after the disturbance. Using fish predation as a disturbance and considering that aquatic insects have been shown to avoid fish cues (e.g. Resetarits et al., 2005), we predict that habitat choice will increase resilience, but decrease resistance relative to random dispersal. Our predictions for how habitat choice will affect resistance and resilience are illustrated in Figure 3.1.

METHODS

A factorial mesocosm experiment was conducted at Brackenridge Field Laboratory in Austin, TX to determine the effects of colonization behavior and disturbance on aquatic insect communities. Aquatic insects have been shown to respond to a variety of biotic and abiotic factors, such as competitor and predator density, canopy cover, nutrient levels, and pesticides, during natural colonization from the surrounding environment (Resetarits, 2001; Holyoak et al., 2005; Binckley and Resetarits, 2007; Binckley and Resetarits, 2009; Vonesh and Kraus, 2009; Yee et al., 2009). Mesocosms have been used extensively to study habitat choice in pond taxa (Resetarits, 2005; Binckley and Resetarits, 2007), and they provide a tractable system for controlled factorial experiments (Chalcraft et al. 2005).

Mesocosms were established March 10, 2014, and each mesocosm was filled with 300L of well water and inoculated with 800 ml of concentrated pond water and 250 g of pine needles, which served as a source of nutrients and substrate. The ecosystems were given 81 days to develop via natural colonization and oviposition of aquatic insects. Two factors were manipulated over the course of the experiment: disturbance (presence/absence) and habitat choice behavior (presence/absence), for a total of 4 treatments (Figure 3.2a). Six replicates of each treatment were established in a 2 by 3 block structure, with treatments within each block assigned using a random number generator.

The disturbance was a pulse of predation by juvenile green sunfish (*Lepomis cyanellus*). A single sunfish was introduced into the disturbed tanks on day 81 (total length mean + SE: 7.75 ± 0.21 cm). The fish were removed after 14 days. Fish affect insect communities via consumptive effects on density, and via nonconsumptive effects when colonists can choose to avoid mesocosms with fish.

Habitat choice behavior was manipulated using fiberglass screens which covered each mesocosm, with the center of the screen weighted down into the water to allow colonization on top of the screen (sensu Binckley and Resetarits, 2007; Vonesh et al., 2009). These methods allowed control over whether individuals were choosing where to colonize naturally or whether individuals were randomly assigned to the disturbed and undisturbed treatment in each block. In the “choice” treatment, the colonist insects on top of the screen were counted and then placed under the screen of their chosen mesocosm. In the “random” dispersal treatment, the colonists from different disturbed and undisturbed mesocosms within each block were mixed together in a water sample, then the sample was split in half with a plankton splitter wheel (Figure 3.2b). Each randomized sample was haphazardly placed under the screen of the disturbed or undisturbed mesocosm from which the colonists were collected. These treatments represent two different dispersal scenarios. The choice treatment represents the natural colonization behavior of the insects, where they are free to choose where to colonize and oviposit. The random treatment represents a scenario in which there is variation in disturbance across the landscape, but insects cannot detect this variation and their movements are undirected. In these scenarios, we assume that variation in colonist abundance is driven by preferences of the pool of actual colonists. If individuals have a preference, then colonists are concentrated in the preferred habitat and diluted in the undesirable habitat. Random dispersal can thus be simulated by mixing colonists in preferred and undesirable habitats.

Response Variables

Our response variables include a variety of community and ecosystem properties. The main variables of interest were total abundance and morphotype/species richness (hereafter just “richness”) of insects in each mesocosm. To explore the mechanism of changes in richness and abundance within each mesocosm, the abundance and richness of insect colonists arriving to each tank were assessed as well. We also measured total productivity and total respiration estimated by measuring changes in dissolved oxygen concentrations. The colonist and resident community composition of aquatic insects, productivity, and respiration in each mesocosm was estimated once per week starting at the onset of the disturbance (Week 6) and continuing until the end of the experiment (Week 10). Samples of the assemblage of insects (hereafter “insect community”) were attempts at censusing the entire community of all individuals larger than 2 mm. Water was collected from each tank into 2 or more 5-gallon buckets, and then a net with 2 mm mesh was used to sweep through the mesocosms until 10 consecutive sweeps had no insects. Insects and detritus were placed into the buckets of water, then insects were counted and identified to the lowest level possible without magnification and placed back into the mesocosm. If abundance for a given species exceeded 100 individuals, the abundance was recorded as 100.

Productivity and respiration were measured using daily cycles of dissolved oxygen (DO) concentration following Downing and Leibold (2010). These measures were an attempt to include a response variable at the whole-ecosystem scale to see whether changes in the insect community impact the function of ecosystems. DO in these ecosystems depends on physical factors such as temperature and wind, but also upon the respiration and productivity of the organisms in the mesocosms, with phytoplankton contributing the most to both respiration and productivity (Downing and Leibold, 2002; 2010). Given that all mesocosms were in the same place, differences in DO among the mesocosms must be primarily driven by differences in the productivity and respiration of the organisms, rather than by physical factors. DO tends to be highest in lentic waters about 30 minutes before sunset as a result of accumulating oxygen levels from primary producers during the day as a result of the light reactions of photosynthesis. DO levels tend to be lowest about 30 minutes before sunrise as community respiration has continued in the absence of oxygen production in the dark. DO was measured using a Eureka Manta II multiprobe. Respiration rates were calculated as the rate of DO loss per hour between sunset and sunrise on one day per week. Productivity rates were calculated as rate of DO increase per hour between sunrise and sunset of the next consecutive day. Both measures provide an estimate of respiration and productivity of all organisms, with respiration rate encompassing the gross rate of all organisms and productivity representing a net value (gross productivity minus the respiration of all organisms). While these variables are related and depend on overall dissolved oxygen levels, each corresponds to different ecosystem processes that were measured independently (i.e. different daily cycles) each week.

Data Analysis

A repeated-measures ANOVA was used to examine how time and treatment affected each response variable directly, as in Figure 3.1a. Note that the control treatment was the treatment with natural colonization and no disturbance. The undisturbed treatment with random colonization, while measured, was excluded from all analyses: that treatment only existed as a means to randomize the colonization in the "random" treatment. When significant effects were found, pairwise comparisons with Bonferroni corrections were used to determine which groups differed.

In addition to the direct analysis of response variable dynamics among treatments, resistance and resilience were calculated directly using linear regressions of the proportional difference between the control and treatment tanks following Downing and Leibold (2010; see Figure 3.1b). These calculations consisted of taking the average value of the response variable for the undisturbed, natural colonization treatment (control), and subtracting the value of the response variable for each treatment tank for each time step after the disturbance. Linear regression was used to calculate resistance (extent of initial displacement) and resilience (convergence slope) for all 6 replicates of each treatment. Given the formula for the linear regression of proportional difference (PD = a*time + b), displacement can be calculated by the absolute value of the y-intercept (b). Resistance can be calculated as 1 – displacement, since more displacement means less resistance.

The convergence slope can be calculated as -1*(sign of b)*a. After calculating these values of displacements and convergence slopes, t-tests were used to compare the random-colonization disturbed and choice-colonization disturbed treatments. All univariate analyses were performed in R version 3.5.1.

Multivariate analyses were also used to compare community structure among our treatments. These comparisons were achieved using PERMANOVA (Permutational multivariate ANOVA) on a Bray-Curtis dissimilarity matrix of all samples in Primer–E ver. 6 (Clarke and Gorley 2006). We square-root transformed the abundance data before analysis: the square root transformation weakens the influence of the most abundant species on observed differences, and this transformation is recommended when comparing abundance data (Clarke and Warwick 2001). These data were visualized using NMDS on the Bray-Curtis dissimilarity matrix. In addition, the taxa that contribute most to the observed dissimilarity among times and treatments were explored using the SIMPER (similarity percentages) procedure in Primer-E. The SIMPER results can be used to determine which specific taxa contribute most to any observed differences in community composition. It lists the taxa that differ most in abundance among the groups of communities that are being compared, and it tells how much each taxon contributes to observed dissimilarity among the communities (Clarke and Gorley 2006).

RESULTS

The results indicate that fish disturbance resulted in fewer colonist insect species, and this lower colonist richness was successfully eliminated by randomization of colonization, resulting in fewer colonist species in the Choice treatment than in either the Random or Control treatment (Figure 3.3A, Table 3.1). Colonist abundance decreased over time, and was unaffected by treatment (Figure 3.3B, Table 3.1). In the census samples, treatment interacted with time to affect species richness: the Choice treatment had fewer species than the Control treatment when the fish were present in Week 8. Census richness in the Random treatment was intermediate between the Control and Choice treatments at that time (Figure 3.4A, Table 3.1). Census abundance was affected by time, with lower abundance in all communities later in the experiment than near the beginning. Census abundance was unaffected by treatment, however (Figure 3.4B, Table 3.1).

Productivity and respiration were both affected by a treatment*time interaction. Treatments with fish tended to have higher productivity and respiration rates when the fish were present. However, the only significant difference among treatments is the unexpected drop in both productivity and respiration in week 9 after the removal of the fish in the Random treatment relative to the Control and Choice treatments (Figure 3.5, Table 3.1).

For direct measures of resistance and resilience, Choice treatments show less resistance in species richness, productivity, and respiration than Random treatments, indicating higher sensitivity to disturbance. However, Choice treatments show higher resilience than Random treatments for productivity and respiration, as well as species richness if a 1-tailed t-test is used, indicating faster recovery after a disturbance (Figure 3.6, Table 3.2).

Multivariate community composition was affected by both time and treatment, but these factors did not have a significant interaction (Figure 3.7, Table 3.3). Choice treatments differed significantly from both Random and Control treatments, while the two disturbed treatments did not differ significantly from one another. Control treatments were characterized by higher abundance of Baetid mayfly nymphs and *Pantala* sp. dragonfly nymphs and lower abundance of *Culex* sp. and Chironomid fly larvae than either of the disturbed treatments (Table 3.4). Community composition significantly changed over time, with each week differing from all others except weeks 9 and 10. To get a sense of the trajectory of this changing composition, SIMPER comparisons of Week 6 and Week 10 are given in Table 3.5. Most taxa decreased in abundance over time, including *Culex, Pantala, Tropisternus, Laccophilus,* and Chironomids. A few taxa, including both Baetid and Caenid mayflies, and *Paracymus* beetles increased in abundance over time.

DISCUSSION

As expected, the results suggest that choice behavior reduced resistance to disturbances caused by a predator. Colonizing insects in the Choice treatment tended to detect and avoid predators, and this dispersal behavior reduced species richness beyond the effects of consumption by predators alone. However, upon removal of the predator, choice increased the resilience of community and ecosystem properties: Choice treatments had higher rates of convergence to control conditions relative to Random treatments. So, while choice behavior exacerbated the effects of disturbance on species richness and ecosystem properties, choice resulted in faster recovery relative to random dispersal. The results highlight the importance of colonization behavior as both a source of stability and a source of sensitivity to disturbances, and they suggest that the effects non-random dispersal should be considered when predicting species' responses to change.

Any reduction in density can be considered a disturbance (Rykiel, 1985). The presence of fish can represent a natural, temporary disturbance: small ponds vary dramatically in hydroperiod and presence of predators such as fish (De Meester et al., 2005), especially in ponds in the same watershed that can be linked by periods of rain. The avoidance of predators during colonization is a well-known pattern of non-random dispersal, and predator presence often supersedes the effects of resources on habitat preference (Gilliam and Fraser, 1987; Savino and Stein, 1989; Rosenzweig, 1991; Resetarits, 2001; Resetarits et al., 2005; Binkley and Resetarits, 2008). Reductions in prey density caused by predators include both consumptive effects (predation) and non-consumptive effects (emigration, avoidance, death via stress or altered nutrition, etc., Preisser et al., 2005). While our results corroborate the observation that colonizing insects avoid ongoing disturbances from predators, this might not be the case in all types of disturbance. When might a disturbance have these nonconsumptive effects?

Some types of disturbances other than predation can certainly have both consumptive and nonconsumptive effects. Stream insects have been shown to actively avoid chemical toxins via dispersal away from affected areas (Araújo & Ribeiro, 2016). Many animals move away from areas under threat of fire, flooding, storms, and other catastrophes (Komarek, 1969; Lytle, 2000; Streby et al., 2015). In addition, organisms in disturbed areas might have induced stress responses that alter nutrition and survival as well. We predict that disturbances will have negative nonconsumptive effects on species survival or abundance when the disturbance causes lower ability for resource-gathering or when dispersing organisms sense and avoid disturbed patches.

Given our focus on measuring insects alone, we cannot determine the mechanism by which treatment affected productivity and respiration in this experiment. When fish were added, both respiration and productivity tended to increase, perhaps due to direct respiration of the fish, whose biomass was probably an order of magnitude more than all the insects in the tank, or due to indirect effects of fish on alga abundance. However, the drop in both respiration and productivity in the Random treatment in Week 9 is more difficult to ponder, since the Choice treatment (which also had fish) maintained high productivity and respiration. The dissolved oxygen concentrations used to quantify these variables are much more dependent on the microbial members of the community, particularly phytoplankton, than on insects or fish directly (Downing and Leibold 2002). Therefore, differences among our treatments likely represent an indirect effect of insects driven by changes in the phytoplankton community. An alternative hypothesis is that the act of mixing water samples from the Random treatment with the undisturbed mesocosm we used to achieve random colonization caused unintentional dispersal of microbial taxa that affected dissolved oxygen dynamics.

Other patterns in our data warrant more discussion as well. First, there is a slight increase (not significant) in colonist richness and abundance in the Control treatment during Weeks 7 and 8 when the fish were present in the other treatments, likely representing a concentration/compression of colonists based on preference for fishless habitats. The Control treatments were meant to provide a reference condition to explore the recovery process, but disturbances around the undisturbed patches might have created a “moving baseline” if colonists preferred fishless mesocosms. However, this isn’t necessarily a problem with the design; these types of spatial interactions (i.e. spatial contagion, Resetarits and Binkley 2009) among patches likely exist in natural metacommunities that vary in local disturbance patterns. Plus, the same preference would have been present in the undisturbed, random colonization mesocosm, ensuring that the manipulations of colonization worked as intended.

Second, the lack of significant fish effects on abundance, both of colonizers and of residents, is unusual in natural ponds and mesocosm experiments involving fish (e.g. Batzer and Wissinger 1996; Resetarits et al. 2005, Binkley and Resetarits 2005). By including the entire insect community (at least all species >2mm), perhaps we included more fish-tolerant taxa that are usually not quantified. The most abundant taxon in our experiment, Chironomid midges, may survive in the presence of fish by building cases of detritus and hiding in the benthic portions of ponds. Many taxa that live in small ephemeral ponds have cyclic, opportunistic dispersal patterns among temporary (usually fish-less) and permanent (often fish-containing) water bodies as well, suggesting that these taxa may have strategies that allow them to coexist temporarily with fish (Batzer and Wissinger 1996).

Habitat choice behavior is not part of the species sorting process in most community models (Leibold et al., 2004; Svensson et al., 2012; Haegeman and Loreau, 2014), but our results suggest that non-random dispersal is very important form of non-lethal sorting that can contribute to stability in the structure and function of ecosystems. Therefore, habitat choice should be considered when predicting spatial dynamics or species' long-term responses to disturbance and other environmental change.

FIGURES AND TABLES:

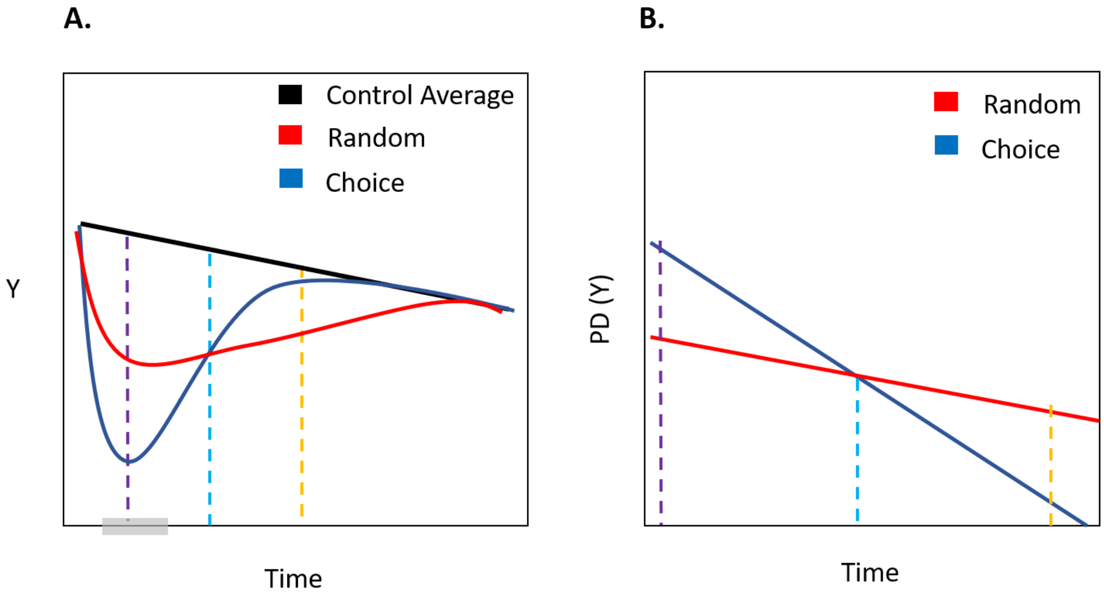


Figure 3.1: Predicted dynamics of undisturbed, naturally assembling patches (control, black line), and disturbed patches with either natural choice behavior (blue line) or randomized colonization (red line). The gray period in Panel A shows the onset and extent of the disturbance. Panel A shows the predicted results for the raw data treatment averages, while Panel B shows the predicted results of linear regressions, with characteristic y-intercepts (displacement from control values) and slopes (rate of convergence toward control values) after the proportional difference between control and treatment tanks is calculated. Each of the dotted vertical lines represents a sampling point. Comparing each sample point shows the how predicted qualitative treatment differences change over time.

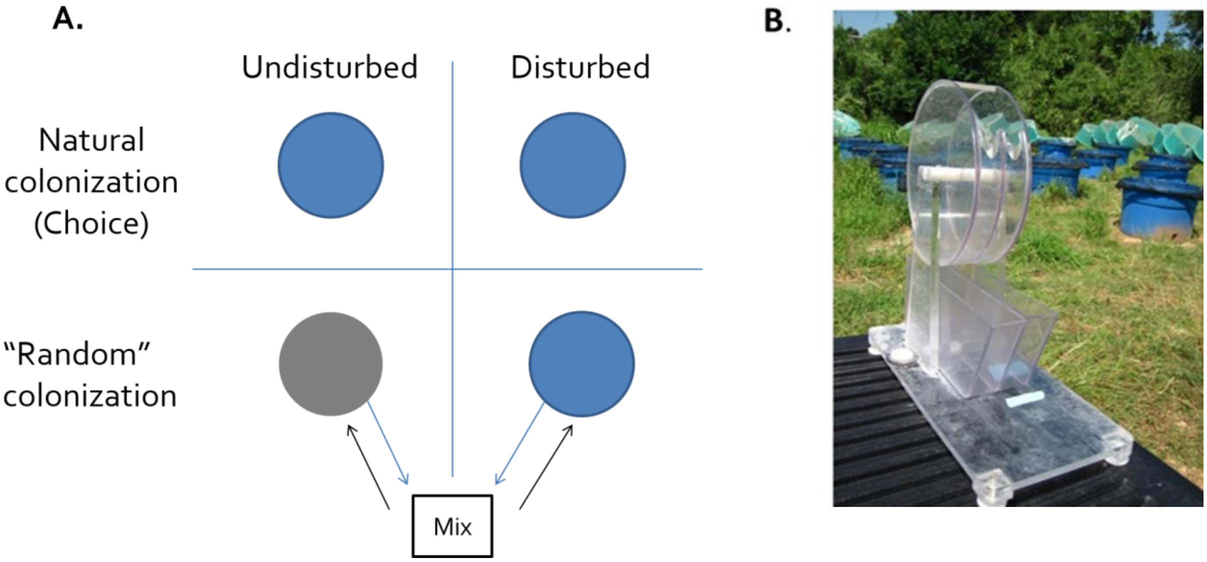


Figure 3.2: Panel A shows the experimental design used to explore the effect of insect habitat choice behavior on resistance and resilience. Disturbed tanks received a 2-week pulse of fish predation 81 days after mesocosms were established. Panel B shows the plankton splitter used to mix and divide the insect colonists of the disturbed and undisturbed tanks assigned to the random colonization treatment. Note that the undisturbed, random colonization treatment only existed to randomize the colonization in the “Random” treatment, and that combination was excluded from all analyses.

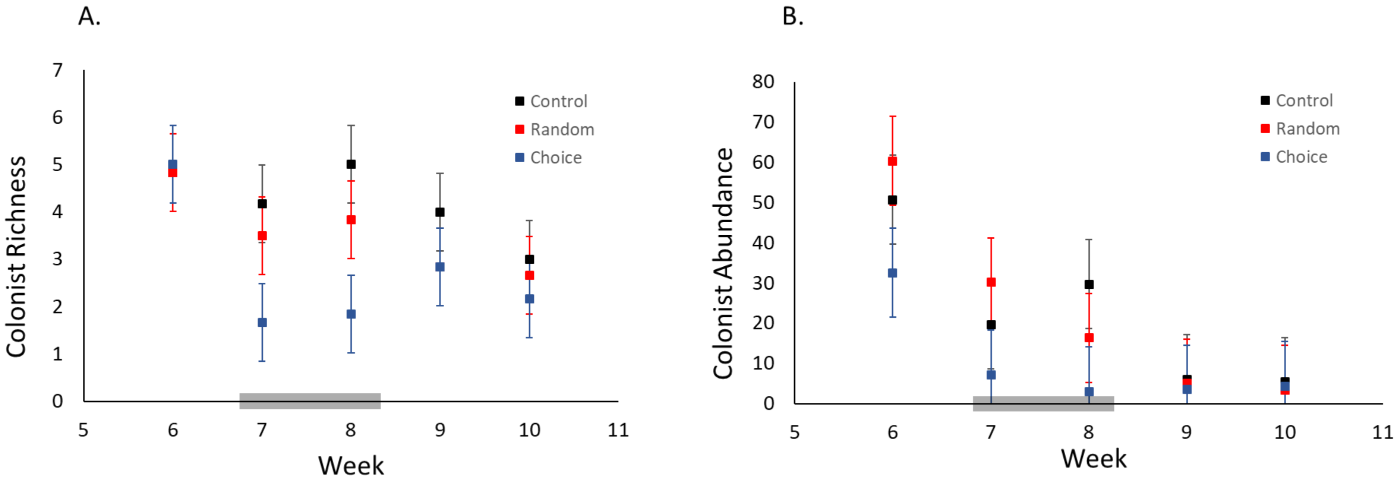


Figure 3.3: The temporal effects of treatment on insect colonization. Panel A shows the average species richness of colonists for each treatment, while Panel B shows the average abundance of colonists for each treatment. Numbers were tallied after immigration was manipulated in the random treatment, so that each week's measurements included colonization. The period in which fish were placed into disturbed tanks appears in gray on the x-axis. Fish significantly reduced colonist richness in the choice treatment during the disturbance. Treatment did not significantly affect colonist abundance.

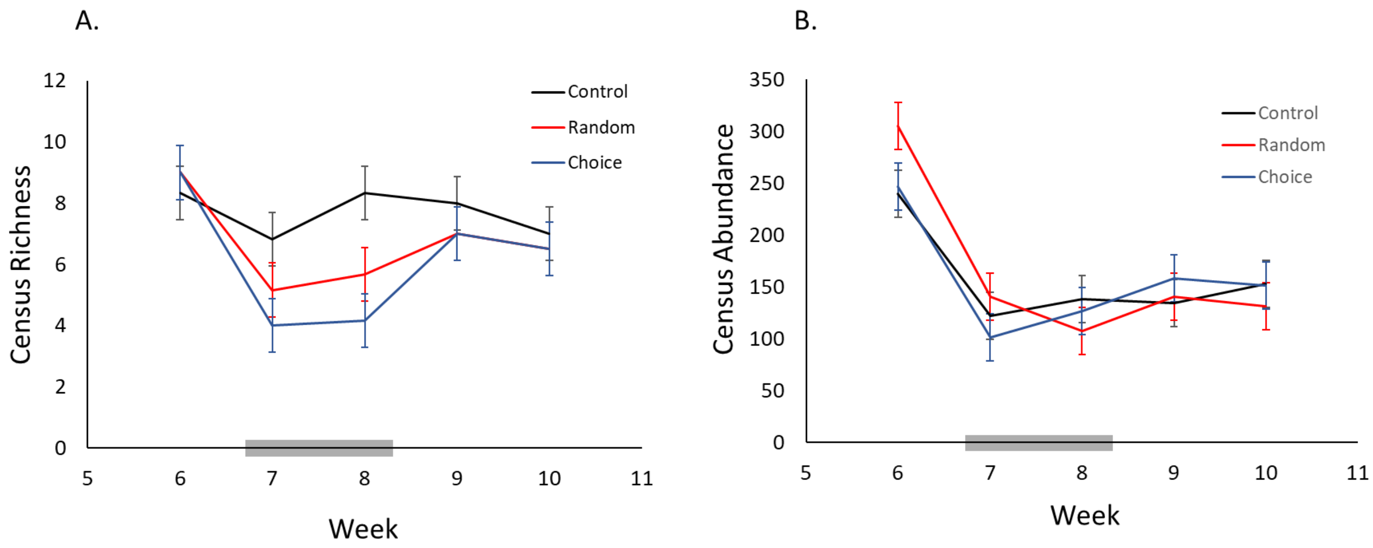


Figure 3.4: The temporal effects of treatment on insect communities. Panel A shows the species richness of the weekly census samples from each mesocosm, while Panel B shows the total abundance of all insects from the same census. The period in which fish were placed into disturbed tanks appears in gray on the x-axis. While fish were present, they significantly altered insect richness, but only in the choice treatment. The random treatment did not differ statistically from either the control or the choice treatment. Treatment did not affect insect abundance.

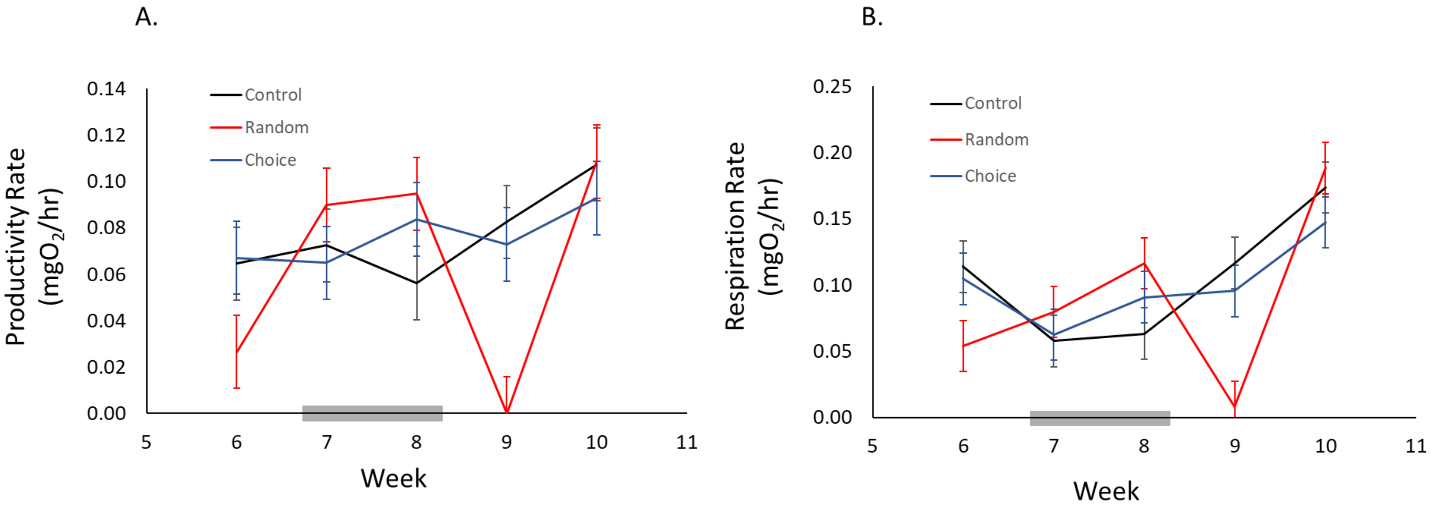


Figure 3.5: The temporal effects of treatment on ecosystem productivity and respiration. Panel A shows the productivity while Panel B shows the respiration rate based on weekly measurements of dissolved oxygen dynamics. The period in which fish were placed into disturbed tanks appears in gray on the x-axis.

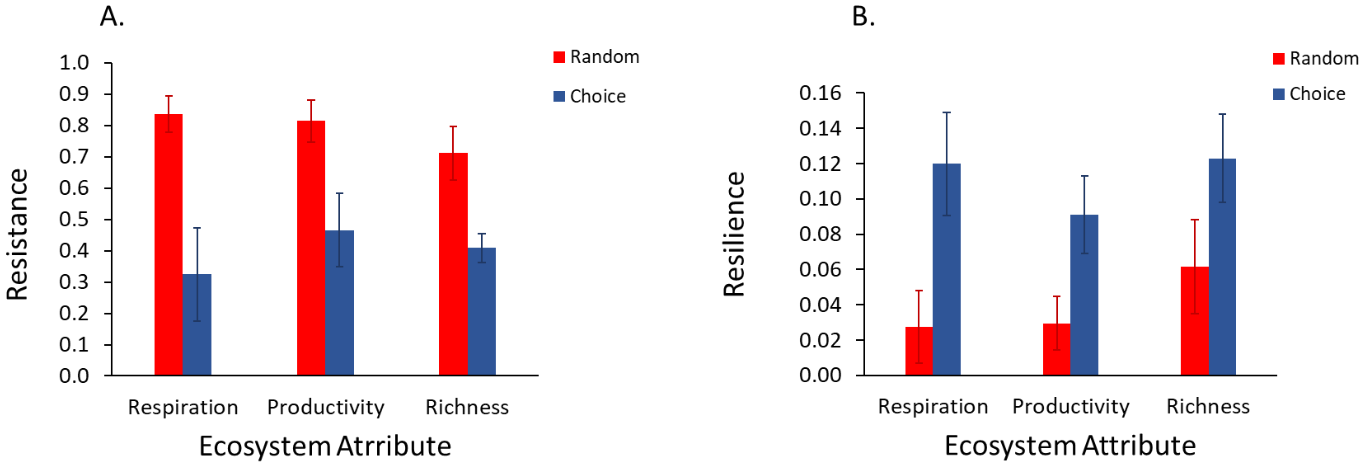


Figure 3.6: Resistance and resilience from linear regressions of the proportional difference, a comparison of treatment tanks versus control tanks (see Fig. 1B), through time after the disturbance. Panel A shows resistance effects (1 – displacement), while Panel B shows resilience (convergence slope) effects. In general, choice behavior reduces resistance, but increases resilience relative to random dispersal in both community and ecosystem properties ($p<0.06$ for all comparisons).

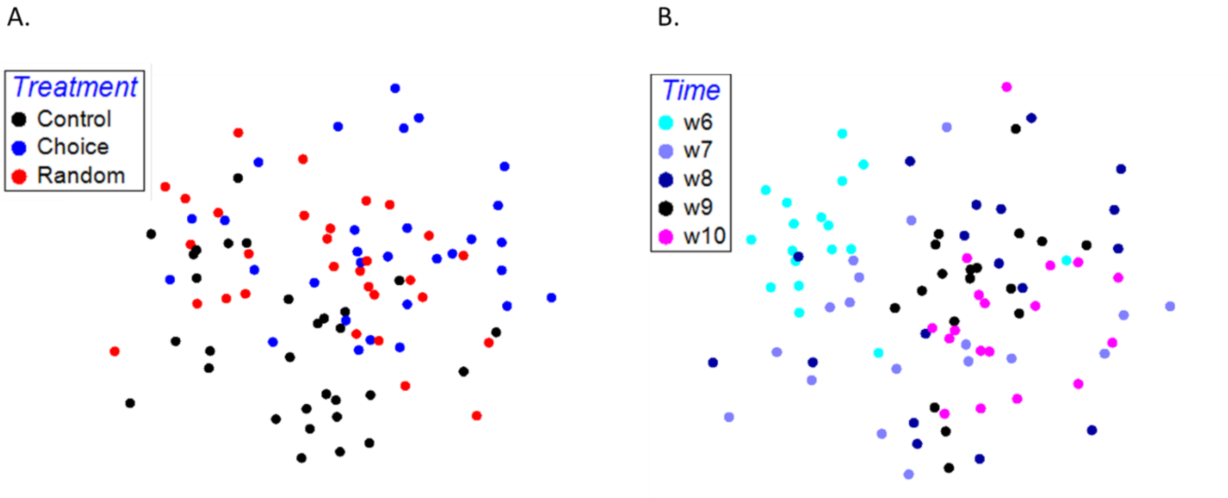


Figure 3.7: NMDS plots showing similarity in insect community composition in each mesocosm based on treatment (Panel A) and sampling time (Panel B). Communities that share similar composition based on Bray-Curtis dissimilarity appear closer together on the ordination plots. Both time and treatment significantly affected community composition based on PERMANOVA.

Table 3.1: Results of repeated measures ANOVA on raw data. When significant overall effects or interactions involving treatment were found, pairwise comparisons were conducted.

	Colonist Richness				Colonist Abundance			
Source of Variation	DFn	DFd	F	p	DFn	DFd	F	p
Overall Time	4	60	6.597	**1.81E-04**	4	60	15.344	**1.08E-06**
Overall Treatment	2	15	6.028	**0.012**	2	15	2.143	0.152
Choice vs. Random				0.115				ns
Control vs. Random				0.353				ns
Control vs. Choice				**0.004**				ns
Overall Time*Treatment	8	60	1.533	0.165	8	60	1.018	0.432

	Census Richness				Census Abundance			
Source of Variation	DFn	DFd	F	p	DFn	DFd	F	p
Overall Time	4	60	13.539	**6.34E-08**	4	60	40.919	**1.64E-16**
Overall Treatment	2	15	5.323	**0.018**	2	15	0.22	0.805
Overall Treatment*Time	8	60	2.529	**0.019**	8	60	2.047	0.056
Choice vs. Random*Week 8				0.572				ns
Control vs. Random*Week 8				0.101				ns
Control vs. Choice*Week 8				**0.012**				ns

	Respiration Rate				Productivity Rate			
Source of Variation	DFn	DFd	F	p	DFn	DFd	F	p
Overall Time	4	60	27.365	**6.05E-13**	4	60	10.753	**1.23E-06**
Overall Treatment	2	15	1.047	0.375	2	15	1.092	0.361
Overall Treatment*Time	8	60	7.052	**1.59E-06**	8	60	5.873	**1.53E-05**
Choice vs. Random*Week 9				**1.70E-05**				**1.27E-03**
Control vs. Random*Week 9				**0.002**				**3.10E-04**
Control vs. Choice*Week 9				0.4904				0.706

Table 3.2: T-test results comparing the resistance and resilience of disturbed treatments based on calculations of proportional difference to control treatments.

	Resistance		
T-test P-values	Respiration	Productivity	Richness
Choice vs. Random (1-tailed)	**0.008**	**0.016**	**0.008**
Choice vs. Random (2-tailed)	**0.017**	**0.033**	**0.015**

	Resilience		
T-test P-values	Respiration	Productivity	Richness
Choice vs. Random (1-tailed)	**0.015**	**0.023**	**0.062**
Choice vs. Random (2-tailed)	**0.030**	**0.046**	0.125

Table 3.3: PERMANOVA results showing how time, treatment, and treatment*time affect community composition. When significant overall effects were found, pairwise comparisons were conducted.

Source of Variation	df	Pseudo-F	p
Treatment	2	8.183	**0.001**
Control vs. Choice			**0.001**
Control vs. Random			**0.001**
Choice vs. Random			0.056
Time (Weeks)	4	6.943	**0.001**
6 vs. 7			**0.001**
6 vs. 8			**0.001**
6 vs. 9			**0.001**
6 vs. 10			**0.001**
7 vs. 8			**0.012**
7 vs. 9			**0.001**
7 vs. 10			**0.001**
8 vs. 9			**0.001**
8 vs. 10			**0.003**
9 vs. 10			0.073
Time*Treatment	8	1.051	0.378

Table 3.4: SIMPER results showing the 10 taxa that contributed most to differences in community composition among treatments, and their average abundance in each treatment.

	Species	Av.Abund Control	Av.Abund Choice	Contrib%
Control vs. Choice (Av. Dissimilarity = 39.1)	Baetid naiad	0.75	2.93	16.64
	Pantala sp.	6.69	4.76	13.62
	Culex sp.	2.97	1.85	11.58
	Chironomid larva	8.02	9.01	8.39
	Microvelia sp.	1.16	1.09	5.36
	Tropisternus lateralis	0.84	0.13	4.9
	Paracymus sp.	1.11	0.45	4.84
	Berosus ordinatus	0.64	0.11	3.59
	Tropisternus sp. larva	0.78	0.26	3.41
	Caenid naiads	0	0.56	2.89

	Species	Av.Abund Control	Av.Abund Random	Contrib%
Control vs. Random (Av. Dissimilarity = 34.3)	*Pantala* sp.	6.69	5.18	13.22
	Culex sp.	2.97	3.57	12.96
	Baetid naiad	0.75	1.53	11.01
	Chironomid larva	8.02	9.1	9.82
	Microvelia sp.	1.16	1.2	6.42
	Paracymus sp.	1.11	0.72	5.55
	Tropisternus lateralis	0.84	0.4	4.68
	Tropisternus sp. larva	0.78	0.31	4.07
	Berosus ordinatus	0.64	0.18	3.92
	Enochrus sp.	0.28	0.26	2.53

	Species	Av.Abund Choice	Av.Abund Random	Contrib%
Choice vs. Random (Av. Dissimilarity = 32.3)	Baetid naiad	2.93	1.53	21.72
	Culex sp.	1.85	3.57	16.3
	Pantala sp.	4.76	5.18	11.47
	Chironomid larva	9.01	9.1	7.5
	Microvelia sp.	1.09	1.2	6.23
	Caenid naiads	0.56	0.18	4.57
	Paracymus sp.	0.45	0.72	3.47
	Laccophilus larva	0.34	0.43	2.99
	Tropisternus lateralis	0.13	0.4	2.97
	Liodessus sp.	0.67	0.5	2.86

Table 3.5: SIMPER results showing the taxa that contributed most to differences in community composition among the most different time points (week 6 and week 10), and their average abundance at each time point.

Week 6 vs. Week 10 (Avg. Dissimilarity = 44.9)

Species	Av.Abund Week 6	Av.Abund Week 10	Contrib%
Culex sp.	8.31	0.11	30.6
Baetid naiad	1.24	2.78	11.92
Pantala sp.	6.57	5.86	7.05
Chironomid larva	10	8.5	5.75
Tropisternus sp. larva	1.4	0.11	5.28
Laccophilus larva	1.22	0.06	4.53
Microvelia sp.	1.88	1.18	4.3
Paracymus sp.	0.7	1.12	4.1
Liodessus sp.	0.66	0.6	2.45
Caenid naiads	0	0.68	2.34
Tropisternus lateralis	0.51	0.25	2.09
Helophorus sp.	0.5	0.11	2.02
Berosus ordinatus	0.48	0.17	2.02
Helochares sp.	0.34	0.21	1.56
Agabus sp.	0.36	0.06	1.44
Rhantus sp. larva	0.36	0	1.41
Enochrus sp.	0.16	0.25	1.25

Chapter 4: Metaecosystems--Pulsed nutrient and plankton inputs have little effect on the stability of assembling rock pool communities

INTRODUCTION:

In Chapter 2 and Chapter 3, I discussed the influences of dispersal on metapopulations and metacommunities respectively. Chapter 4 represents an attempt to study the interaction between dispersal and flows of resources in a metaecosystem framework. Metaecosystems are systems of connected ecosystems, with dispersal of organisms as well as abiotic flows (e.g. of nutrients) connecting patches of similar habitat. Flows of abiotic components of ecosystems have long been recognized as important components of ecosystems (Odum and de la Cruz, 1963; Wallace et al., 1999), and have been studied mostly as inputs into a receiving ecosystem patch (i.e. “spatial subsidies” or “allochthonous inputs” of materials; Polis et al., 1997). Both theory and experiments have been used to show that nutrient flows can affect diversity and stability in ecosystems (e.g. Anderson and Polis, 2004; Butzler and Chase, 2009; Gravel et al., 2010). There may be multiple mechanisms responsible for the effect of these inputs on communities, since resource inputs can affect birth rates, death rates, and movement rates of species, both directly and indirectly (Yang et al., 2008; Holt, 2008).

Theory predicts that flows of nutrients from outside a patch can sometimes stabilize communities and promote population persistence, coexistence, and greater biodiversity within patches. This stabilization can occur if nutrient flows weaken trophic interactions (Huxel and McCann, 1998; Huxel et al., 2002) or promote population growth of less abundant species or resource pulse specialists (Holt, 2008; Gravel et al. 2010). However, nutrient flows can also destabilize communities if they promote stronger predator-prey interactions or they benefit abundant species more strongly than less abundant species (i.e. the “Paradox of Enrichment” sensu Rosenzweig, 1971; Huxel and McCann, 1998; Huxel et al., 2002; Gravel et al., 2010). Most theoretical models of such nutrient flows consider inputs to be constant over time (Huxel and McCann, 1998; Huxel et al., 2002; Gravel et al., 2010), but many observations of nutrient inputs show that they can occur in pulses that vary in timing and magnitude (Nowlin et al., 2007). Pulsed inputs have been modeled less frequently, but these models also predict that the effects of inputs on stability and diversity still depend on whether the inputs covary with species abundances and how the inputs affect the strength of competitive and trophic interactions (Tilman and Kilham, 1982; Huston and DeAngelis, 1994; Chesson, 2000; Takimoto, 2002; Holt, 2008). Pulsed inputs may have strong effects on ecosystems, possibly even promoting switches to alternative stable states (Holt, 2008).

Many of the theoretical predictions of how nutrient inputs affect biodiversity and stability have been tested experimentally, since there is extensive interest in anthropogenic nutrient pollution (Vitousek et al., 1997; Jeffries, 2000). While many predictions of theory are supported, such as the destabilizing effects of large nutrient inputs (e.g. Anderson and Polis, 2004), some studies show idiosyncratic effects of nutrients inconsistent with the predictions of theory, perhaps due to species-specific responses to nutrient addition, unpredictable trophic interactions, or differing scales of these experimental studies (Leibold et al., 1997; Chalcraft et al., 2008; Butzler and Chase, 2009; Weber and Brown, 2018). This inconsistency suggests that more empirical tests of theory isolating different aspects of resource inputs might help understand this variation in results. Butzler and Chase (2009) show that the timing of pulsed inputs (i.e. the nutrient “loading rate”) might be as important as the total amount of material moving.

Here, we report the results of an experiment manipulating the loading rate of dry sediment inputs in small aquatic ecosystems. Movement of sediment in aquatic systems is a particularly important flow of materials that can affect biodiversity and ecosystem function (Van der Meulen et al., 2016). Sediments are a major source of nutrients such as nitrogen and phosphorus in these systems, and inputs of sediment can have large impacts on productivity (e.g. Barko and Smart, 1981). However, in ephemeral aquatic systems such as rock pools, sediments are also a major source of dormant or diapausing organisms, including bacteria, algae, and invertebrate eggs, with adaptations to survive dry periods (Hairston and Kearns, 2002; Jones et al., 2010). Therefore, sediments allow some taxa to disperse both spatially (via sediment flows, Brendonck and De Meester, 2003) and temporally (via delayed hatching/regeneration; Evans and Dennehy, 2005; McCarthy, 2015). Therefore, our experiment simultaneously explores inputs of nutrients and organisms. Movement of individuals can also affect stability in populations and communities (see Chapters 2 and 3). We attempt to disentangle the effects of these different aspects of sediment inputs by including a treatment in which the sediment was sterilized, thus presumably only containing non-living material.

Many empirical studies of abiotic flows test the effects of inputs on already-assembled communities (e.g. Nowlin et al., 2007; Butzler and Chase, 2009; Weber and

Brown, 2018). Experiments exploring the effects of nutrient flows and colonization/community assembly simultaneously are rare (but see Binckley and Resetarits, 2008; McCarthy, 2015). Given that nutrient flows might affect dispersal and colonization behavior (Yang et al., 2008; Holt, 2008), focusing on assembling communities can provide insight into how variable sediment inputs impact the community of organisms that develops both through local processes of birth and death and through regional processes of spatial dispersal. Our overall question is therefore the following: how do variable inputs of diapausing organisms and/or nutrients in sediment affect diversity and stability of communities in small ephemeral pools? We predict that a large pulse of sediment will be destabilizing, promoting large unstable fluctuations as in Anderson and Polis (2004), resulting in more temporal variability in abundance and lower species diversity. We predict that smaller pulses of sediment (both relative to large pulses and relative to no sediment inputs) will promote weaker interactions and population persistence, therefore stabilizing abundances and promoting diversity as predicted by Huxel and McCann (1998).

METHODS:

Model System

Our experiment was conducted in artificial containers that replicate the conditions found in small, ephemeral freshwater systems such as rock pools. Rock pools and other temporary water bodies are common in most places (Vanschoenwinkel et al., 2010), and Central Texas is no exception. Only about 20% of Texas streams and rivers are considered permanent; the remaining 80% experience dry-down during times with little rainfall and/or high evapotranspiration (TCEQ, 2009). Dry stream beds often contain numerous depressions that hold water long after flow has ceased and can fill independently of stream flow during rain events (e.g. Baron et al., 1998). Our experiment models these types of pools that experience occasional flooding and sediment deposition. These pools make a good model system because they have discrete borders and relatively simple communities, and thus artificial mesocosms can be used to recreate temporary pond communities that approach the complexity of natural systems (Wilbur, 1997).

Small freshwater pools are often characterized by dry and wet stages, with predictable successional changes during a period of inundation. Typically, the first colonists of a newly flooded pool are those that are present in the sediment "egg bank", including microbes and zooplankton. If overland flow fills a pool, then organisms can also be transported from upstream as well. Aerial and terrestrial colonists such as aquatic insects, snails, and frogs become increasingly important as the pool persists (Vanschoenwinkel et al., 2010).

Mesocosm Experiment

To explore how flows of materials interact with community assembly, a mesocosm experiment was conducted across different sites in Central Texas. Eight sites were chosen, with one replicate of the experiment at each site. One benefit of using different sites is that it allowed exploration of the process of community assembly in sites with different pools of aerial colonists, ensuring each replicate was an independent test of how input dynamics affect colonization and community assembly. To determine whether any large-scale variation among sites might account for variation in the effects of the experimental treatments on community dynamics, the sites were divided into 2 spatial blocks. The “western” block included 4 sites in western Travis County and Hays County, TX in the Edward’s Plateau ecoregion, while the “eastern” block included 4 sites in eastern Travis County and Bastrop County, TX in the Blackland Prairie and East Central Texas Plains ecoregions (TPWD, 2011; Figure 4.1).

Within each site, four mesocosms were established: one for each sediment input treatment. One treatment (0g) received no sediment at all and was set up with water alone. The community that developed in these mesocosms were thus completely reliant on leaf fall and dust inputs for carbon and most nutrients (those not found in well water). The other three treatments all received 250 grams of sediment but differed in the nature of the inputs. One treatment (250g) received all 250 grams as a single pulse at the beginning of the experiment. The second sediment treatment (50g) consisted of 50-gram pulses of living sediment every two months over the course of a year. The final sediment treatment (50ga) had input dynamics like the 50g treatment, but after the initial dose of sediment, the sediment inputs for the rest of the experiment were sterilized in an autoclave to kill any resting stages of organisms. The 50ga treatment thus contained the nutrients in the sediment, but presumably no organisms after the initial inoculation.

Sediment was collected from 4 ponds in Travis county: two in the Edward’s Plateau ecoregion and two in the Blackland Prairie ecoregion. All sediment was mixed and homogenized by hand before being introduced into the mesocosms. Mesocosms were established with water and the initial sediment dose on 9 July 2016. These mesocosms consisted of clear polyurethane containers with a volume of 53 L. Well water from a single source at Brackenridge Field Laboratory in Austin, TX was used to fill all mesocosms. They were left open to natural colonization and leaf fall. However, disturbance by mammals (using the pools as a water source) was evident after the first sampling, and so all mesocosms were covered with coated wire fencing with 5*10cm mesh size. After initial filling, the hydrology of the mesocosms varied naturally with rain events. The experiment was sampled opportunistically following rain events if they occurred about two months after the preceding sampling event. These rain events did not affect all sites equally, and some sites had low water levels at the time of sampling. Any mesocosm with a water depth of <10 cm was not sampled.

We focused on all macroinvertebrates for community measurements. The community of insects and crustaceans in each mesocosm was sampled approximately every two months over the course of a year (sampling dates in October, December, February, May, and July). All macroinvertebrates that were visible from the surface were counted and identified non-destructively (i.e. without removing them) in the field. Identification was based on previous sampling and identification efforts in Central Texas following Merritt and Cummings (1996). Zooplankton could not be identified in the field, and thus were sampled destructively and identified in the lab following Thorp and Covich (2009). A 500-mL water sample, which consisted of a 250-mL subsample at the surface and a 250-mL subsample near the sediment, was filtered through a 100-µL sieve and washed into a sample vial with 70% ethanol in order to estimate crustacean zooplankton abundance in each mesocosm. Two sweeps with a 10*7cm aquarium net (mesh size 2mm) were taken to look for any unobserved species of benthic macroinvertebrates, which were counted and returned to the tank.

Response Variables and Data Analysis

Species richness and total community abundance based on all sampling techniques together was recorded for each mesocosm. To explore temporal variability in richness and abundance, the temporal coefficient of variation (CV) of richness and abundance was calculated for each treatment. In order to see if egg bank and aerial colonizers responded differently to sediment inputs, the communities of egg bank colonizers (mostly crustaceans) and aerial/terrestrial colonizers (mostly insects) were also analyzed separately. A split-plot, repeated-measures ANOVA was used to examine how time and treatment affected these response variables. When significant effects were found, pairwise comparisons with False Discovery Rate (fdr) corrections were used to determine which groups differed. Spatial block (eastern vs. western sites) was included in the model as a random factor. All univariate analyses were performed in R version 3.5.1. Samples that were not taken due to low-water conditions were excluded from all analyses.

Multivariate analyses were also used to compare community structure over time and among sediment treatments. Permutational multivariate ANOVA (PERMANOVA) was performed on a Bray-Curtis dissimilarity matrix of all samples in Primer–E ver. 6

(Clarke and Gorley 2006). Abundance data was square-root transformed before analysis: the square root transformation weakens the influence of the most abundant species on observed composition differences, and this transformation is recommended when comparing abundance data (Clarke and Warwick 2001). NMDS on the Bray-Curtis dissimilarity matrix were created as a visual representation of the differences observed in the PERMANOVA. The SIMPER (similarity percentages) procedure in Primer-E was employed to determine the taxa that contribute most to the observed dissimilarity among times and treatments. This procedure lists the taxa that differ most in abundance among the groups of communities that are being compared, and it tells how much each taxon contributes to observed dissimilarity among the communities (Clarke and Gorley 2006).

RESULTS:

Species richness (Figure 4.2) was low; there were usually only 2-6 species per mesocosm. When comparing species richness among treatments and sampling dates, there was a significant overall effect of treatment ($F_{3,28}$=3.123, p=0.042) and time ($F_{1,79}$=25.697, p<0.0001), but no treatment-by-time interaction ($F_{3,79=}$0.908, p=0.441). Pairwise differences indicate that the 50g treatment had significantly higher richness than the 0g treatment over the course of the experiment (fdr-corrected p=0.021), but no other sediment treatments differed (all other p>0.129). Species richness generally increased with time, with the highest values in May and the lowest values in December. Richness differed in the following comparisons: Dec-Feb, Oct-May, Dec-May, Feb-May, Dec-Jul (fdr-adjusted $p<0.004$). All other time comparisons did not differ (fdr-adjusted $p>0.065$).

Total community abundance (Figure 4.3) did not vary with sediment treatment ($F_{3,28}=0.949$, $p=0.431$), nor was there a treatment-by-time interaction ($F_{3,79}=2.273$, $p=0.0865$). Abundance did vary over time ($F_{1,79}=11.204$, $p=0.001$), with higher abundances in May (May vs. all other times, fdr-adjusted $p<0.031$). Abundance was also higher in July than in December (fdr-adjusted $p=0.030$), but all other time comparisons had similar total abundance (all other $p>0.200$).

Variation in richness and abundance was explored by comparing the temporal CV among treatments (Figure 4.4). The CV of species richness did not vary among treatment (F3,21=0.922, $p=0.447$), but the CV of abundance did ($F_{3,21}=4.044$, $p=0.020$). Pairwise comparisons indicate that abundance was more variable in the 0g treatment relative to the 250g treatment and the 50ga treatment (fdr-corrected $p<0.05$).

Looking at only the organisms that hatch from the egg bank (crustaceans, mites, and flatworms; Figure 4.5), richness and abundance changed seasonally ($F_{1,77}>19.3$, $p<0.0001$) similar to the observed pattern for the entire community, but richness and abundance were not affected by sediment treatment ($F_{3,28}<2.34$, $p>0.090$) or the interaction between treatment and time ($F_{3,77}<0.748$, $p>0.527$). The CV of richness and abundance did not vary with treatment when looking at only the egg bank community ($F_{3,21}<1.51$, $p>0.242$; Figure 4.6).

Looking at the aerial/terrestrial colonists alone (insects and amphibians; Figure 4.5), richness patterns mirrored the patterns from the egg bank taxa, with a seasonal increase in richness ($F_{1,79}$=5.66, p=0.020), but no effect of sediment treatment ($F_{3,28}$<1.65, p>0.200) or the interaction between treatment and time ($F_{3,79}$<1.06, p>0.373). Insect abundance was not significantly effected by treatment, time, or the interaction between treatment and time (F<2.07, p>0.111). However, the CV of abundance varied with treatment ($F_{3,21}$=3.651, p=0.029), with the 0g treatment showing higher variability in abundance than the 50ga treatment (fdr-corrected p=0.022). The CV of richness was not affected by treatment in the terrestrial colonist data ($F_{3,21}$=1.01, p=0.409; Figure 4.6).

Multivariate analyses showed significant effects of time (Pseudo-F=5.678, p<0.001), but neither treatment nor the treatment-by-time interaction affected multivariate community structure (Pseudo-F<0.929, p>0.564; Figure 4.7). Pairwise differences in community composition among the different sampling dates showed no differences in the Oct-Dec comparison (p=0.074), but all other times differed from each other in multivariate community composition (all other p<0.015). The SIMPER procedure showed a seasonal change in which *Culex* sp. mosquitoes and *Pantala* sp. dragonflies decreased in abundance from fall to spring, while *Ceriodaphnia* sp., chironomids, *Culiseta* sp., ostracods, *Aedes* sp., and *Anopheles* sp. increased in abundance from fall to spring. Multivariate analyses could not be performed on egg bank taxa vs. aerial/terrestrial colonizers because these community subsets were absent in several samples, resulting in undefined comparisons in the Bray-Curtis dissimilarity matrix (Table 4.1).

DISCUSSION:

Our results show little support for the idea that small pulses of sediment inputs are stabilizing relative to no sediment inputs or large sediment inputs, as predicted by theory (Huxel and McCann, 1998; Huxel et al., 2002; Takimoto, 2002; Gravel et al. 2010). Small pulses of live sediments resulted in higher species richness than the “no sediment” treatment. This result suggests that pulsed inputs of resting-stage individuals might have spatially subsidized rare species in the zooplankton, promoting coexistence and increasing diversity (*sensu* Mouquet and Loreau, 2003). Small pulses of sterilized sediment resulted in more stable total abundance values relative to no sediment inputs. The mechanism of this stabilization in our experiment is difficult to determine but is likely due to nutrient flows weakening predator-prey interactions (Huxel and McCann, 1998; Morrin, 1999; Huxel et al., 2002) and/or promoting population growth of less abundant species (Holt, 2008; Gravel et al. 2010; see discussion of egg bank vs. aerial colonizers below). The treatment with one large pulse of sediment at the beginning showed intermediate levels of stability: not as stable as the smaller sediment inputs, but not as unstable as the no-sediment treatment. Overall, our data show that sediments can affect stability, and smaller pulsed inputs might be more stabilizing than a single large pulsed input, as predicted by theory and supported by some empirical studies of input dynamics (Huxel and McCann, 1998; Takimoto, 2002; Holt, 2008; Weber and Brown, 2016).

When comparing the results for taxa that hatch from the egg bank vs. taxa that colonized the mesocosms aerially/terrestrially, the effects of sediment treatments were generally weaker for egg bank taxa. This seems somewhat counter-intuitive since the sediment input treatments should have directly affected the egg bank taxa by moving resting-stage individuals. The cues used by egg bank taxa to initiate hatching are not completely understood, but they include temperature, inundation, dissolved oxygen concentration and photoperiod (Hairston and Kearns, 2002; Gyllström and Hansson, 2004). There is little evidence that egg bank taxa terminate diapause in response to resource levels (Gyllström and Hansson, 2004). Therefore, input of resources in the sediment in our experiment is decoupled from most hatching cues in egg bank taxa, and thus their responses to resource levels are likely more controlled by birth/death processes after hatching. A meta-analysis by Yang et al. (2010) suggests that strong numerical responses to resource pulses are most often driven by immigration rather than increases from within a community. In addition, in taxa that respond to inputs via reproductive processes, responses to resource availability tend to be more lagged relative to taxa that respond to inputs via dispersal (Yang et al., 2010). These patterns are corroborated by our data: taxa that colonized aerially or terrestrially showed stronger responses to sediment treatments, with higher diversity and lower variation in abundance in the treatments with small pulses of sediment. The assembling community of aerial/terrestrial colonizers mostly consist of species with active dispersal, and many may have the ability to choose habitats based on resource levels (e.g. Resetarits, 2005; Binckley and Resetarits, 2008). Habitat choice can both weaken predator-prey interactions (e.g. spatial avoidance by prey, Resetarits, 2005) and promote population growth of less abundant taxa (e.g. density-dependent dispersal, Holt, 1993; Amarasekare, 2010; Chapters 2 and 3).

Thus, habitat choice is the likely reason that sediment input dynamics affected stability more in actively dispersing taxa relative to egg bank taxa in our experiment.

Another interesting result regarding egg bank species is that most of these taxa (6/11 species) were able to colonize the no-sediment treatment. Not much is known about the spatial dispersal capacity of egg bank species independent of sediment flows (McCarthy, 2015), but it is known that the resting stages of some taxa can disperse aerially as dust in the wind (Vanschoenwinkel et al., 2008), and that resting stages and active stages can disperse among patches via insect, bird, and mammal vectors (Van de Meutter et al. 2008; Allen, 2007, but see Jenkins and Underwood, 1998). In our experiment, there was strong evidence of raccoons and other mammals interacting with the mesocosms (tracks, disturbance, and rapid water loss), providing one likely source of vectored dispersal among the sediment treatments within a site. While this interaction may have weakened the differences among our treatments, it does represent a natural phenomenon that could affect community dynamics in nature, and the opportunity for mammal-mediated dispersal was similar among all replicates in the experiment.

Pulse magnitude in our experiment seemed to have only weak effects on stability. Weak or inconsistent effects of pulse magnitude have been found in other empirical studies of pulsed inputs. Weber and Brown (2018) manipulated inputs of dead fish in mesocosms, simulating winter fish mortality in lakes. They found little effect of the amount of fish inputs on ecosystem stability, perhaps due to the limited biomass of inputs in the experiment. Nowlin et al. (2007) manipulated inputs of cicadas into mesocosms and found that increasing input biomass stabilized populations of predatory taxa, but herbivores and primary producers showed greater stability at low or intermediate input levels. This is like the large effect of nutrient loading rates on phytoplankton observed by Butzler and Chase (2009). The weak effects of sediment input magnitude could therefore be due to too little variation in magnitude among sediment treatments or differential responses to pulse magnitude by different taxa. A more likely explanation, however, is that the time scale of sampling in our experiment was too broad to see all the effects of pulsed inputs. Pulses in aquatic systems tend to happen quickly, and responses tend to happen over short time scales with little lag (Yang et al. 2010). This transient effect is likely even stronger in small rock pools, where many species are specialists in rapid colonization and short generation times as adaptations to ephemeral water sources (Vanschoenwinkel et al., 2010). Many of the community responses to resource pulses in our experiment could have happened over shorter time scales. Transient dynamics after a single pulse event and the interacting effects of recurring inputs over longer periods are both important to understanding the effects of inputs in ecosystems (Holt, 2008), and while we focused on long-term effects, future studies could strive to characterize effects at both scales. Even with this limitation, we still observed some of the stabilizing effects of inputs in our experiment. In ephemeral communities such as rock pools, exploring the long-term effects of inputs and disturbance can help us understand how the populations that inhabit these systems are able to persist (Holt, 2008).

The inclusion of the treatment with autoclaved sediments was an attempt to isolate the effects of inputs of resting-stage organisms and the effects of nutrient/material input in the long-term sediment pulses. In general, the two long-term low-magnitude pulse treatments (50g and 50 ga) showed similar results: higher richness and more stable populations than the no-sediment treatment and the single large pulse treatment. However, the effects for species richness were slightly stronger with living sediments and the effects for abundance stability was slightly stronger with nutrients only. There is a possibility that the nutrient inputs of these two treatments are not completely equivalent despite using the same amount of sediment in each treatment: autoclaving sediments can increase the amount of nutrients released from them (Tuominen et al., 1994). However, these two treatments are still representative of long-term, low-magnitude inputs relative to the treatment with a single large pulse and the treatment with no sediment inputs, and so while direct comparisons of these two aspects of sediment inputs are difficult, the overall conclusions of the experiment are not affected.

While the effects of pulsed inputs of nutrients and detritus on food web structure, composition, and productivity in aquatic ecosystems have received considerable attention (e.g. Jeffries, 2000; Rubbo and Kiesecker, 2004; Williams et al., 2008), the role of these inputs on temporal stability has been tested less frequently (Anderson and Polis, 2004; Nowlin et al., 2007; Weber and Brown, 2018). Resource pulses are increasingly recognized as an important phenomenon in ecosystems, and both theoretical and empirical work suggests the can have large impacts on diversity and stability (Huxel and McCann, 1998; Huxel et al., 2002; Takimoto, 2002; Anderson and Polis, 2004; Nowlin et al., 2007; Gravel et al. 2010; Weber and Brown, 2018). Ecosystem stability is expected to be particularly important in many applications, including the design of reserves, prediction of species responses to disturbance, conservation of rare species, and the control of pests (Kendall et al., 2000). Given that resources pulses are common in many ecosystems (Yang et al., 2010), studying the effects of such pulses is integral to our understanding of temporal variation in ecosystems.

FIGURES AND TABLES:

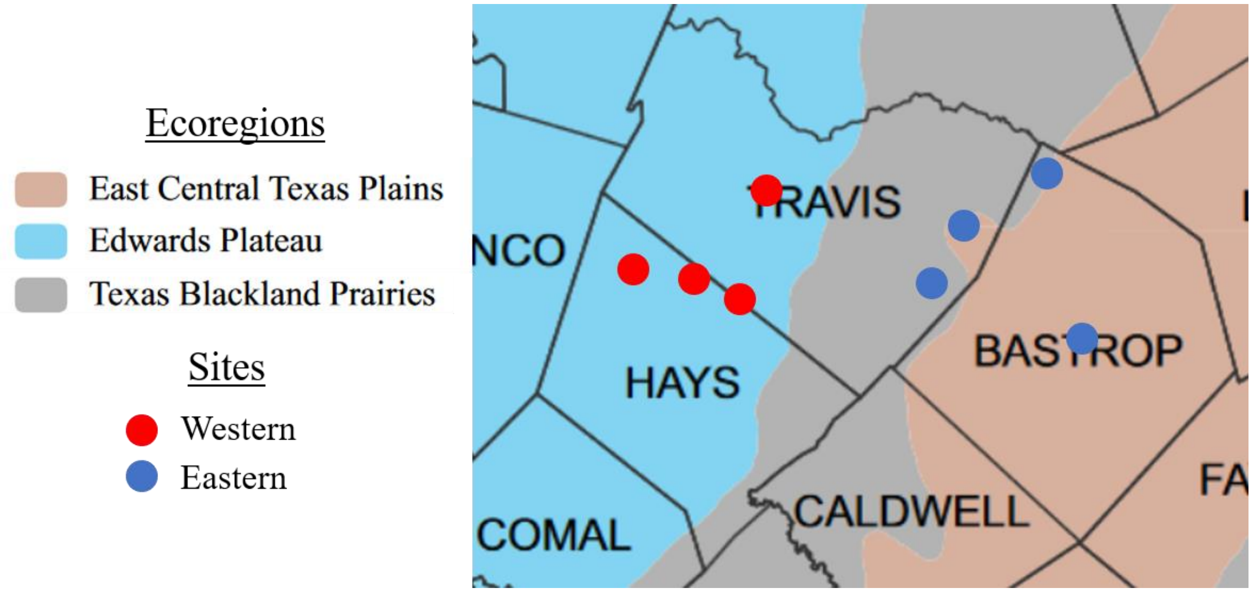


Figure 4.1: Location of all 8 experimental replicates, showing which replicates are in the western block and which are in the eastern block. Ecoregions map is from TPWD (2011).

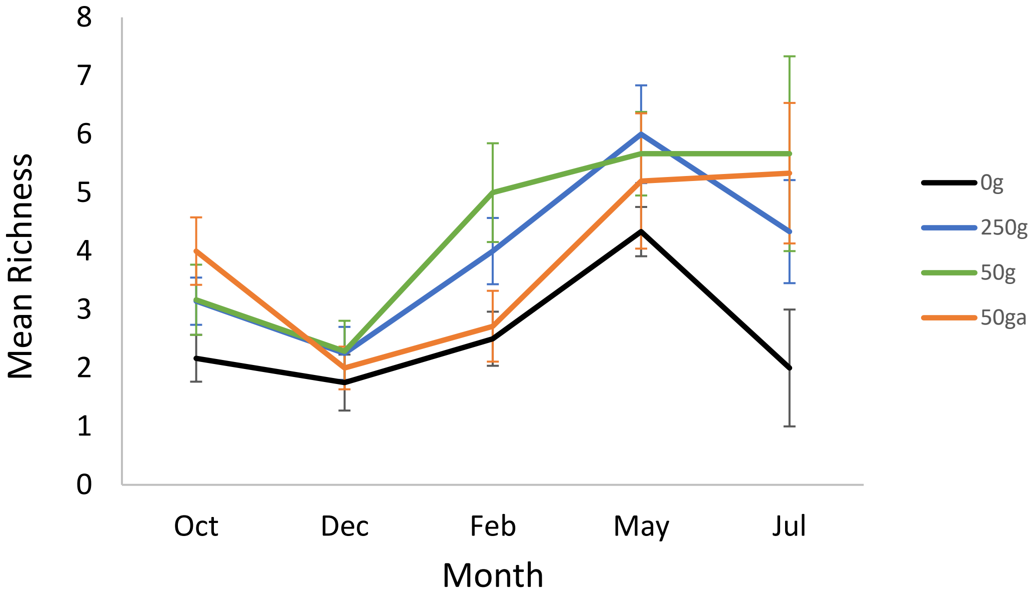


Figure 4.2: Mean species richness (± SE) over time for each of the four sediment input treatments. Species richness changed seasonally, with a peak in diversity in May. In addition, the 50g treatment had significantly higher species richness than the 0g treatment over the course of the experiment. The effect of treatment on species richness did not change over time.

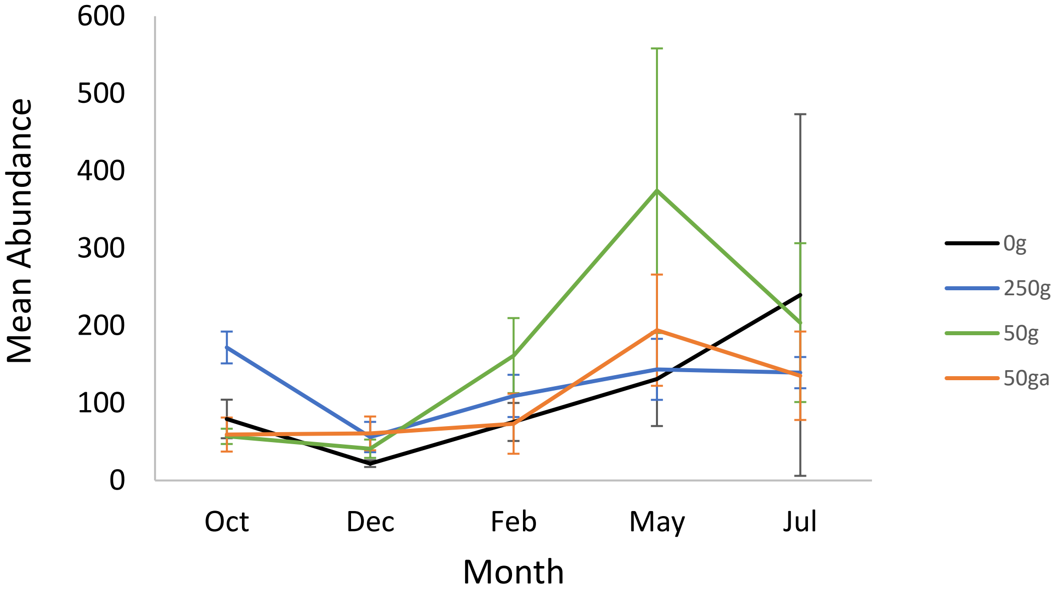


Figure 4.3: Mean total community abundance (± SE) over time for each of the four sediment input treatments. Total abundance changed seasonally, but it was not affected by sediment treatment or a treatment-by-time interaction.

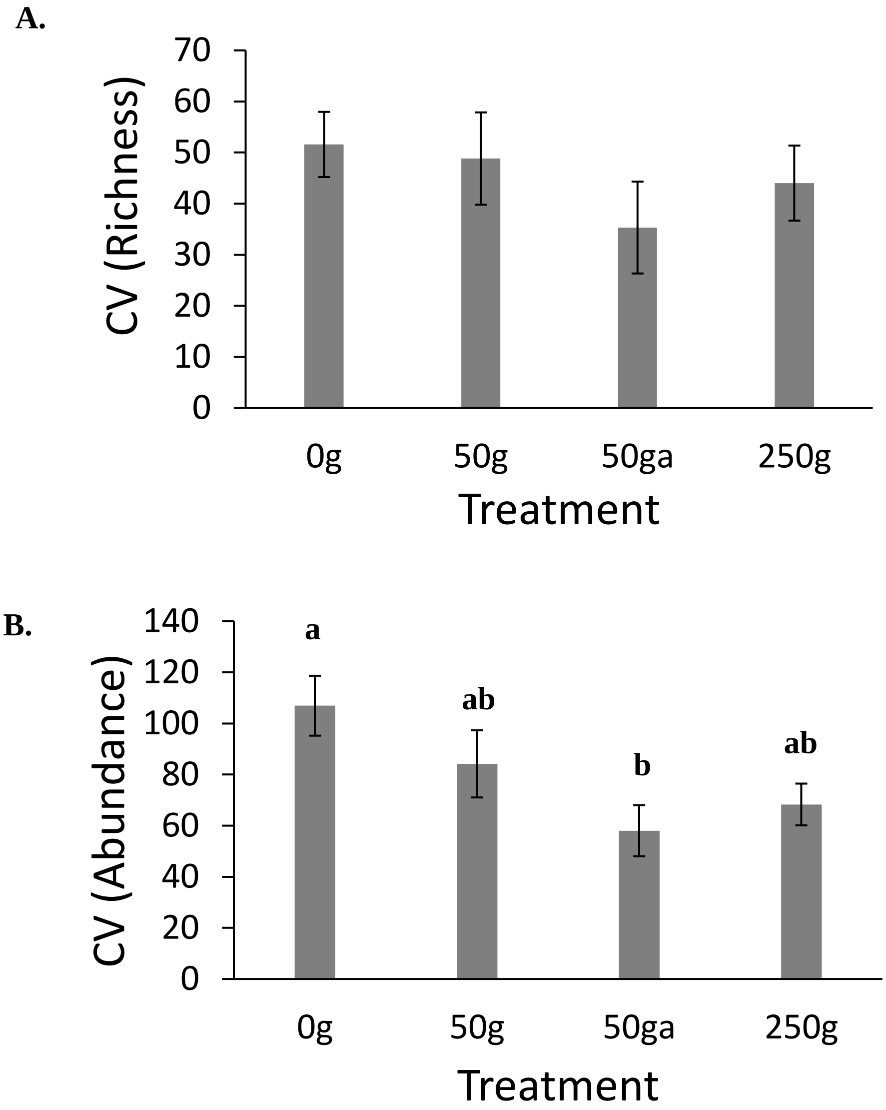


Figure 4.4: Coefficient of variation (mean ± SE) in species richness (Panel A.) and abundance (Panel B.) among treatments for the entire macroinvertebrate community. Variation in species richness was similar across treatments. Variation in abundance was highest in the 0g treatment and lowest in the 50ga treatment.

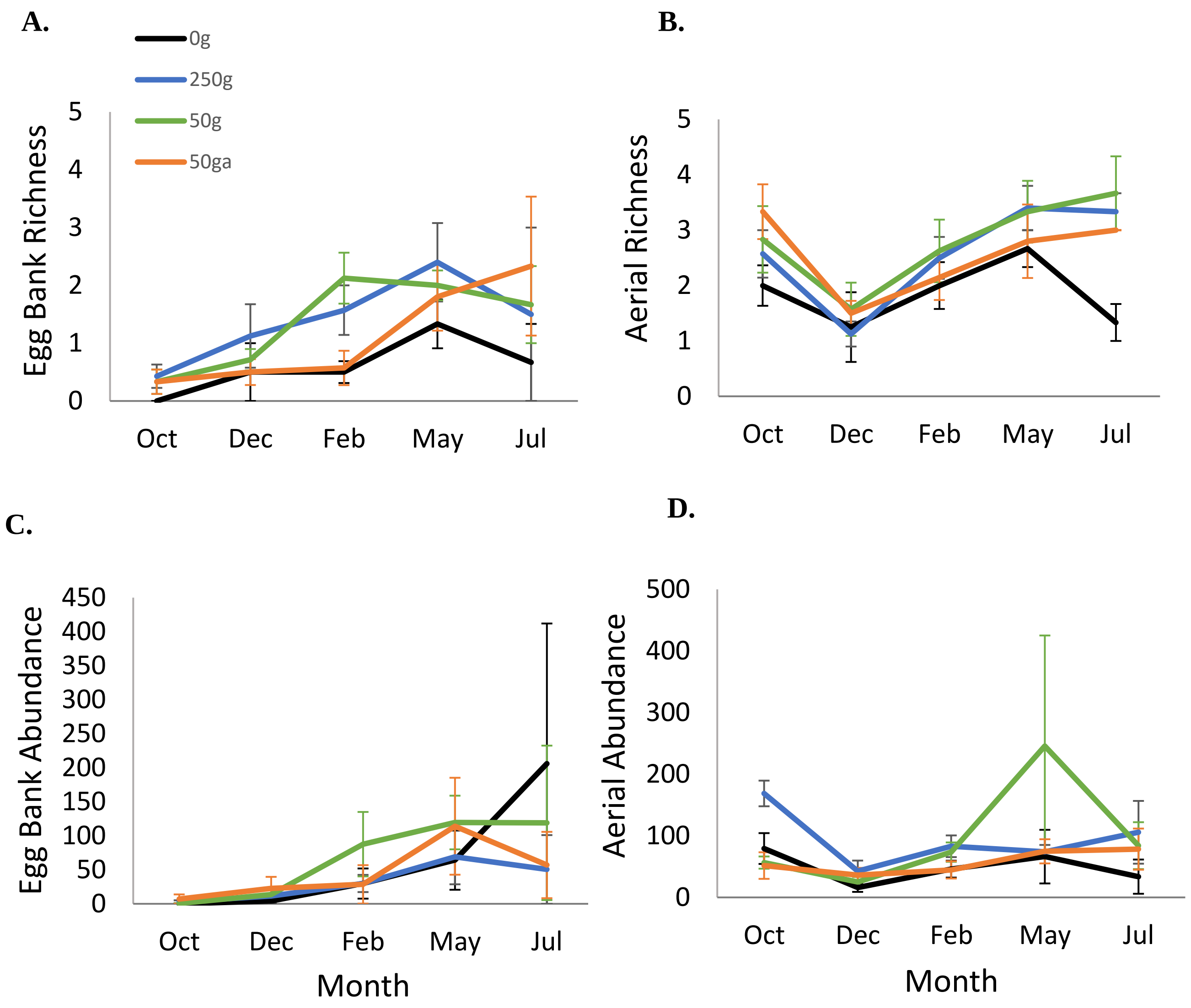


Figure 4.5: Richness and abundance data for taxa that hatch from the egg bank (Panels A. and C.) and taxa that colonize aerially or terrestrially (Panels B. and D.). Richness and abundance for both sets of taxa varied over time, but sediment treatments did not differ.

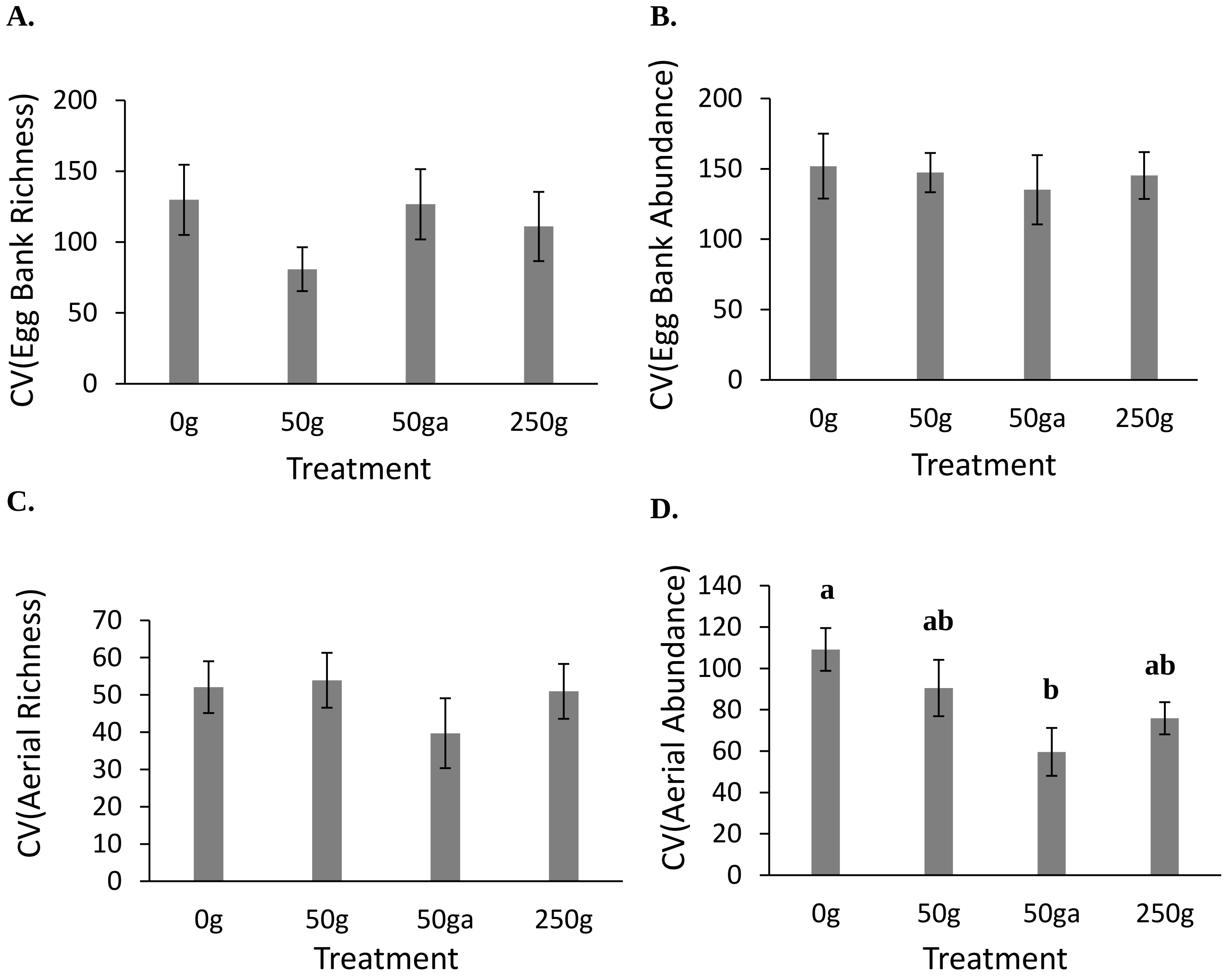


Figure 4.6: Coefficient of variation (±SE) in richness and abundance data for taxa that hatch from the egg bank (Panels A. and C.) and taxa that colonize aerially or terrestrially (Panels B. and D.). Only the aerial colonizers showed treatment differences, with more variable abundance in the 0g treatment relative to the 50ga treatment.

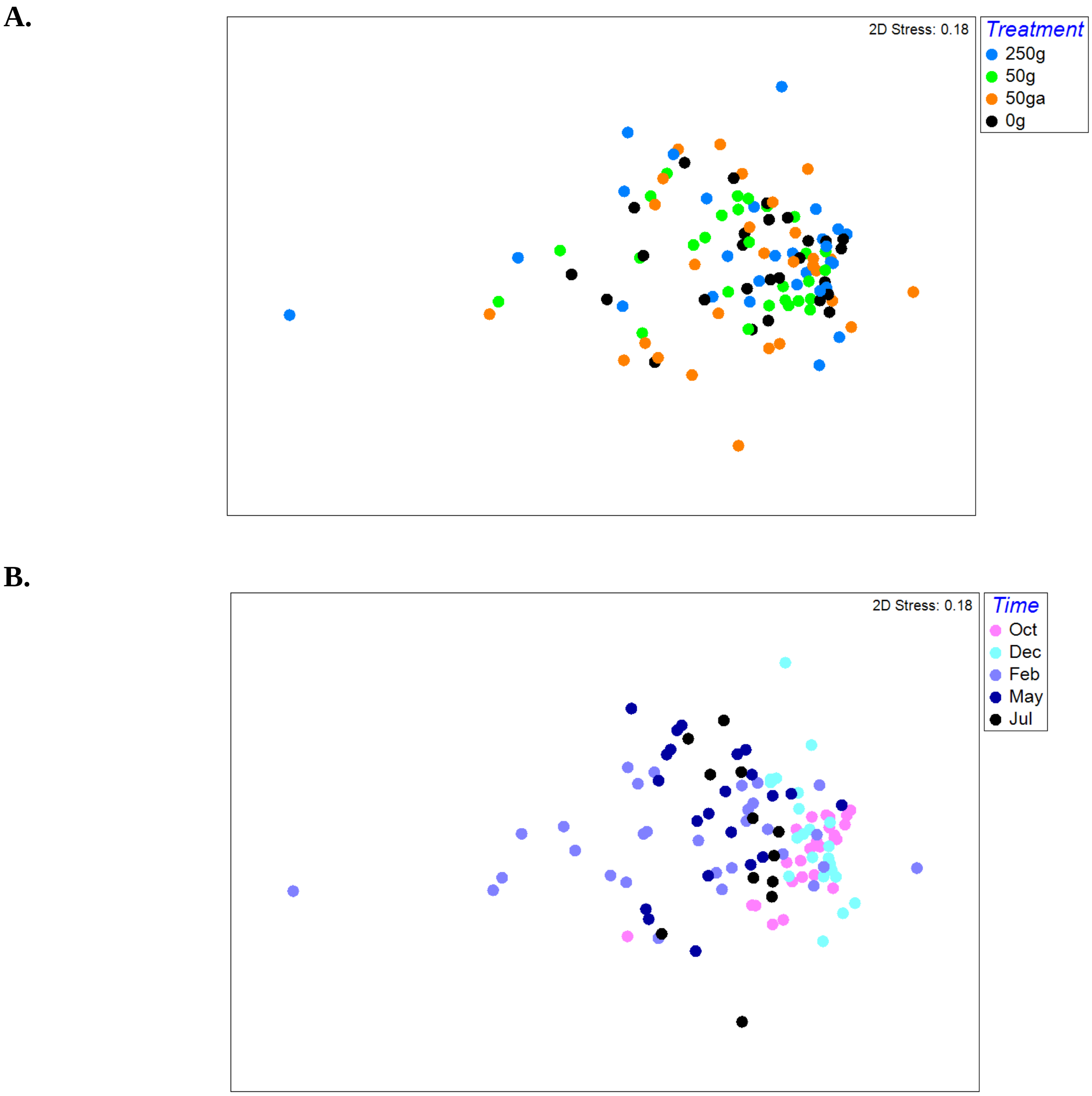


Figure 4.7: NMDS plots showing similarity in community composition in each mesocosm based on treatment (Panel A) and sampling time (Panel B). Communities that share similar composition based on Bray-Curtis dissimilarity appear closer together on the ordination plots. There were seasonal changes in community composition, but sediment input treatment did not affect community composition.

Table 4.1: Temporal change in community composition, showing the taxa that contribute most to the difference in the two most dissimilar sampling dates: October and February.

October vs. February (Average Dissimilarity = 79.63)

Species	Avg. Abundance October	Avg. Abundance February	Contrib%
Culex sp. A	7.06	3.72	26.15
Ceriodaphnia sp.	1.24	3.71	13.86
Chironomidae	0.99	2.55	11.14
Culiseta sp.	0	1.86	8.6
Ostracod A	0.15	2.7	8.53
Aedes sp.	0.55	1.44	6.38
Anopheles sp.	0.05	1.08	4.24
Mite	0.15	0.71	2.89
Pantala sp.	0.6	0	2.64
Culex sp. B	0	0.86	2.46
Collembola	0.34	0.3	2.23
Ostracod B	0	0.62	1.95

Chapter 5: Conclusions--The effects of habitat selection behavior on the stability of populations, communities, and ecosystems

POPULATIONS:

In an experiment manipulating dispersal among local snail populations, the results indicated that dispersal *per se* was important for dampening fluctuations of density caused by stochastic disturbances. Dispersal stabilized fluctuations in population size and contributed to increasing the persistence of local populations because the net movement of snails was away from areas of high density and towards areas of low density, promoting asynchrony among populations. The snails seemed to have a slight preference for low density when immigrating, and the treatment where immigration choices were allowed had the longest metapopulation persistence and the least variable local population size. However, most of the stabilizing effect of dispersal seems to come from increased emigration when snail density was high, analogous to a diffusive process. But because diffusion tends to result in movements that show negative density-dependence, even in scenarios where immigration is undirected or only slightly directed, dispersal can still be a strong stabilizing force relative to landscapes with no dispersal or landscapes with dispersal that does not depend on density.

COMMUNITIES:

In communities of competing species, habitat choice and density-dependent dispersal might also contribute to asynchrony among species, thus promoting diversity and more stable communities over time. However, inclusion of multiple trophic levels complicates the effects of habitat choice behavior on stability. In an experiment manipulating immigration behavior of aquatic insects during and after a pulse of fish predation, the results showed that choice behaviors initially decrease stability: when insects can choose where to colonize, most species avoid fish and thus patches experience losses in diversity and ecosystem function. However, upon removal of the predator, choice increased the resilience of community and ecosystem properties. So, while choice behavior exacerbated the effects of disturbance on species richness and ecosystem properties, choice resulted in faster recovery relative to random dispersal. The results highlight the importance of colonization behavior as both a source of stability and a source of sensitivity to disturbances when multiple trophic levels are involved.

ECOSYSTEMS:

Flows of individuals among patches can be important for stability of populations and communities as discussed above, but how do abiotic flows affect stability? In an experiment manipulating sediment inputs in mesocosms mimicking small rock pool communities, the data suggest that sediment inputs had weak effects on community stability, and smaller pulsed inputs are not more stabilizing than a single large pulsed input. There were small effects of sediment inputs on stability, with small pulses of nutrients showing more stable community abundance than ecosystems with no sediment inputs. This stabilization effect was likely driven by habitat choice behavior, since the sediment input treatments affected organisms with active dispersal more than those with passive dispersal. This experiment shows that habitat choice is not just a force for stability in the face of disturbance: systems with pulses of resource abundance might also be stabilized by this type of dispersal behavior.

IMPLICATIONS:

Dispersal in many theoretical models is often assumed to consist of random, undirected movements where the probability of immigration depends only on spatial factors, such as patch size and isolation (Binckley and Resetarits, 2005; e.g. Haegeman and Loreau, 2014). In nature, many species can make choices about when and where to disperse based on environmental cues. In environments that vary over time, organisms may be able to track changes in resource availability or predation risk and thus have populations that are less prone to extinction (Diamond, 1975). In addition, negative density-dependent dispersal should result in decreased population growth rates in high-density patches, and increased population growth rates in low-density patches (Holt, 1993; Amarasekare, 2010). Thus, habitat selection could dampen oscillations in population sizes among linked patches and contribute to the rescue of populations in low-density patches. The experiments in this dissertation are useful as direct empirical tests of these predictions. Experiments linking dispersal behavior to temporal stability in populations, communities, and ecosystems are rare (Ohgushi, 1995; Howeth and Leibold, 2010; Steiner et al., 2011), and so these represent significant contributions to our understanding of ecological stability.

All ecosystems experience environmental changes over time, with important consequences on populations and communities (Row et al. 2014). Understanding changes in community structure and factors that affect stability in the face of change is a central goal in Ecology, with many practical applications. Human society depends on ecosystem functions, which are affected by community structure (Holyoak et al. 2005, Cardinale et al. 2012). In order to make predictions about how ecosystems will respond in changing environments, it is critical to understand the role of habitat selection on species' responses to change, and how this can alter the stability of ecosystems over time. Habitat selection is common (Morris, 2003; Edelaar and Bolnick, 2012), and therefore studying the effects of habitat selection is important to our basic understanding of ecosystems as well.

Works Cited

Abbott, K. C. 2011. A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. Ecology letters, 14(11), 1158-1169.

Abrams, P. 2007. Habitat choice in predator-prey systems: spatial instability due to interacting adaptive movements. The American Naturalist 169: 581-594.

Abrams, P. and L. Ruokolainen. 2011. How does adaptive consumer movement affect population dynamics in consumer-resource metacommunities with homogeneous patches? Journal of Theoretical Biology 277: 99–110.

Allen, M.R. 2007. Measuring and modeling dispersal of adult zooplankton. Oecologia 153: 135-143.

Amarasekare, P. 2010. Effect of non-random dispersal strategies on spatial coexistence mechanisms. Journal of Animal Ecology 79: 282–293.

Anderson, W. B., and Polis, G. A. 2004. Allochthonous nutrient and food inputs: consequences for temporal stability. Food webs at the landscape level. University of Chicago Press, Chicago, 82-95.

Araújo, C. V., Moreira-Santos, M., and Ribeiro, R. 2016. Active and passive spatial avoidance by aquatic organisms from environmental stressors: a complementary perspective and a critical review. Environment international, 92, 405-415.

Barko, J. W., and Smart, R. M. 1981. Sediment-based nutrition of submersed macrophytes. Aquatic Botany, 10, 339-352.

Baron, J. S., LaFrancois, T., and Kondratieff, B. C. 1998. Chemical and biological characteristics of desert rock pools in intermittent streams of Capitol Reef National Park, Utah. The Great Basin Naturalist, 250-264.

Bartumeus, F., da Luz, M. G. E., Viswanathan, G. M., and Catalan, J. 2005. Animal search strategies: a quantitative random-walk analysis. Ecology, 86(11), 3078-3087.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18: 1482-1491.

Belgacem, F., and Cosner, C. 1995. The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment. Canad. Appl. Math. Quart, 3(4), 379-397.

Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B, 57, 289–300.

Benton, T. and D. Bowler. 2012a. Linking dispersal to spatial dynamics. In Dispersal ecology and Evolution. Ed. Clobert, J., M. Baguette, T. Benton, and J. Bullock. Oxford University Press. Oxford, U.K.

Benton, T. and D. Bowler. 2012b. Dispersal in invertebrates: influences on individual decisions. In Dispersal ecology and Evolution. Ed. Clobert, J., M. Baguette, T. Benton, and J. Bullock. Oxford University Press. Oxford, U.K.

Binckley, C. A., and Resetarits Jr, W. J. 2008. Oviposition behavior partitions aquatic landscapes along predation and nutrient gradients. Behavioral Ecology, 19(3), 552-557.

Binckley, C. and W. Resetarits. 2007. Effects of forest canopy cover on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. Oecologia 153: 951-958.

Binckley, C. and W. Resetarits. 2009. Spatial and temporal dynamics of habitat selection across canopy gradients generates patterns of species richness and composition in aquatic beetles. Ecological Entomology 34: 457-465.

Bovbjerg, R. V. 1968. Responses to food in lymnaeid snails. Physiological Zoology, 41(4), 412-423.

Bowler, D. E., and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews, 80(2), 205-225.

Brendonck, L. and L. De Meester. 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia 491: 65-84.

Brown, J. S., Laundré, J. W., and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of mammalogy, 80(2), 385-399.

Butzler, J. and J. Chase. 2009. The effects of variable nutrient additions on a pond mesocosm community. Hydrobiologia 617: 65-73.

Cameron, R. A. D., and Carter, M. A. 1979. Intra-and interspecific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). The Journal of Animal Ecology, 237-246.

Cantrell, R. S., Cosner, C., and Lou, Y. 2006. Movement toward better environments and the evolution of rapid diffusion. Mathematical biosciences, 204(2), 199-214.

Cantrell, R. S., Cosner, C., and Lou, Y. 2008. Approximating the ideal free distribution via reaction–diffusion–advection equations. Journal of Differential Equations, 245(12), 3687-3703.

Cantrell, R., C. Cosner, and Y. Lou. 2010. Evolution of Dispersal and the Ideal Free Distribution. Mathematical Biosciences and Engineering 7: 17–36.

Cardinale, B., J. Duffy, A. Gonzalez, D. Hooper, C. Perrings, P. Venail, A. Narwani, G. Mace, D. Tilman, D. Wardle, A. Kinzig, G. Daily, M. Loreau, J. Grace, A. Larigauderie, D. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486: 59-67.

Chalcraft, D. R., Cox, S. B., Clark, C., Cleland, E. E., Suding, K. N., Weiher, E., and Pennington, D. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. Ecology, 89(8), 2165-2171.

Chalcraft, D., C. Binckley, and W. Resetarits. 2005. Experimental venue and estimation of interaction strength: comment. Ecology 86: 1061-1067.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics, 31(1), 343-366.

Clarke, K. and Gorley, R. 2006. PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth, UK.

Clarke, K. and Warwick, R. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E: Plymouth, UK.

Conradt, L., Roper, T. J., and Thomas, C. D. 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. Oikos, 95(3), 416-424.

Cottingham, K., B. Brown and J. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4: 72-85.

De Meester, L., S. Declerck, R. Stoks, G. Louette, F. De Meutter, T. De Bie, E. Michels, and L. Brendonck. 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 715-725.

DeAngelis, D. and W. Mooij. 2005. Individual-based modeling of ecological and evolutionary processes. Annual Review of Ecology, Evolution, and Systematics 36: 147–168.

Den Boer, P. J. 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). Oecologia, 4(1), 1-28.

Denno, R. F., and Roderick, G. K. 1992. Density-related dispersal in planthoppers: effects of interspecific crowding. Ecology, 73(4), 1323-1334.

Diamond, J. 1975. Assembly of species communities. In Ecology and Evolution of Communities, ed. M. Cody and J. Diamond, 342-444. Cambridge, MA, Harvard University Press.

Downing, A. and M. Leibold. 2010. Species richness facilitates ecosystem resilience in aquatic food webs. Freshwater Biology 55: 2123-2137.

Downing, A. L., and M. Leibold. 2002. Ecosystem consequences of species richness and composition in pond food webs. Nature, 416: 837-841.

Downing, A., B. Brown, E. Perrin, T. Keitt, and M. Leibold. 2008. Environmental fluctuations induce scale-dependent compensation and increase stability in plankton ecosystems. Ecology 89: 3204-3214.

Edelaar, P. and D. Bolnick. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. Trends in Ecology and Evolution 27: 659-665.

Eisenberg, R. M. 1970. The role of food in the regulation of the pond snail, Lymnaea elodes. Ecology, 51(4), 680-684.

Evans, M.E.K., and J.J. Dennehy. 2005. Germ banking: bet-hedging and variable release from egg and seed dormancy. Quarterly Review of Biology 80: 431-451.

Fahrig, L., and Paloheimo, J. E. 1987. Interpatch dispersal of the cabbage butterfly. Canadian Journal of Zoology, 65(3), 616-622.

Farnsworth, K. D., and Beecham, J. A. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. The American Naturalist, 153(5), 509-526.

Fretwell, S. and H. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16-36.

Gilliam, J. F., and Fraser, D. F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology, 68(6), 1856-1862.

Gonzalez, A., Lawton, J. H., Gilbert, F. S., Blackburn, T. M., and Evans-Freke, I. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science, 281(5385), 2045-2047.

Gouhier, T., F. Guichard, and A. Gonzalez. 2010. Synchrony and stability of food webs in metacommunities. The American Naturalist 175: E16-E34.

Grand, T. 2002. Foraging-predation risk trade-offs, habitat selection, and the coexistence of competitors. The American Naturalist, 159: 106-112.

Gravel, D., Mouquet, N., Loreau, M., and Guichard, F. 2010. Patch dynamics, persistence, and species coexistence in metaecosystems. The American Naturalist, 176(3), 289-302.

Gray, D.K. and S.E. Arnott. 2011. Does dispersal limitation impact the recovery of zooplankton communities damaged by a regional stressor? Ecological Applications 21: 1241-1256.

Green, D. M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biological conservation, 111(3), 331-343.

Grimm, V., T. Wyszomirski, D. Aikman, and J. Uchmanski. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115: 275–282.

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jorgensen, W. M. Mooij, B. Mueller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Rueger, E. Strand, S. Souissi, R. A. Stillman, R. Vabo, U. Visser, and D. L. DeAngelis. 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198:115–126.Haegeman, B. and M. Loreau. 2014. General relationships between consumer dispersal, resource dispersal and metacommunity diversity. Ecology Letters 17: 175-184.

Gripenberg, S., Mayhew, P. J., Parnell, M., and Roslin, T. 2010. A meta-analysis of preference–performance relationships in phytophagous insects. Ecology letters, 13(3): 383-393.

Grosberg, R. K. 1981. Competitive ability influences habitat choice in marine invertebrates. Nature, 290(5808): 700-702.

Gundersen, G., Andreassen, H. P., and Ims, R. A. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. Ecology Letters, 5(2), 294-301.

Gyllström, M., and Hansson, L. A. 2004. Dormancy in freshwater zooplankton: induction, termination and the importance of benthic-pelagic coupling. Aquatic Sciences, 66(3), 274-295.

Haegeman, B., and Loreau, M. 2014. General relationships between consumer dispersal, resource dispersal and metacommunity diversity. Ecology letters, 17(2), 175-184.

Hairston, N.G., Jr., and C.M. Kearns. 2002. Temporal dispersal: Ecological and evolutionary aspects of zooplankton egg banks and the role of sediment mixing. Integrative and Comparative Biology 42: 481-491.

Hanski, I. 1998. Metapopulation dynamics. Nature, 396(6706), 41.

Hanski, I. and M. Singer. 2001. Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. The American Naturalist 158: 341-353.

Hanski, I., and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In Metapopulation Biology (pp. 5-26). Academic Press.

Hanski, I., and Woiwod, I. P. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology, 656-668.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological journal of the Linnean Society, 42(1-2), 89-103.

Hauzy, C., M. Gauduchon, F. Hulot, and M. Loreau. 2010. Density-dependent dispersal and relative dispersal affect the stability of predator–prey metacommunities. Journal of Theoretical Biology 266: 458-469.

Hawkins, C. P. 1984. Substrate associations and longitudinal distributions in species of Ephemerellidae (Ephemeroptera: Insecta) from western Oregon. Freshwater Invertebrate Biology, 3(4): 181-188.

Heithaus, M. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92: 542-554.

Henry, P. Y., Vimond, L., Lenormand, T., and Jarne, P. 2006. Is delayed selfing adjusted to chemical cues of density in the freshwater snail Physa acuta? Oikos, 112(2), 448-455.

Holling, C. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4: 1-23.

Holt, R. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. Evolutionary Ecology 1: 331-347.

Holt, R. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In Species diversity in ecological communities: historical and geographical perspectives, ed. R. Ricklefs and D. Schluter. University of Chicago Press, Chicago, IL.

Holt, R. D., 2008. Theoretical perspectives on resource pulses. Ecology 89: 671–681.

Holyoak, M., M. Leibold, and R. Holt. 2005. Metacommunities: spatial dynamics and ecological communities. The University of Chicago Press, Chicago, IL, USA.

Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. The American Naturalist 144:954–977.

Huston, M., D. DeAngelis, and W. Post. 1988. New Computer Models Unify Ecological Theory. BioScience 38: 682–691.

Huxel, G. R., and McCann, K. 1998. Food web stability: the influence of trophic flows across habitats. The american naturalist, 152(3), 460-469.

Huxel, G. R., McCann, K., and Polis, G. A. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. Ecological Research, 17(4), 419-432.

Jefferies, R. L. 2000. Allochthonous inputs: integrating population changes and food-web dynamics. Trends in Ecology and Evolution, 15(1), 19-22.

Jenkins, D. G., and Underwood, M. O. 1998. Zooplankton may not disperse readily in wind, rain, or waterfowl. In Rotifera VIII: A Comparative Approach (pp. 15-21). Springer, Dordrecht.

Johnson MD. 2007. Measuring habitat quality: a review. The Condor109(3):489-504.

Jones, S.E, J.T. Lennon, and D. Karl. 2010. Dormancy contributes to the maintenance of microbial diversity. Proceedings of the National Academy of Sciences of the United States of America 107: 5881-5886.

Kappes, H., and Haase, P. 2012. Slow, but steady: dispersal of freshwater molluscs. Aquatic Sciences, 74(1), 1-14.

Kendall, B., O. Bjørnstad, J. Bascompte, T. Keitt, and W. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. The American Naturalist, 155: 28-636.

Kindlmann, P., and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23:879-890.

Kindvall, O., and Petersson, A. 2000. Consequences of modelling interpatch migration as a function of patch geometry when predicting metapopulation extinction risk. Ecological Modelling, 129(1), 101-109.

Kokkoris, G. D., Troumbis, A. Y., and Lawton, J. H. 1999. Patterns of species interaction strength in assembled theoretical competition communities. Ecology Letters, 2: 70-74.

Komarek, E. V. 1969. Fire and animal behavior. Proceedings Tall Timbers Fire Ecology Conference 9: 160-207.

Křivan, V. and E. Sirot. 2002. Habitat selection by two competing species in a two-habitat environment. The American Naturalist 160: 214-234.

Kuussaari, M., Saccheri, I., Camara, M., and Hanski, I. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. Oikos: 384-392.

Larson, D., Y. Alarie, and R. Roughley. 2000. Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with emphasis on the fauna of Canada and Alaska. NRC Research Press, Ottowa, Ontario, Canada.

Leibold, M. A., and Chase, J. M. 2017. Metacommunity ecology (Vol. 59). Princeton University Press.

Leibold, M. A., J. M. Chase, J. B. Shurin and A. L. Downing, 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics 28: 467–494.

Leibold, M., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601-613.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. American Entomologist, 15(3), 237-240.

Lima, S. L., and Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution, 11(3), 131-135.

Loreau, M. and C. Mazancourt. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecology Letters 16: 106-115.

Lytle, D. A. 2000. Biotic and abiotic effects of flash flooding in a montane desert stream. Archiv für Hydrobiologie, 85-100.

MacArthur, R. and E. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology 1: 1-215.

Martin, T.E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? Ecology, 82(1):175-188.

Matthysen, E. 2012. Multicausality of dispersal: a review. In Dispersal ecology and Evolution. Ed. Clobert, J., M. Baguette, T. Benton, and J. Bullock. Oxford University Press. Oxford, U.K.

McCann, K. and N. Rooney. 2009. The more food webs change, the more they stay the same. Philosophical Transactions of the Royal Society B 364: 1789-1801.

McCann, K., Hastings, A., and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. Nature, 395: 794-798.

McCarthy, L. C. 2015. The Effects of Zooplankton Dispersal on Community Assembly of Temporary Ponds. (Unpublished doctoral dissertation). East Carolina University, Greenville, NC, USA.

McPeek, M. A., and Holt, R. D. 1992. The evolution of dispersal in spatially and temporally varying environments. The American Naturalist, 140(6), 1010-1027.

Merritt, R. W., and Cummins, K. W. (Eds.). 1996. An introduction to the aquatic insects of North America. Kendall Hunt. Dubuque, IA, USA.

Morin, P. 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. Ecology, 80(3), 752-760.

Morris, D. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecological Monographs: 270-281.

Morris, D. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136: 1-13.

Morris, D. W. 2003b. Toward an ecological synthesis: a case for habitat selection. Oecologia 136: 1-13.

Morris, D. W. 2003a. How can we apply theories of habitat selection to wildlife conservation and management?. Wildlife Research, 30(4), 303-319.

Mouquet, N., and Loreau, M. 2003. Community patterns in source-sink metacommunities. The american naturalist, 162(5), 544-557.

Nowlin, W. H., González, M. J., Vanni, M. J., Stevens, M. H. H., Fields, M. W., and Valente, J. J. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. Ecology, 88(9), 2174-2186.

Ohgushi, T. 1995. Adaptive behavior produces stability in herbivorous lady beetle populations. Population dynamics: new approaches and synthesis. Academic Press, San Diego, 303-319.

Otronen, M., and Hanski, I. 1983. Movement patterns in Sphaeridium: differences between species, sexes, and feeding and breeding individuals. The Journal of Animal Ecology, 663-680.

Pandit, S., J. Kolasa, and K. Cottenie. 2013. Population synchrony decreases with richness and increases with environmental fluctuations in an experimental metacommunity. Oecologia, 171: 237-247.

Parrish, J. K., and Edelstein-Keshet, L. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science, 284(5411): 99-101.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology. Annual Review of Ecology and Systematics 28:289–316.

Preisser, E. L., Bolnick, D. I., and Benard, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology, 86(2), 501-509.

Pulliam, H. 1988. Sources, sinks, and population regulation. American Naturalist: 652-661.

Pyron, M., and Brown, K. M. 2015. Introduction to mollusca and the class Gastropoda. In Thorp and Covich's Freshwater Invertebrates (pp. 383-421). Academic Press.

Rausher, M. D. 1979. Larval habitat suitability and oviposition preference in three related butterflies. Ecology, 60(3): 503-511.

Resetarits, W. 2005. Habitat selection behavior links local and regional scales in aquatic systems. Ecology Letters 8: 480-486.

Resetarits, W. 2001. Colonization under threat of predation: non-lethal effects of fish on aquatic beetles, Tropisternus lateralis (Coleoptera: Hydrophilidae). Oecologia 129: 155-160.

Resetarits, W. and C. Binckley. 2014. Species responses of colonising beetles to variation in patch quality, number, and context in experimental aquatic landscapes. Ecological Entomology 39: 226-235.

Resetarits, W. J., and Binckley, C. A. 2009. Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. Ecology, 90(4), 869-876.

Resetarits, W., C. Binckley, and D. Chalcraft. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes. In Metacommunities: spatial dynamics and ecological communities, ed. M. Holyoak, M. Leibold, and R. Holt. The University of Chicago Press, Chicago, IL, USA.

Ricklefs, R. and D. Schluter. 1993. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, IL.

Rohani, P., May, R. M., and Hassell, M. P. 1996. Metapopulation and equilibrium stability: the effects of spatial structure. Journal of Theoretical Biology, 181(2), 97-109.

Roland, J., Keyghobadi, N., and Fownes, S. 2000. Alpine Parnassius butterfly dispersal: effects of landscape and population size. Ecology, 81(6): 1642-1653.

Rosenzweig, M. 1991. Habitat selection and population interactions: the search for mechanism. The American Naturalist, 5-28.

Rosenzweig, M. and Z. Abramsky. 1985. Detecting density-dependent habitat selection. The American Naturalist 126:405–417.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62: 327–335.

Row, J., P. Wilson, and D. Murray. 2014. Anatomy of a population cycle: the role of density dependence and demographic variability on numerical instability and periodicity. Journal of Animal Ecology 83: 800-812.

Rubbo, M. and J. Kiesecker. 2004. Leaf litter composition and community structure: translating regional species changes into local dynamics. Ecology 85: 2519-2525.

Rykiel, E. 1985. Towards a definition of ecological disturbance. Australian Journal of Ecology 10: 361-365.

Saether, B. E., Engen, S., and Lande, R. 1999. Finite metapopulation models with density–dependent migration and stochastic local dynamics. Proceedings of the Royal Society of London. Series B: Biological Sciences, 266(1415), 113-118.

Savino, J. F., and Stein, R. A. 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environmental Biology of Fishes, 24(4): 287-293.

Schmidt, K., J. Earnhardt, J. Brown, and R. Holt. 2000. Habitat selection under temporal heterogeneity: exorcizing the ghost of competition past. Ecology 81: 2622-2630.

Schoener, T. W., and Spiller, D. A. 1992. Is extinction rate related to temporal variability in population size? An empirical answer for orb spiders. The American Naturalist, 139(6), 1176-1207.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19:473-511.

Smith, A. T., and Peacock, M. M. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology, 4(3): 320-323.

Steffen, Will, Paul J. Crutzen, and John R. McNeill. 2007. The Anthropocene: are humans now overwhelming the great forces of nature. Ambio: A Journal of the Human Environment 36: 614-621.

Steiner, C., R. Stockwell, V. Kalaimani, and Z. Aqel. 2011. Dispersal promotes compensatory dynamics and stability in forced metacommunities. The American Naturalist 178: 159-170.

Streby, H. M., Kramer, G. R., Peterson, S. M., Lehman, J. A., Buehler, D. A., and Andersen, D. E. 2015. Tornadic storm avoidance behavior in breeding songbirds. Current Biology, 25(1), 98-102.

Svensson, J., M. Lindegarth, P. Jonsson, and H. Pavia. 2012. Disturbance–diversity models: what do they really predict and how are they tested? Proceedings of the Royal Society B: Biological Sciences 279: 2163-2170.

Takimoto, G., T. Iwata, and M. Murakami. 2002. Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. Ecological Research 17:433–439.

TCEQ (Texas Commission on Environmental Quality). 2009. A guide to freshwater ecology. www.tceq.state.tx.us/goto/publications

Tessier, A. J., and Leibold, M. A. 1997. Habitat use and ecological specialization within lake Daphnia populations. Oecologia, 109(4), 561-570.

Thorp, J. H., and Covich, A. P. (Eds.). 2009. Ecology and classification of North American freshwater invertebrates. Academic press.

Tilman, D., and Kilham, P. 1982. Community Ecology: The Role of Limiting Nutrients. Annual Review of Ecology and Systematics, 13, 349-372.

TPWD (Texas Parks and Wildlife Department). 2011. Level III Ecoregions of Texas. tpwd.texas.gov/publications/pwdpubs/media/pwd_mp_e0100_1070z_08.pdf

Tuominen, L., Kairesalo, T., and Hartikainen, H. 1994. Comparison of methods for inhibiting bacterial activity in sediment. Appl. Environ. Microbiol., 60(9), 3454-3457.

Turner, A. M., Fetterolf, S. A., and Bernot, R. J. 1999. Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia, 118(2), 242-247.

Urban, M., M. Leibold, P. Amarasekare, L. De Meester, R. Gomulkiewicz, M. Hochberg, C. Klausmeier, N. Loeuille, C. de Mazancourt, J. Norberg, J. Pantel, S. Strauss, M. Vellend, and M. Wade. 2008. The evolutionary ecology of metacommunities. Trends in Ecology and Evolution 23: 311–317.

Van de Meutter, R. Stoks, and L. de Meester. 2008. Size-selective dispersal of Daphnia resting eggs by backswimmers (Notonecta maculata). Biology Letters 4: 494-496.

Van der Meulen, E. S., Braat, L. C., and Brils, J. M. 2016. Abiotic flows should be inherent part of ecosystem services classification. Ecosystem Services, 19, 1-5.

Vanschoenwinkel, B., Gielen, S., Seaman, M., and Brendonck, L. 2008. Any way the wind blows-frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos, 117(1), 125-134.

Vanschoenwinkel, B., Waterkeyn, A., Jocqué, M., Boven, L., Seaman, M., and Brendonck, L. 2010. Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. Journal of the North American Benthological Society, 29(4), 1267-1278.

Vellend, M. 2010. Conceptual Synthesis in Community Ecology. Quarterly Review Of Biology: 1–30.

Vitousek, P., J. Aber, R. Howarth, G. Likens, P. Matson, D. Schindler, W. Schleinger, and D. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7: 737-750.

Vonesh, J. and J. Kraus. 2009. Pesticide alters habitat selection and aquatic community composition. Oecologia 160: 379-385.

Vonesh, J. R., Kraus, J. M., Rosenberg, J. S., and Chase, J. M. 2009. Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. Oikos, 118(8), 1219-1229.

Weber, M. J., and Brown, M. L. 2016. Effects of resource pulses on nutrient availability, ecosystem productivity, and temporal variability following a stochastic disturbance in eutrophic glacial lakes. Hydrobiologia, 771(1), 165-177.

Weber, M. J., and Brown, M. L. 2018. Effects of resource pulse magnitude on nutrient availability, productivity, stability, and food web dynamics in experimental aquatic ecosystems. Hydrobiologia, 814(1), 191-203.

Wilbur, H. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78: 2279-2302.

Williams, B., T. Rittenhouse, and R. Semlitsch. 2008. Leaf litter input mediates tadpole performance across forest canopy treatments. Oecologia 155: 377-384.

Williams, D. D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the North American Benthological Society, 15(4), 634-650.

Wojdak, J. M. 2009. Foraging and refuge use by a pond snail: Effects of physiological state, predators, and resources. Acta Oecologica, 35(5), 746-751.

Yang, L. H., Bastow, J. L., Spence, K. O., and Wright, A. N. 2008. What can we learn from resource pulses? Ecology 89: 621– 634.

Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N., and Spence, K. O. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs, 80(1), 125-151.

Yee, D., S. Taylor, and S. Vamosi. 2009. Beetle and plant density as cues initiating dispersal in two species of adult predaceous diving beetles. Oecologia 160: 25-36.

Email: deansr12@utexas.edu

This dissertation was typed by Robert Andrew Deans.