8-2006

Explaining Species Diversity By Linking Local and Large Scale Processes

Marc William Cadotte
University of Tennessee - Knoxville

Recommended Citation

Cadotte, Marc William, "Explaining Species Diversity By Linking Local and Large Scale Processes. " PhD diss., University of Tennessee, 2006.
https://trace.tennessee.edu/utk_graddiss/1648

To the Graduate Council:

I am submitting herewith a dissertation written by Marc William Cadotte entitled "Explaining Species Diversity By Linking Local and Large Scale Processes." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

James A. Drake, Major Professor

We have read this dissertation and recommend its acceptance:

Dan Simberloff, Nathan Sanders, Michael McKinney

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the graduate council:

I am submitting herewith a dissertation written by Marc William Cadotte entitled “Explaining species diversity by linking local and large scale processes.” I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

__James A. Drake____
Major Professor

We have read this dissertation
and recommend its acceptance:

____Dan Simberloff______

____Nathan Sanders______

____Michael McKinney___

Accept for the council:

___Anne Mayhew_____
Vice Chancellor and
Dean of Graduate studies

(Original signatures are on file with official student records.)

EXPLAINING SPECIES DIVERSITY BY LINKING LOCAL AND LARGE SCALE PROCESSES

A Dissertation Presented for the
Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Marc William Cadotte
Aug 2006

Thank you Shirley and Isabella for making everything worth it.

ACKNOWLEDGMENTS

Undertaking doctoral research is a daunting task, something that people cannot do alone. I am grateful to a number people who helped make this work possible and who supported my endeavors. Jon Lovett-Doust has been a constant encouragement and for him I never would have considered graduate education. I am extremely grateful to my family for all their support and especially to Shirley Lo-Cadotte for her love and patience, and to Isabella Cadotte for making the last few months exciting.

Jim Drake, my advisor, has been a wonderful source of moral and scientific support. He allowed me the freedom to grow and spread my wings. From Jim I learned that doing good science is as much about being creative has running a good experiment. To my committee members, Bob Holt (courtesy member), Mike McKinney, Nate Sanders and Dan Simberloff, I am extremely grateful for their input and guidance. Aaron King, who had to be removed from the committee because of a recent move, was also very helpful.

Being at the Department of Ecology and Evolutionary Biology has been one of the best experiences of my life; I have greatly enjoyed interactions with such diverse and skilled group of colleagues. I benefited from advice from and discussions with the following people: Arijana Barun, Monica Beals, Chris Boake, Marguerite Butler, Michael Collins, Greg Crutsinger, Rob Dunn, Sandy Echternacht, Mike Fuller, Matt Fitzpatrick, Jim Fordyce, Tad Fukami, Lou Gross, Colleen Iverson, Sean McMahon, Martin Nunez, Massimo Pigliucci, Kevin Smith, Lara Souza, Justin Walguarnery, and Jake Weltzin.

A number of people provided comments on portions of this dissertation, and to them I am indebted. They include: Bradley Cardinale, Karl Cottenie, Jim Drake, Tad Fukami, Bob Holt, Marcel Holyoak, Jamie Kneitel, Michel Loreau, Jon Lovett-Doust, Brad Murray, William Resetarits, Nathan Sanders, Dov Sax, Dan Simberloff and a number of anonymous reviewers.

The laboratory work presented in Chapters 3-6 could not have been completed without assistance from Kristin Clark, Allison Fortner, Tad Fukami, Sam Jantz, Monica Keele, Eli Kennedy, Jeff Lowder, Donny Mai, Amanda MacDonald and Manish Rana. Further, unpublished manuscripts or preprints were provided by Jonathan Chase, Helmut Hillebrand, Ronen Kadmon, Jamie Kneitel, Birte Matthiessen and Roly Russell.

Funding was generously provided by Department of Ecology and Evolutionary Biology, Science Alliance and Scholarly Activity and Research Incentive Funds, all at the University of Tennessee, and from the National Science Foundation (Doctoral Dissertation Improvement Grant (DEB 0206598) to Tad Fukami.

ABSTRACT

Large-scale processes are known to be important for patterns of species richness, yet the ways in which local and larger scale processes interact is not clear. I first examined published experiments that manipulated dispersal among local communities using meta-analyses. I show that local communities often readily increase diversity, but that there may be declines at larger spatial scales. I then used metacommunities consisting of microbial aquatic communities to examine how processes at different scales affect local and metacommunity richness. Specifically, I manipulated the potential dispersal rate, whether dispersal was localized or global, and variation in initial community composition. I showed that a low dispersal rate and intermediate distance dispersal enhanced local richness. Initial assembly variation had no effect on local richness, while a lack of dispersal or global dispersal reduced local richness. I also show that predation undoes any diversity increases associated with dispersal. At the metacommunity scale, richness was enhanced throughout the time course of the experiment by initial compositional variation and was reduced by high or global dispersal. Also predation identically structured local communities, and thus reveals large impacts at the metacommunity scale. I further show that these organisms exhibit competition-colonization tradeoffs, and examine how local scale disturbances can structure species diversity. If species are evenly distributed along this tradeoff, then diversity is maximized at intermediate disturbance rates. However if the tradeoff is colonist-skewed then diversity increases with disturbance, and declines is the tradeoff is competitor-skewed. But patterns of diversity at scales larger than the local community always show that diversity is maximized at intermediate disturbances, regardless of the distribution of species along the competition-colonization tradeoff. These results indicate that the effects of dispersal on species richness have a complex relationship with scale and are not solely divisible in to "regional" versus "local" scales. Finally, predictions of how dispersal structures communities appear dependent on local-scale processes, species interactions and historical assembly and disturbance frequency.

TABLE OF CONTENTS

1. General background and overview 1

2. Dispersal and species diversity: a meta-analysis
    - Abstract 3
    - Introduction 3
    - Methods 5
    - Results 10
    - Discussion 12

3. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment
    - Abstract 17
    - Introduction 17
    - Methods 20
    - Results 22
    - Discussion 27

4. The effects of resource enrichment, dispersal, and predation on local and meta-community structure
    - Abstract 31
    - Introduction 31
    - Methods 33
    - Results 36
    - Discussion 41

5. On testing the competition-colonization tradeoff in a multispecies assemblage
    - Abstract 43
    - Introduction 43
    - Methods 45
    - Results 47
    - Discussion 48

6. Competition-colonization tradeoffs and the intermediate disturbance hypothesis
    - Abstract 51
    - Introduction 51
    - Methods 53
    - Results 57
    - Discussion 59

7. Synthesis: Act locally, think regionally: incorporating ecological scale into conservation thinking.
    - Abstract 64
    - Introduction 64

1. Metapopulations extended to the community 68
2. Dispersal: predicting increases in diversity 70
3. Community saturation and invasions: it depends on the region 73
4. Invasive species dynamics at multiple spatial scales 75
5. Tradeoffs, neutral dynamics and spatial coexistence 77

Conclusions and conservation implications 81

Literature cited 84

Appendices

1. Supplemental material for Chapter 2 101
2. Supplemental material for Chapter 3 104

Vita 112

LIST OF TABLES

2.1. Summary of the studies used in this study...6-7
2.2. Results of homogeneity tests for the fixed effects model, and the mixed effect model if needed...10

3.1. Results of repeated measures ANOVAs testing the effect of dispersal rate, pathway and initial beta on number of patches occupied by each species............26
3.2. Mean time to colonize four other patches in single species metacommunity (n = 3 trials) and the corresponding dispersal rank (Cadotte et al. in review)................28

4.1. The 11 protozoan and rotifer species, plus the basal trophic species used in this experiment. 35
4.2. Results of the loglinear model, modeling main effects and their two-way interactions on local and regional species richness...37
4.3. Results of the loglinear model, showing within class effects on local and regional species richness...38

5.1. Mean colonization time in weeks, the associated colonization rank and the competition rank for each species used in this experiment...................................45

6.1. The two traits, colonization (*c*) and competitive ability (*i*), defining the 20 species used in the disturbance simulations...54
6.2. Disturbance treatments used in the microcosm experiment.................................56

7.1. Ecological scales at which ecological processes occur and measures of species diversity are made...67
2.A.1 Species used, their taxonomic affiliations, maximum size, relative size class, and dietary needs...105

LIST OF FIGURES

2.1. The hypothesized interaction between dispersal rate and species diversity at different spatial scales (Adapted from Mouquet and Loreau 2003)........................5
2.2. Dispersal enhances richness despite a rate effect..8
2.3. The standardized effect size of the studies used to test hypothesis 1 (local diversity)...11
2.4. The effect of the standardized dispersal rate on the standardized diversity of treatment for animal experiments...11
2.5. There was no effect of the standardized dispersal rate on the standardized diversity of treatment for plant experiments...13
2.6. The standardized effect size of the studies used to test hypothesis 3 (regional diversity)...13

3.1. Dispersal scale designs and the relative probabilities of species dispersal from community A to the other communities in the metacommunity............................19
3.2. Local, beta and regional richness for the 14 treatments used in the experiment...23
3.3. The effects of dispersal rate and initial beta on local, beta and regional richness on day 50...24
3.4. The effect of the three-way interaction among dispersal rate, scale and initial beta on local richness on day 50..24
3.5. Community similarity on day 50 as affected by A) dispersal scale; and B) both dispersal rate and initial beta, which also reveals the interaction between these two factors...25

4.1. Local prey community species richness during the 8 week study in each combination of predation/dispersal treatment...39
4.2. Regional (metacommunity) species richness during the 8 week study for Predation and Dispersal (P+D), Predation (P), Dispersal (D), Control (C), (mean ± SE, n=5)...40
4.3. The number of *Stentor coeruleus* (log +1) at high, medium and low resource levels, (mean ± SE, n= 5) with (a) dispersal and (b) no dispersal........................40

5.1. Hypothesized relationships between competitive and colonization abilities.........44
5.2. Colonization rates for individual species...47
5.3. The relationship between the number of extinctions caused by a species and the number of trials in which it persisted..49
5.4. The relationship between competitive and dispersal abilities, which support a competition-colonization tradeoff...49

6.1. At the (a) local, intra-patch, scale, disturbance frequency (here defined as number of disturbances per patch per time step) can produce unimodal or linear (increasing and decreasing) richness patterns dependent upon the distribution of species along a competition-colonization tradeoff gradient.................................58

6.2. Results of the microcosm experiment showing that (a) local richness linearly declines with increasing disturbance frequency, while richness at (b) beta and (c) regional scales conforms to the IDH..59
6.3. Patch occupancy patterns for each of 13 species across increasing disturbance frequencies...60
6.4. The species used in this experiment reveal a general tradeoff between relative competitive and colonization ability (from Cadotte et al. in review)...................61

7.1. Graphical representation of Hanski’s (1981) metapopulation model....................68
7.2. Number of citations using the term “metacommunity”...69
7.3. The hypothesized interaction between dispersal rate and species diversity at different spatial scales (Adapted from Mouquet and Loreau 2003)......................71
7.4. The relationship between local and regional richness given saturated and unsaturated local community models..74
7.5. Hypothesized relationship of time since introduction on a relative measure of abundance or occupancy..76
7.6. Number of ecology citations using the term “neutral theory”...............................79
7.7. Graphical representations of relationship between species pool (metacommunity membership) and local diversity...80
7.8. The relationship between ecological scale and the actions available to the conservation and management of ecological resources...82

2.A.1. The potential complete food web for the organisms used in this experiment.....106
2.B.1. The temporal richness trajectories for dispersal rate, dispersal pathway and initial beta at the three spatial scales..107
2.C.1. Occupancy patterns for each species over time...108
2.C.2. Species occupancy patterns for the three dispersal treatments............................109
2.C.3. Species occupancy patterns for the four dispersal pathway treatments...............110
2.C.4. Species occupancy patterns for the two initial beta treatments...........................111

Chapter 1

General background and overview

Ecologists' understanding of the processes driving patterns in community ecology is undergoing a fundamental change. Historically, ecologists tried to understand how communities were assembled by local interactions among species, between species and the abiotic environment, and historical effects (e.g., MacArthur 1958, Hutchinson 1959, Tilman 1982, Drake 1991), perhaps with limited success as pointed out by Lawton (1999) and Simberloff (2004). Yet ecologists are increasingly coming to view communities as the product of numerous processes operating across multiple spatial scales (e.g., Allen and Starr 1982, Ricklefs 1987, Wilson 1992, Holt 1993, Zobel 1997, Peterson and Parker 1998, Whittaker et al. 2001, Leibold et al. 2004, Holyoak et al. 2005).

The realization that dispersal was a fundamental ecological process made explicit the need to incorporate spatial scale into ecological understanding. Dispersal has had continued success as a potential explanation for community and biogeography patterns – at least as it affects local community composition (e.g., Gleason 1917, MacArthur and Wilson 1967, Levins 1969, Levins and Culver 1971, Horn and MacArthur 1972, Brown and Kodric-Brown 1977, Hastings 1980, Terborgh and Faaborg 1980, Cornell 1985, 1993, Shmida and Wilson 1985, Cornell and Lawton 1992, Rees 1995, Zobel 1997, Chesson 2000, Cadotte 2006a). MacAurthur and Wilson (1967) perhaps changed ecologists' understanding of the role of dispersal more than any other publication. They explicitly examined the role of dispersal and colonization in regulating island diversity.

The incorporation of space and dispersal now links community-structuring processes to a larger "metacommunity" (Leibold et al. 2004, Holyoak et al. 2005). The general definition of a metacommunity is a set of local communities linked by dispersal of potentially interacting species (Wilson 1992, Leibold et al. 2004). Metacommunity theory can be parsed into four main processes (reviewed in Leibold et al. 2004). The first process, patch dynamics, is a direct outgrowth of metapopulation theory, and essentially examines predator-prey or competitor-competitor dynamics as a series of extinctions and colonizations, such that coexistence occurs at larger spatial scales. Here, as with the traditional metapopulation approach, local populations are impermanent, and so species interactions should not be viewed as local dynamics, which may appear unstable, but rather as part of a larger dynamic (Holt 1997, Nee 1997).

Whereas patch dynamics assumes that there are no substantial or biologically important differences among local patches, the second process, species sorting, explicitly uses patch heterogeneity as a basis of coexistence (Amarasekare and Nisbet 2001, Cottenie et al. 2003, Cottenie and DeMeester 2004, Mouquet et al. 2006). As the environment changes species assemblages may track these changes, granted that the appropriate species are part of the metacommunity and thus can disperse into local communities. Again, we see that local coexistence may be limited by localized environmental conditions, but regional coexistence is possible in heterogeneous systems.

The third process, mass effects, combines the first two. Here local species diversity is enhanced because of immigrants entering from other patches (Brown and Kodric-Brown 1977, Shmida and Wilson 1985). Populations in patches with unfavorable local conditions will experience negative growth rates but are supplemented by immigrants from better patches with positive growth rates, allowing them to persist. For the community, this means that in any given patch a number of declining species are supplemented, thus local diversity is increased. However, if all patches are identical, then the best adapted to those conditions will likely come to dominate all patches in the metacommunity (Amarasekare and Nisbet 2001, Mouquet et al. 2006). Similarly, if patches are too different then species will simply sort according to local conditions (Mouquet et al. 2006).

The final process, neutral dynamics describe metacommunities in which trophically-similar species are functionally equivalent, thus mechanisms controlling species diversity do not depend upon species identity (such as determining who are good competitors or good colonizers) (Bell 2000, 2001, Hubbell 2001). Local diversity depends upon species abundances in the metacommunity, the dispersal rate into local habitats, stochastic deaths and the creation of new species (speciation) into the metacommunity.

My goal in this dissertation is to explore how space and dispersal can structure patterns of species diversity at both the local community and at larger scales. Further, ecologists have described how processes such as predation, competition or disturbance structures local communities, and I re-examine these fundamental processes across scales. In Chapter 2, I use meta-analyses of published experiments to examine how dispersal affects diversity. Dispersal appears to increase local diversity, while simultaneously reducing diversity at larger scales. Further, the dispersal effect on local communities seems to show rate dependency. In Chapter 3, I use aquatic microcosms to test how dispersal interacts with both the connectivity of patches and the initial variation in composition among local patches, and I show that both are important, specifically that dispersal increases local diversity when there is initial variation among the patches of the metacommunity. In Chapter 4, I again use microcosms to test how competition, predation and resources interact with dispersal. I show that dispersal increases diversity in the absence of the generalist predator, and that the predator itself does not benefit from dispersal. In Chapter 5, with microcosm I show that the species used in my experiments show a competition-colonization tradeoff, where the better colonizers are poor competitors, and vice versa. The competition-colonization tradeoff is an important explanation for spatial coexistence. I then explore how this tradeoff can be used to make predictions about the role of disturbance in a metacommunity, in Chapter 6. Here I show that depending on how species are distributed along the competition-colonization tradeoff gradient (e.g., more colonizers versus competitors) can fundamentally change how we expect diversity to vary across a disturbance gradient. Finally in Chapter 7, I review how modern advances in our use of ecological scale and metacommunity ecology can inform conservation and management activities.

Chapter 2

Dispersal and species diversity: a meta-analysis[1]

Abstract Species diversity in communities of interacting organisms is thought to be enhanced by dispersal, yet mechanisms predicting this have little to say about what effects differing rates of dispersal have on diversity, and how dispersal affects diversity at larger spatial scales. I performed meta-analyses on 23 studies comprising 50 experiments that manipulated species migration and measured community richness or diversity, to test three hypotheses: 1) that dispersal increases local diversity; 2) that this effect depends upon the rate of dispersal, specifically, that local diversity should be maximized at intermediate dispersal rates or else linearly related to dispersal rate; and 3) that regional diversity may be either unaffected or negatively impacted by dispersal, since dispersal tends to homogenize local communities. I found that immigration increased local diversity. Further, in animal studies, diversity appears maximized at intermediate dispersal rates, but not with plant studies, however more standardized studies are needed. Finally, results are ambiguous as to what happens at larger scales, with studies either finding declines or no change in regional diversity, with dispersal. Taken together, these results reveal that dispersal has a complex, spatially contingent relationship with patterns of species diversity.

Introduction

Dispersal as a community-structuring mechanism has a long and recurring history in ecology. For example, shortly after the turn of the last century, Volney Spalding, an early plant ecologist, showed that dispersal was an important factor structuring desert plant communities (Spalding 1909). Since then, dispersal has had continued success as a potential explanation for community and biogeography patterns (e.g., Gleason 1917, MacArthur and Wilson 1967, Levins 1969, Levins and Culver 1971, Horn and MacArthur 1972, Brown and Kodric-Brown 1977, Hastings 1980, Terborgh and Faaborg 1980, Cornell 1985, 1993, Shmida and Wilson 1985, Cornell and Lawton 1992, Rees 1995, Chesson 2000). However, only recently have ecologists further developed explicit predictions about the role of dispersal in structuring communities (e.g., Mouquet and Loreau 2003, Leibold et al. 2004, Mouquet et al. 2006) and used controlled experiments to test how dispersal affects species diversity (e.g., Kneitel and Miller 2003, Cadotte 2006b). To-date no one has quantified how important dispersal is across differing habitats and organisms.

Many ecologists now dichotomize ecological processes into those operating at local and regional spatial scales (e.g., Ricklefs 1987, Cornell and Lawton 1992, Cornell and Karlson 1997, c.f. Levins and Lewontin 1985). Local processes generally describe species interactions at small spatial scales, especially competition, niche partitioning and predation, which serve to limit the number of locally coexisting species (e.g., Grinnell

---

[1] A slightly modified version of this chapter is in press as: Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. The American Naturalist 168.

1917, Hutchinson 1957, Chase and Leibold 2003, Kneitel and Miller 2003). On the other hand, processes operating at regional scales refer to organisms moving among local communities, new species entering local communities from a species pool, or over long temporal scales, speciation, all of which likely enhance local species diversity (Ricklefs 1987, Hubbell 2001, Leibold et al. 2004).

However, increasing evidence from studies of species invasions reveals that local communities are not saturated, with diversity increasing as new species establish in extant communities (Simberloff 1981, Sax et al. 2002, Smith and Shurin 2006). Dispersal enhancing local diversity is certainly not a controversial concept (e.g., Loreau and Mouquet 1999), but how dispersal affects local communities has been shown to depend upon a number of processes such as the species interactions present. For example, dispersal may potentially differentially affect communities primarily structured by competition compared to those structured by a generalist predator (Shurin and Allen 2001, Kneitel and Miller 2003). The presence of differing species interactions may reduce certainty in the prediction that dispersal increases local diversity. Furthermore, experiments using laboratory systems to examine predator-prey interactions show that dispersal can either increase the persistence of species (Huffaker 1958, Holyoak and Lawler 1996, Holyoak 2000) or increase the extinction risk (Burkey 1997, Holyoak 2000, Cadotte and Fukami 2005) depending upon the nature and stability of the interactions.

Yet more basic than these contingencies is the fact that dispersal is often more than an all or nothing process: species vary in their dispersal abilities, and local communities vary in their levels of isolation and connectedness (MacArthur and Wilson 1967, Mouquet and Loreau 2003, Cottenie et al. 2004). While dispersal is generally thought to increase local coexistence, too high a dispersal rate can be detrimental to species coexistence, hence dispersal rate may have non-linear effects on diversity (Fig. 2.1; Mouquet and Loreau 2003, Kneitel and Miller 2003). Mouquet and Loreau (2003) modeled competitive differences and stochastic extinctions to show that intermediate dispersal rates maintain the greatest local diversity (Fig. 2.1). Mechanistically, too low a dispersal rate means that both stochastic extinctions and negative interactions cause local populations to go extinct without rescue, while at high rates dominant competitors are introduced into all local communities. However, the models of Mouquet and Loreau (2003) assume that negative interactions ultimately limit coexistence, and others assume that such negative interactions imply an upper limit to the number of species that can coexist (e.g., Ricklefs 1987, Cornell and Lawton 1992, Cornell and Karlson 1997). Other authors question whether communities can be saturated, predicting that as the size of the regional species pool increases, immigration should increase local diversity (e.g., Hubbell 2001, Smith and Shurin 2006 –and references therein, but see a discussion of spatial scale contingencies by Loreau 2000).

Beyond dispersal effects on local community diversity is what happens at larger spatial scales. A number of authors have argued that dispersal among local communities serves to homogenize and therefore reduce among-habitat variation, or beta diversity (Loreau 2000, Mouquet and Loreau 2003, Cottenie and DeMeester 2004). But how this reduction affects regional, or gamma, diversity is not clear (Loreau 2000, Kneitel and Chase 2004). The difficulty is that as dispersal increases local diversity, beta diversity decreases. Since we can view local and beta diversity as additive quantities, equaling

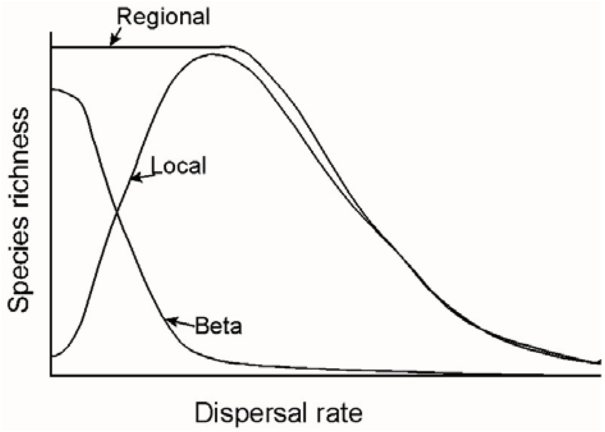

Figure 2.1: The hypothesized interaction between dispersal rate and species diversity at different spatial scales (Adapted from Mouquet and Loreau 2003).

regional diversity (Lande 1996, Veech et al. 2002), the relative change in regional diversity will depend upon which of local and beta diversity shows a greater response. Mouquet and Loreau (2003) show that at lower rates of migration, regional diversity remains unchanged as the loss in beta is offset by increases in local diversity (Fig. 2.1). However, at higher rates of migration, losses in both local and beta diversity mean that regional diversity declines.

In this study I used meta-analyses of published studies examining the following: 1) that the presence of dispersal increased local diversity (e.g., Shmida and Wilson 1985); or possibly 2) that this effect depended upon rate of dispersal, and that local diversity was either a) maximized at some intermediate rate (Mouquet and Loreau 2003) or b) increased with increasing dispersal rate; and finally, 3) that regional diversity was either unaffected or negatively affected by dispersal (Mouquet and Loreau 2003).

Methods

I conducted meta-analyses on experimental studies that manipulated species dispersal and measured this effect on species richness or diversity. In June 2005, I searched two databases, Biological Abstracts (WebSPIRS 5, Ovid Technologies, New York, NY) and Web of Science (Thompson Scientific Corporation, Stamford, CT), using various combinations of the following keywords: diversity, richness, local, regional, community, dispersal, immigration and saturation. I used studies that: 1) manipulated immigration of individuals (either in a binary fashion or by rate); 2) contained at least five species; and 3) examined species for more than a single generation, in order to allow competitive interactions to occur. A total of 23 studies representing 50 experiments were included (Table 2.1). These experiments represent a diverse array of organisms and study systems, and, surprisingly, given how long immigration has been viewed as important for diversity, were all published within the last ten years.

Table 2.1: Summary of the studies used in this study.

Authors	Organisms	Dispersal treatment	Hypotheses tested	Number of experiments	Used in rate analysis?
Brown and Fridley 2003	Plants	Seed sowing	Local	2	No
Cadotte 2006b	Protozoans	Open corridors	Local	2 2	No
Cadotte and Fukami 2005	Protozoans	Community subsample	Local Regional	1 1	Yes
Cadotte et al. 2006a	Protozoans	Community subsample	Local Regional	6 2	Yes
Forbes and Chase 2002	Zooplankton	Connectivity among local communities	Local Regional	1 1	Yes
Foster 2001	Plants	Seed sowing	Local	1	No
Foster and Tilman 2003	Plants	Seed sowing	Local	1	Yes
Foster et al. 2004	Plants	Seed sowing	Local	1	No
Gehring et al. 2002	Soil fungus	Exclusion of mammal vectors	Local	1	No
Gilbert et al. 1998	Arthropods	Patch connectivity	Local	1	No
Gonzalez and Chaneton 2002	Arthropods	Patch connectivity	Local	1	No
Gross et al. 2005	Plants	Seed sowing	Local	1	Yes
Kellogg and Bridgham 2004	Plants	Seed sowing	Local	1	Yes
Kneitel and Miller 2003	Protozoans	Individuals moved among communities	Local	2	Yes
Matthiessen and Hillebrand, unpublished MS	Algae		Local Regional	3 2	No
Mouquet et al. 2004	Plants	Seed rain exclusion	Local	1	Yes
Rantalainen et al. 2004	Arthropods	Patch connectivity	Local	3	No
Shurin 2001	Zooplankton	Individuals moved among communities	Local	4	No

Table 2.1 continued

Authors	Organisms	Dispersal treatment	Hypotheses tested	Number of experiments	Used in rate analysis?
Spencer and Warren 1996	Protozoans	Individuals moved among communities	Local	1	No
Tilman 1997	Plants	Seed sowing	Local	1	Yes
Warren 1996	Protozoans	Individuals moved among communities	Local Regional	2 2	Yes
Xiong et al. 2003	Plants	Seed sowing	Local	1	Yes
Zobel et al. 2000	Plants	Seed sowing	Local	1	Yes

Despite recommendations from various authors (e.g., Gurevitch et al. 2000, 2001), most studies used in this analysis did not explicitly state mean values ($\bar{x}$) or a measure of variation such as standard deviation (*s*), so these values had to be extrapolated from figures using a program called Data Thief II, version 1.1.0 (Bas Tummers, http://www.nikhef.nl/~keeshu/datathief/). The studies used here all included the sample size. In studies reporting multiple sampling dates I only used the final sampling date, in order to analyze outcomes over the most generations. Studies where classified into one or more of three groups: 1) those comparing effects of the presence/absence of dispersal of individuals among commuities or immigration into communities on local diversity (referred to as local studies); 2) those that gave requisite information to calculate dispersal rate (rate studies); and 3) those comparing the effects of dispersal on regional or metacommunity diversity (regional studies). Therefore, with the local and regional studies, dispersal simply refers to individuals entering or moving among communities, while the rate studies refer to the standardized measure defined below.

It seems that hypotheses 1 and 2a are mutually exclusive, when in reality they are not. Fig. 2.2 shows that even when there is an underlying rate effect, the mean dispersal effect on local diversity will be larger than that of the no-dispersal control. Furthermore, whereas testing hypotheses 1 and 3 with existing studies was rather straightforward, the ability to examine hypothesis 2 was problematic, because different studies variously defined dispersal rates. For example, most experiments used in this meta-analysis categorize treatments, for example into “high” and “low” treatments, without any obvious standardization among studies.

In order to test hypothesis 2 adequately, one must standardize dispersal. A simple standardized rate of immigration (D) is the rate of immigration (*i*) per community resident density (ρ):

$$D = i/\rho , \qquad \text{eq(1)}$$

where *i* is the number of individuals (*n*) per generation time (*t*), such that:

$$D = \left(\frac{n}{t}\right)\Big/\rho \qquad \text{eq(2)}$$

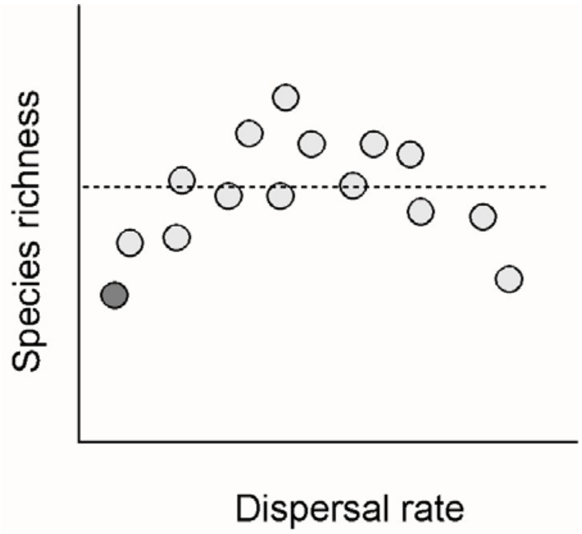

Figure 2.2: Dispersal enhances richness despite a rate effect. The dark circle represents a no-dispersal control and the light circles are a hypothesized rate effect. The dashed line is the mean of dispersal treatments.

Here, ρ is a measure of the number of individuals per unit area (or volume). This type of standardization has the added benefit of allowing immigration rate to be analyzed in predictive regression models, and permitting any study, even those which manipulate a single dispersal rate could be included, so long as they provide the requisite information.

Some information required in eq(2) had to be determined from the primary and secondary literatures. For example some of the plant-based studies gave a single species' proportion of total seed mass added and so I had to find seed masses for the species used. Similarly, generation times needed to be located in the literature.

Experiments used to test the rate effect were divided into separate analyses, for animals and for plants. This was done because, first, plant and animal studies used very different measures of resident density, with plant studies using percent cover and animal studies using an estimate of the numbers of individuals. Secondly, the unit of dispersal differed greatly. In animal studies juveniles or adults were the units of dispersal, while in plant studies seeds dispersed. These dispersal units have very different survivorships resulting in animal studies dispersing tens to hundreds of individuals and plant studies dispersing thousands to tens of thousands of seeds.

Statistical analyses. The approach was adapted from Gurevitch and Hedges (2001) and all the equations used are shown in the Appendix. The basis of meta-analysis is to combine independent studies into some overall measure of effect size. In this case, the effect is of immigration on species diversity.

I employed a test for homogeneity of effects for the different treatments using Cochran's Q. If effects were found to be homogeneous then a fixed effects model for calculating the grand mean effects was used; otherwise I used a mixed model (see Appendix). I calculated the confidence interval (CI), and the standard approach to assessing significance is to see if the CI intersects 0. However, I also used a non-directional test, analogous to a χ^2 test, as an independent estimation of P-values (see Appendix). For all cases, I subtracted the mean control diversity from the treatment diversity, thus a positive effect size implies dispersal increases diversity.

The data compiled for hypothesis 2 included a continuous dependent variable (dispersal rate), so the standard meta-analytic approach had to be modified in this case. For each experiment included, I calculated a standardized dispersal effect as:
(treatment diversity - control diversity)/control diversity.

This dependent variable was regressed against the standardized immigration rate in both a linear and non-linear (quadratic) model. If both models revealed a significant relationship, they were compared using Akaike's information criteria (AIC). Since the dependent variable was standardized by the control, all regression models were constrained by an intercept of zero.

Criticisms of meta-analyses. Though an efficacious statistical tool, meta-analyses in ecology may be epistemologically problematic. One could view ecological processes as universal laws that transcend local vagaries of time and space, in which case meta-analyses are an appropriate tool for synthesizing results across experiments. However, if one subscribes to the idea that ecological patterns are driven by a multitude of spatially and temporally contingent processes, or that many different processes can produce similar patterns, then meta-analyses falsely reify trends into a single hypothesis test (D. Simberloff, pers. comm.). If contingency and multiplicity of processes are important, ecologists should be primarily trying to understand how individual communities are structured, rather than search for general processes or laws that cannot predict or explain the workings of particular communities except at a very high level (Simberloff 2004).

Osenberg et al. (1999) critiqued the use of meta-analysis in ecology and called for the use of a variety of effect size metrics. However, Gurevitch et al. (2001) disagreed with Osenberg et al. (1999) and instead supported the use of a single mean effect size metric that can be universally understood by ecologists and argued that a lack of a standard makes evaluation of results difficult. Here, I use the standard approach advocated by Gurevitch et al. (2001).

Further, Murtaugh (2002) revealed that the data used in meta-analyses might be affected by journal 'quality'. However, even if effect size increases with journal quality, that does not mean that a journal's quality caused the effect size (as would be interpreted from Murtaugh's use of regression); rather, this correlation could simply mean that more powerful experiments with more conclusive results are generally published in better journals. As long as researchers employing meta-analyses use studies from all recognized, peer-reviewed journals, then their analyses should represent an unbiased sample. Nevertheless, I regressed effect size on the log of ISI impact factor (Thompson Scientific Corporation, Stamford, CT). Effect size slightly increased with impact factor (slope = 2.1115) but this relationship was not significant (P = 0.2317).

Table 2.2: Results of homogeneity tests for the fixed effects model, and the mixed effect model if needed. ***P < 0.001; and 'ns', non-significant.

Test	*k*	Q_f	Q_m
Local-binary	40	117.241***	50.890^{ns}
Regional	11	10.182^{ns}	---

Results

The studies used in this analysis represent a diverse range of organisms and dispersal treatments (Table 2.1). The potential existed for these disparate experiments to exhibit diverse effects. I calculated standardized effect sizes for each study, for hypotheses 1 and 3. Before interpreting the overall grand effect, I tested for homogeneity among studies and found that the local comparisons (hypothesis 1) had heterogeneous effects (Table 2.2). For these comparisons I used the mixed effects model, and the fixed effects model for the comparison among regional studies. It is important to note that the mixed model for the local studies was considered homogeneous, which means these studies did not need to be analyzed in smaller, more homogeneous groups (i.e., plants vs. animals).

Hypothesis 1: dispersal increases local diversity. Using a fixed model I found that the studies comprising this comparison were heterogeneous, but they were found to be homogeneous with the mixed model (see Table 2.2), so the mixed model was used. Most experiments testing this hypothesis revealed a positive effect of dispersal on local diversity (Fig. 2.3). In terms of confidence intervals, two experiments showed significantly negative responses, nine no response, and 29 a positive response. The grand effect was significantly positive (Fig. 2.3, χ^2_{40} = 113.870, P < 0.0001), meaning that the presence of dispersal strongly increased local diversity.

Hypothesis 2: non-linear effect of dispersal rate on local diversity. The animal and plant data had to be separated in order to test the hypothesis that there was a unimodal relationship between diversity and standardized dispersal rate. For the animal analysis (Fig. 2.4), both the quadratic and linear models revealed a significant relationship between the standardized immigration rate and the treatment effect on diversity ($F_{2,16} = 5.771$; P = 0.016; $R^2 = 0.47$ for the quadratic and $F_{1,16} = 11.307$; P = 0.005; $R^2 = 0.45$ for the linear model). Further, AIC indicated that the linear model better fit the data (AIC = 101.137 for the linear and 119.017 for the quadratic models). However, it is clear from figure 2.4 and from regression diagnostics that there was an outlying data point with an extremely high dispersal rate. When this point was removed, the results indicated that the quadratic was a significant predictor while the linear model was not ($F_{2,15} = 5.97$; P = 0.013; $R^2 = 0.46$, vs. $F_{1,15} = 3.085$; P = 0.099; $R^2 = 0.17$) (Fig. 2.4).

The results of the plant analyses revealed that neither quadratic nor linear models were significant predictors of treatment effects on diversity ($F_{2,6} = 0.35$; P = 0.73; R^2 = 0.19,and $F_{1,6} = 0.932$; P = 0.389; $R^2 = 0.19$, respectively). The plant data were

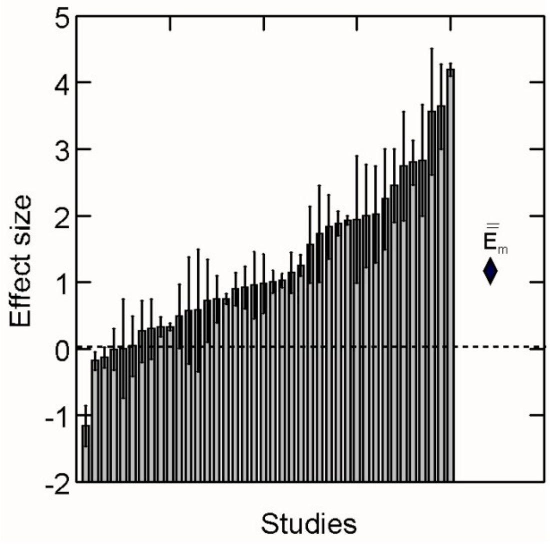

Figure 2.3: The standardized effect size of the studies used to test hypothesis 1 (local diversity). *E* is the grand mean effect size using the mixed model, m. Error bars represent the 95% confidence intervals.

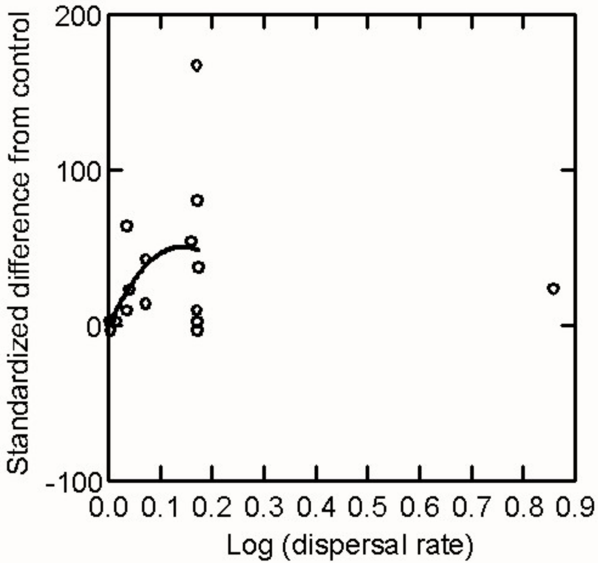

Figure 2.4: The effect of the standardized dispersal rate on the standardized diversity of treatment for animal experiments. The line represents the quadratic model including all data points except the outlier (see results).

represented by a small number of data points, with a lot of scatter at low dispersal rates (Fig. 2.5). Further, an outlying data point with an extremely large dispersal rate was removed (not shown).

Hypothesis 3: dispersal decreases regional diversity. The fixed model was found to be homogeneous (see Table 2.2), and so was appropriate. In six of the eleven studies comprising this comparison, dispersal negatively affected regional diversity (Fig. 2.6). Four studies had a confidence interval that overlapped with 0, indicating no effect, and one had a positive effect. The grand effect and its CI were well below 0, indicating a significant negative effect associated with dispersal. However the result of the non-directional test indicated non-significance (χ^2_{11} = 14.653, P = 0.1989), revealing that this result needs to be carefully considered, especially in lieu of the small sample size, and perhaps that meta-analyses in general need carefully to consider what is a “significant” result. The non-directional test is a more conservative test and is less likely to find significance with small sample sizes and large variances.

Discussion

Individual studies exploring the effect of dispersal on patterns of species diversity may be influenced by various spatially and temporally dependent ecological processes (Zobel and Kalamees 2005). A meta-analysis can overcome these vagaries and highlight general effects of dispersal. I have shown that immigration had a strong positive effect on local diversity (hypothesis 1; Fig. 2.3). This positive effect was apparent over a diverse assembly of study systems and organisms. If communities are available for colonization by new species, then larger scale processes may be important for patterns of local diversity (Cornell and Lawton 1992). These results support the general notion that local communities are not necessarily saturated, and that local species interactions may not limit future species invasions (e.g., Simberloff 1981, Sax et al. 2002, Smith and Shurin 2005). These diversity increases may not even be permanent, and without continued dispersal, diversity would decrease. Regardless, dispersal-dependent increases reveal that mechanisms such as mass effects (Shmida and Wilson 1985, Mouquet et al. 2006) can overcome negative interactions.

Further, there is a potential non-linear effect of dispersal rate on species diversity (Fig. 2.4), qualitatively supporting the claims for this made by Mouquet and Loreau (2003). The results would have benefited from a greater sample size. The animal studies (Fig. 2.4) were missing higher rate treatments, with the exception of the single outlier from Cadotte and Fukami (2005). In fact, several animal studies claimed to examine more than a single dispersal rate treatment, yet the different rates within a single study were surprisingly similar once entered into eq(2). The obvious conclusion from of these results is that empirical studies need to conceptualize dispersal rate better to test hypotheses about the effect of dispersal rate on patterns of species diversity.

However, focusing on a single scale of organization can lead to erroneous conclusions about processes occurring at other scales. That local communities are not saturated does not necessarily lead to the conclusion that communities are under the control of regional processes. The processes defining patterns of local diversity may have different effects at larger spatial scales and vice versa (Huston 1999, Loreau 2000, Sax et

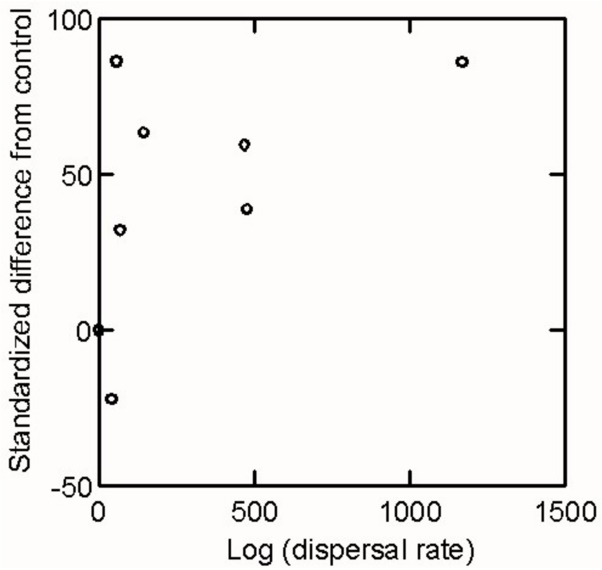

Figure 2.5: There was no effect of the standardized dispersal rate on the standardized diversity of treatment for plant experiments.

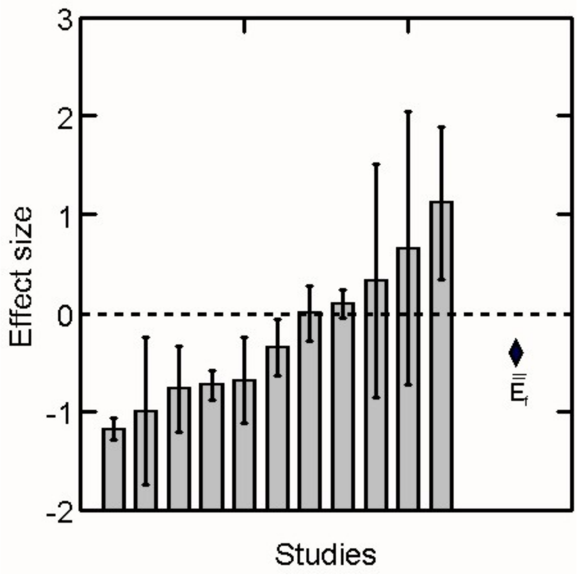

Figure 2.6: The standardized effect size of the studies used to test hypothesis 3 (regional diversity). *E* is the grand mean effect size using the fixed model, *f*. Error bars represent the 95% confidence intervals.

al. 2002). Dispersal may increase local diversity, but dispersal will also likely affect beta, or among community diversity (Loreau 2000, Kneitel and Chase 2004). My analysis revealed that dispersal experiments often observe declines in regional diversity, at least more often than they observe increases (hypothesis 3), but again there is a dearth of studies testing this hypothesis, and there were certainly too few studies to examine the role of rate of migration on regional diversity. The likely explanation for the decline is that, by allowing increased numbers of individuals to move among local communities, beta diversity declines as these communities become increasingly homogenized. This homogenization means that dominant competitors or generalist predators have impacts in all local communities and likely structure the region in a monotonous fashion (e.g., Cadotte and Fukami 2005, Cadotte et al. 2006a). Kneitel and Chase (2004) thought that if coexistence-promoting mechanisms are local in nature (resource use, environmental stress, predation, etc.), then local diversity should be high, and perhaps increasable, while beta diversity should be low. Kneitel and Chase (2004) were uncertain about what should happen to regional diversity, but the present results show that the magnitude of the increase in local diversity is not likely to be greater than declines in beta diversity, meaning that, in the presence of dispersal, regional diversity will decline or remain unchanged compared to no-dispersal treatments. Therefore, species in dispersal treatments are either just as likely or more likely to go extinct as in no-dispersal treatments.

These scale-dependent results have important conservation implications because the perspective of conservation managers in regard to migration depends upon their scale of concern. For example, if managers are interested in maintaining maximal diversity over a fragmented landscape, then perhaps restricting, or at least not enhancing, dispersal would best ensure regional diversity. However, if the concern is a single local community, then enhancing immigration may be the best option. There is a long-running debate in conservation ecology as to the benefit of using corridors to link habitats (e.g., Noss 1987, Simberloff and Cox 1987). I would argue, based on the current results, that this is a debate about the scale of effects, rather than the nature of effects.

Limitations on interpretation. The studies making up this meta-analysis may not be adequate to draw firm conclusions about how dispersal interacts with species diversity at different spatial scales. I have four main concerns.

First, most of the studies either used homogeneous local conditions or failed to measure micro-environmental conditions. Metacommunity theory predicts that heterogeneity among local communities can have important consequences on species diversity (Mouquet et al. 2006). Heterogeneity should enhance the relative importance of mass effects, as heterogeneity likely results in spatial variation in a species' growth rate. Mouquet et al. (2006) showed that when heterogeneity is measured as resource supply rate differences among local communities, richness was maximized at intermediate levels of heterogeneity. Essentially, little or no heterogeneity results in regional domination by species best adapted to resource supply rates. While at high heterogeneity levels, local patches are exclusively inhabited by species adapted to local supply rates. In the intermediate case, large populations are able to subsidize slowly declining populations (e.g., mass effects). More than a mechanism for local coexistence, environmental heterogeneity can potentially drive diversity patterns at different spatial scales, such that heterogeneity can be seen as a diversifying or beta increasing processes (Cottenie and De Meester 2004), which would maintain greater regional diversity. This is an important criticism because, when heterogeneity is not explicitly measured or addressed, a researcher's ability to interpret tests of hypotheses can be affected, as processes that can potentially enhance or reduce diversity may be in operation. Only two studies included local environmental differences (Kneitel and Miller 2003, Cadotte et al. 2006a). For example, Cadotte et al. (2006a) manipulated resource availability in local communities of aquatic protozoans and metazoans, and found that low resource communities showed a greater benefit from dispersal, presumably because extinction risks were higher in the absence of dispersal. Unfortunately a couple of further studies that adequately included natural variation by using natural ponds had to be excluded because of a lack of a no-dispersal control. Cohen and Shurin (2003) examined the effect that distance gradients (as dispersal rate surrogate) had on pond diversity, and concluded that distance had a strong effect on colonization, and potentially upon species diversity. Similarly, in a natural pond survey using distance as a dispersal surrogate, Chase and Ryberg (2004) showed that a region with closer ponds (higher dispersal rate) had lower regional diversity.

A second issue is the nature of the dispersal treatments. Most studies simply introduced set amounts of propagules without any explicit consideration for species-specific attributes. The natural movement of individuals influences patterns of species coexistence through a number of possible mechanisms: an evolutionarily derived competition-colonization tradeoff (Levins and Culver 1971, Hastings 1980, Yu and Wilson 2001, Amaresekare 2003, Kneitel and Chase 2004); source-sink dynamics (Brown and Kodric-Brown 1977) or mass effects (Shmida and Wilson 1985, Kunin 1998). By removing a set amount of the community, or introducing a set number of propagules, studies are using a density-dependent dispersal probability that is antithetic to potential competition-colonization tradeoffs, which require inferior competitors (lower abundance) be superior dispersers. The drawback of incorporating natural dispersal abilities is that dispersal is less tractable. However, one study (Mouquet et al. 2004) explicitly manipulated dispersal to test potential competition-colonization tradeoffs in plant communities. They had dispersal scenarios in which dispersal was either positively, negatively, or un-correlated with competitive ability and they showed that allowing for competition-colonization tradeoffs enhanced coexistence and occupancy patterns for poor competitors.

Third, specific ecological interactions may change how dispersal impacts patterns of coexistence. For example, predation is thought to have profound effects on dispersal-mediated patterns of diversity (Shurin and Allen 2001). Kneitel and Miller (2004) and Cadotte et al. (2006a) both reveal that the presence of a predator can undo any positive effect of dispersal. However, Shurin (2001) showed that predation could offer openings for colonizers and in fact appears to enhance diversity increases through dispersal. Besides predation, variation in competitors could also impact the dispersal effect on diversity. For example, Cadotte (2006a) showed that in competitively structured communities, variation in initial species assembly could result in supporting or rejecting the Mouquet-Loreau hypothesis, revealing the importance of community history.

Finally, dispersal (as used in this study) is quite ambiguous. The studies used to test the first two hypotheses include either immigrants arriving from outside the local species pool or individuals moving among local communities, within the local pool. Species pool effects can have important consequences for patterns of local diversity (Zobel 1997, Chase 2003). The first immigration type (from beyond the local pool) is often used in studies examining plant communities, and provides greater tractability as novel species are easy to enumerate. The second type (within pool) may be more realistic, and explicitly draws links among spatial scales. This type of migration is an essential component of metacommunity dynamics. Metacommunities are sets of local discrete communities that interact via migration (Wilson 1992, Leibold et al. 2004). The studies used to test the regional diversity hypothesis used the within pool method and are explicit examinations of metacommunity dynamics. These studies reveal that patterns of metacommunity diversity are a balance between local diversity enhancement and regional diversity limitation (see Holt 1993, Cottenie and DeMeester 2004), and these patterns are likely mediated by dispersal rate (Mouquet and Loreau 2003).

Conclusion. The dispersal of individuals into and among local communities is thought to affect local diversity through a number of mechanisms. However, these mechanisms often do not explicitly predict what would happen to diversity if dispersal rates varied, nor effects at larger spatial scales. The results of the present study show that dispersal increases local diversity while simultaneously decreasing regional diversity in the majority of experiments. This pattern reveals that processes at an intermediate scale may be the best avenue to understanding how community diversity is structured. Further, I offer tentative support to the Mouquet-Loreau hypothesis that dispersal rate has a non-linear effect on diversity. However, more studies that use standardized dispersal rates are needed. Future experiments should explicitly address spatial heterogeneity, the role of species differences such as in competition-colonization tradeoffs, the role of specific ecological interactions, and where immigrants come from.

Chapter 3

Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment[1]

Abstract Large-scale processes are known to be important for patterns of species richness, yet the ways in which local and larger scale processes interact is not clear. I used metacommunities consisting of five interconnected microbial aquatic communities to examine how processes at different scales affect local and metacommunity richness. Specifically, I manipulated the potential dispersal rate, whether dispersal was localized or global, and variation in initial community composition. Using repeated measures ANOVA I showed that a low dispersal rate and intermediate distance dispersal enhanced local richness. Initial assembly variation had no effect on local richness, while a lack of dispersal or global dispersal reduced local richness. At the metacommunity scale, richness was enhanced throughout the time course of the experiment by initial compositional variation and was reduced by high or global dispersal. The effects of dispersal were contingent on the presence of initial compositional variation. The treatments also affected individual species occupancy patterns, with some benefiting from large-scale processes and others being adversely impacted. These results indicate that the effects of dispersal on species richness have a complex relationship with scale and are not solely divisible in to "regional" versus "local" scales. Finally, predictions of how dispersal rate structures communities appears dependent on species compositional variation among communities.

Introduction

Ecology stands at the brink of a paradigm shift, where local scale properties and processes are placed in a broader spatio-temporal framework. In this new "metacommunity" framework, observed pattern and structure are connected across multiple organizational levels (Leibold et al. 2004). The focus of explanations for the maintenance of local species richness has grown to include processes operating at regional scales (Shmida and Wilson 1985, Ricklefs and Schluter 1993). This growth was driven by the need to reconcile seemingly inexplicable patterns at local scales that may be driven by larger scale processes.

I use "space" to refer to processes and patterns observable at different scales (e.g., Holt 1993, Loreau 2000). This differs from the older notion of space in ecology as an explanatory variable in analyses, especially for ordination. This latter use of space is informative and useful, but fails to capture the dynamical nature of space. Many ecological processes are spatially dependent, and others feed back across scales. Further, processes operating across different spatial scales appear necessary to explain patterns of species richness (Whittaker et al. 2001, Amarasekare 2003, Kneitel and Chase 2004, Leibold et al. 2004).

---

[1] A slightly modified version of this chapter has been published as: Cadotte, M. W. 2006. Metacommunity influences on community richness at multiple scales: a microcosm experiment. Ecology 87: 1008-1016.

Space as a process appears necessary to understand mechanisms driving ecological dynamics (e.g., James and Shine 2000, Gering and Crist 2002, Chase and Ryberg 2004, Fukami 2004, Cadotte and Fukami 2005, Hamilton et al. 2005). Yet the salient process linking spatial scales is dispersal, and different dispersal patterns can have scale-dependent effects (Drake et al. 1993, Forbes and Chase 2002). Pertinent to any discussion of dispersal and patterns of species richness is the metacommunity concept (Wilson 1992, Leibold et al. 2004, Cottenie and De Meester 2004). I define a metacommunity as local communities of trophically interacting species linked by dispersal. In the current experiment, these local communities occupy discrete resource patches. By connecting local communities, local species richness is thought to be enhanced despite local interspecific interactions that tend to reduce richness (Cottenie and De Meester 2004, Kneitel and Chase 2004). Further, the rate of dispersal is thought to have a nonlinear effect on the magnitude of these richness reducing interactions, so that richness is maximized at intermediate dispersal rates (e.g., Shurin and Allen 2001, Kneitel and Miller 2003, Mouquet and Loreau 2003). At extremely low dispersal rates, competitive exclusion limits local membership, while at high rates, local communities are homogenized with a suite of dominant competitors maintained in every patch (e.g., Mouquet and Loreau 2003).

The manner in which dispersal influences richness is simply too complex to be captured in a rate function alone. I posit that there are at least two additional processes influencing how dispersal affects richness. First, spatial arrangement of patches may effect how dispersal influences community structure (Cottenie et al. 2003). Secondly, historical stochastic colonization is known to play an important role on local community structure (e.g., Drake 1991, Law and Morton 1993, Price and Morin 2004), and likely alters the among-community dispersal effect on species richness.

This study examined how dispersal rate, spatial scale of dispersal, and initial local community composition affected species richness at different spatial and temporal scales. I examined three scales of dispersal. In the first, organisms have global dispersal to all other communities; the second, organisms are restricted to local dispersal only; and third, is an intermediate dispersal scale (Fig. 3.1). If local communities are largely structured by species interactions at the local level then dispersal at a local scale may impede movement through a metacommunity. However, if dispersal rate is high enough, then perhaps species interactions are determined at larger spatial scales so that the dispersal scale is unimportant. Given these mechanisms, a number of hypotheses follow: 1) low-dispersal communities should maintain the greater local richness than high-dispersal communities (e.g., Mouquet and Loreau 2003); while 2) local dispersal metacommunities should maintain higher beta richness than global dispersal ones; and 3) initial community assembly should have long-term consequences. Specifically, that initial variation should maintain higher beta richness; and finally 4) that these processes should have interactive effects such that dispersal rate may exhibit different patterns at the different dispersal scales.

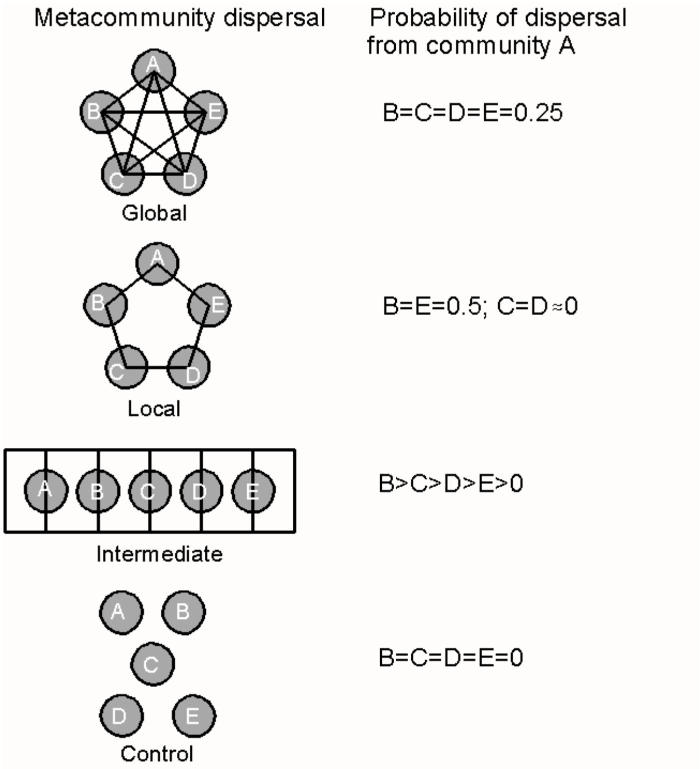

Fig. 3.1: Dispersal scale designs and the relative probabilities of species dispersal from community A to the other communities in the metacommunity.

Methods

Landscape and dispersal treatments. Local patches were 125 ml Nalgene narrow-mouth square bottles with two or four 3/16” holes drilled into opposing sides and tapped. Threaded 3/16” barbed nylon tube fittings (Small Parts Inc., Miami Lakes, FL) were then twisted into the holes and secured with silicone caulk. A concern was that the number of tube connectors in a local community would alter the surface area for bacterial growth (i.e., protozoan food resources). However, a preliminary experiment found no significant differences in protozoan abundances attributable to the number of connectors. Dispersal corridors were clear Nalgene 3/16” tubing. All microcosms were autoclaved prior to use.

The metacommunity designs used in this experiment (Fig. 3.1) were categorized as: 1) "global", with all communities interconnected and organisms having equal probability of migrating to any other community; 2) "local" where species in any community can disperse only to the two neighboring communities; 3) "intermediate", where organisms do not have equal probability of dispersing to other communities; and 4) the no dispersal control (Fig. 3.1). Total length of dispersal pathways was equal between the landscapes, with the control having tubes cut in half and the ends clogged with silicone.

Dispersal rate was manipulated by placing tube clamps on every tube exiting the local communities, and when closed most movement of fluid and organisms was blocked. Three dispersal treatments were used: high dispersal, clamps are always open (except during sampling and nutrient renewal, see below); low dispersal, clamps are open for one hour every other day; and a no dispersal control.

Initial community assembly was divided into two treatments. First each species in the species pool (see *Biological communities*) was initially present in each community and thus initial beta richness was 0. Second was that 7 of the 13 species used were initially randomly introduced into each local community, with a beta of 6. In this treatment, all 13 species were present at the metacommunity scale and the assemblage making up each of the five local communities was repeated for each treatment and replicate (e.g., community A in Fig. 3.1 was identical for all treatments). All species were recorded on at least one sampling date after initialization. Beta values were the values for the additive partition of the among species richness (see *Statistical analyses*).

Dispersal, landscape design and initial composition were combined in a factorial design, except in the case of no dispersal, where landscape design would have no effect. Treatments were replicated four times. One replicate from the high-dispersal/parallel/initial-beta-0 design was removed due to fungal contamination.

Biological communities. Each local patch consisted of 100 ml of sterilized nutrient medium with 0.55 g/l of protozoa pellets (Carolina Biological Supply Company, Burlington, NC), 0.05 g/l powdered vitamins, and two sterilized wheat seeds as a source of slowly released nutrients in spring water (Crystal Springs, Flowery Branch, GA). Six days prior to the initialization of local communities, the stock solution was inoculated with bacteria (*Bacillus cereus*, *B. subtilis*, *Proteus vulgaris*, *Serratia marcescens*) from stock cultures and with unidentified bacteria from filtered protozoan species stock cultures. Four days before initialization, microflagellates and further associated unidentified bacteria were introduced, which were assumed to have a ubiquitous distribution throughout the experiment. The above procedure was repeated each day for 4 days with the first replicate of each of the five treatments being initiated on the first day, and so on.

I used a total of 13 protozoan and rotifer species: *Blepharisma americanum*, *Chilomonas* sp., *Coleps* sp., *Colpidium striatum*, *Euplotes* sp., *Lepadella* sp., *Paramecium aurelia*, *P. bursaria*, *P. caudatum*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, and *Uronema* sp. Three species (*Philodina, Lepadella* and *Euplotes*) were cultured from ponds in and around Knoxville, while the rest were obtained from other laboratories and periodically restocked with individuals ordered from Carolina Biological Supply. Initial number of individuals ranged from 25 to 100 per 100 ml to reduce any strong interactions during the initial phase of the experiment.

The species are protozoan flagellates or ciliates, or metazoan rotifers, all of which naturally inhabit still and stagnant ponds. They range in size from 25-1000 µm in length (Appendix A). Species were quite variable in their dietary habits (Appendix A). Appendix A graphically portrays this complex food web.

Sampling. Twice a week, all clamps were closed and 5 ml of medium was removed from each local community and replaced with fresh nutrient medium. Every other week the extracted 5 ml was used to record presence/absence of species. (In a previous study, Cadotte and Fukami (2005) found that diversity indices incorporating local abundance did not change conclusions drawn from richness observations.) Up to the entire 5 ml aliquot was scanned for the presence of species.

Statistical analyses. I used Lande’s (1996) additive partitioning of richness, and measured species richness at three spatial scales: Local or alpha richness was the number of species per 5-ml aliquot, averaged over the five local communities in the landscape; regional or gamma richness was total species in the 5-ml aliquots from the five local communities in the landscape; and among community or beta richness, measured as gamma minus alpha, or species differences among local communities.

Repeated measures ANOVA's determined whether treatment combinations had a significant effect on species richness across time after day 1 (initial richness). An assumption for the repeated measures *F*-test is that the variance-covariance matrix has compound symmetry. When there was a departure from compound symmetry, I used Greenhouse-Geisser epsilon, and its correction where appropriate. However, since the factorial design was unbalanced, interactive effects (other than time) could not be examined using repeated measures ANOVA's, therefore I examined single treatment effects. To examine interactive effects, I used multiway ANOVA's for the last sampling day (day 50). ANOVAs were performed using SAS version 9 (SAS Institute 2004).

To test whether differential dispersal probabilities resulted in observable differences in composition community similarity was calculated using either the Sorenson index, or between community contrasts within a metacommunity, at day 50. For example, highly connected communities should be more similar than less connected communities. The similarity values were analyzed using a three-way ANOVA with dispersal rate, dispersal pathway and initial beta as factors.

Results

The 50 days of the experiment, or 50-100 generations of the study organisms, represented long-term dynamics. Some treatment combinations showed very different temporal dynamics at different spatial scales (Fig. 3.2a). At the local (alpha) level, treatment combination ($F_{13, 168} = 6.49$, $P < 0.0001$), time ($F_{3, 168} = 49.90$, $P < 0.0001$) and their interaction ($F_{39, 168} = 4.54$, $P < 0.0001$) affected species richness. Similarly, beta richness was affected by treatment combination ($F_{13, 168} = 15.21$, $P < 0.0001$) and time ($F_{3, 168} = 11.25$, $P < 0.0001$), but their interaction was not significant ($F_{39, 168} = 1.37$, $P = 0.090$). Regional (gamma) richness was also affected by treatment ($F_{13, 168} = 9.86$, $P < 0.0001$), time ($F_{3, 168} = 8.40$, $P < 0.0001$), and their interaction ($F_{39, 168} = 1.82$, $P = 0.005$). To highlight the variation among treatments, Fig. 3.2b shows species richness patterns at day 50. Local richness was 5-7 species, while regional richness was 7-11 species.

The three factors manipulated in this experiment all effected species richness at multiple scales across time (see Appendix B), and time also had a highly significant effect ($P < 0.01$ for all tests below). Dispersal rate affected local ($F_{2, 212} = 5.67$, $P = 0.0040$), beta ($F_{2, 212} = 10.92$, $P < 0.0001$) and regional richness ($F_{2, 212} = 5.16$, $P = 0.0065$). Dispersal rate interacted with time to influence species diversity at the local scale ($F_{6, 212} = 2.23$, $P = 0.042$), but not at the other scales of observation. Dispersal scale affected local ($F_{3, 208} = 11.67$, $P < 0.0001$), beta ($F_{3, 208} = 7.82$, $P = 0.0001$), and regional richness ($F_{3, 208} = 5.24$, $P = 0.0017$). Dispersal scale interacted with time to influence species diversity at the local scale ($F_{9, 208} = 2.86$, $P = 0.003$), but not at the other scales of observation. Finally, initial beta did not affect local richness ($F_{1, 216} = 1.80$, $P = 0.1805$) but did affect beta ($F_{1, 216} = 73.99$, $P < 0.0001$) and regional richness ($F_{1, 216} = 55.81$, $P < 0.0001$). Initial beta interacted with time to affect diversity at both the local ($F_{3, 216} = 7.85$, $P < 0.0001$) and beta ($F_{3, 216} = 3.21$, $P = 0.024$) scales, but not at the regional scale.

Generally, for the local community, low dispersal rate and intermediate dispersal scale maintained higher richness over time, with no dispersal or the global dispersal maintaining the lowest richness. A lack of dispersal, or initial species variation maintained greater beta diversity, while high dispersal and the global and intermediate dispersal scales maintained lower beta richness. At the regional level, the control and low dispersal treatments, as well as initial beta diversity of 6 maintained the highest richness, while high dispersal and the all pathway maintained lower richness.

Species richness at day 50 were mainly consistent with the results of the repeated measures ANOVAs. Dispersal affected local ($F_{2, 50} = 6.35$, $P = 0.0035$), beta ($F_{2, 50} = 6.11$, $P = 0.0042$) and regional richness ($F_{2, 50} = 5.30$, $P = 0.0082$). In all cases, a high dispersal rate adversely affected richness (Fig. 3.3). Initial beta had no effect on local richness ($F_{1, 50} = 0.69$, $P = 0.4086$), but did affect beta ($F_{1, 50} = 17.29$, $P = 0.0001$) and regional richness ($F_{1, 50} = 18.20$, $P < 0.0001$). On day 50 an initial beta of 6 led to higher richness at the end of the experiment than initial beta of 0 (Fig. 3.3). However, contrary to the repeated measures ANOVAs, dispersal scale had no direct effects on richness at any scale of observation at day 50.

However, there were some important interactive effects (Figs. 3.3 and 3.4). The affect of dispersal on local richness depended on initial beta ($F_{2, 50} = 3.94$, $P = 0.0257$). With initial beta 6, dispersal produced a unimodal richness pattern (Fig. 3.3), while

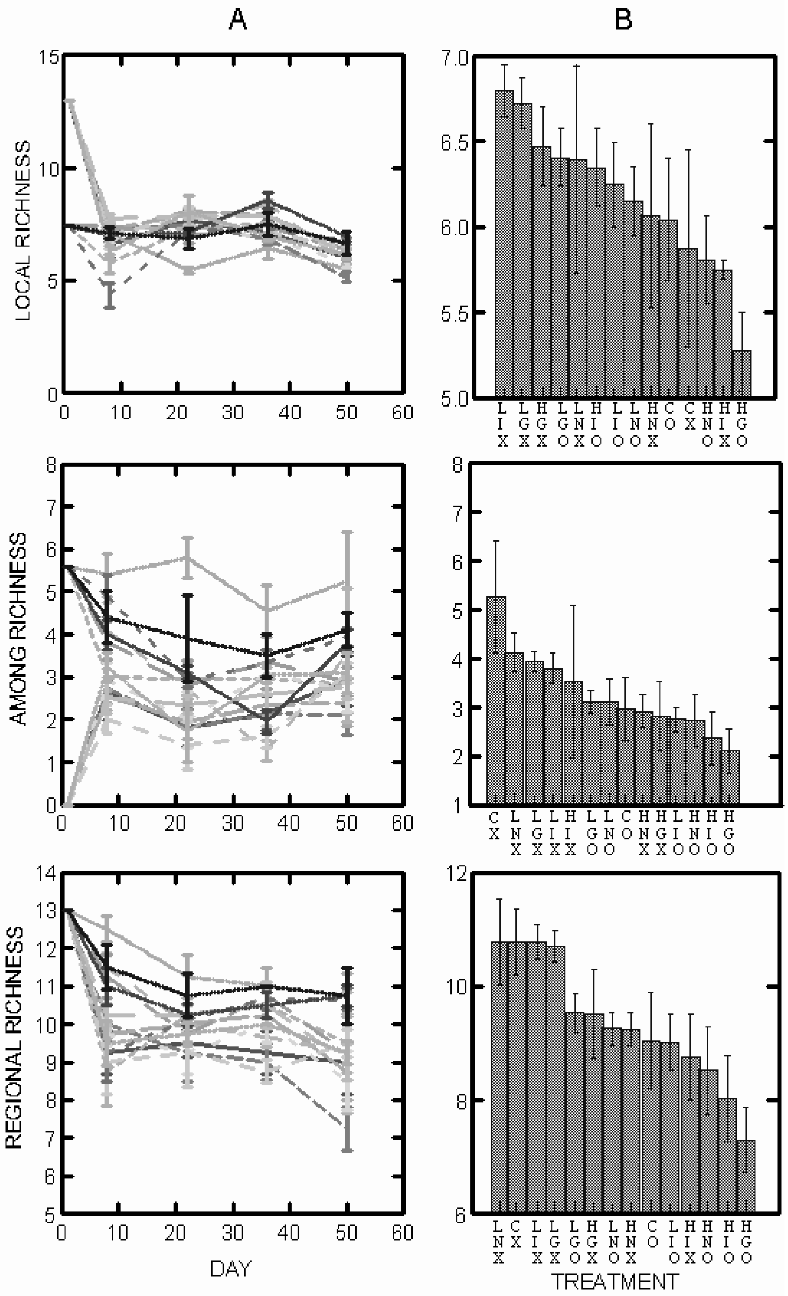

Fig. 3.2: Local, beta and regional richness for the 14 treatments used in the experiment. A) The full temporal dynamics for the treatments. Treatment labels are not present because of the number of treatments, instead this figure shows the dynamics and extent of variation among treatment combinations. B) The treatment effects at day 50, showing the variation among treatment combinations. L and H refer to low and high dispersal rates, respectively and C to the no-dispersal control; G, I and N refer to the global, intermediate and local (neighbor) dispersal scales, respectively; and O and X refer to initial beta of 0 and 6, respectively.

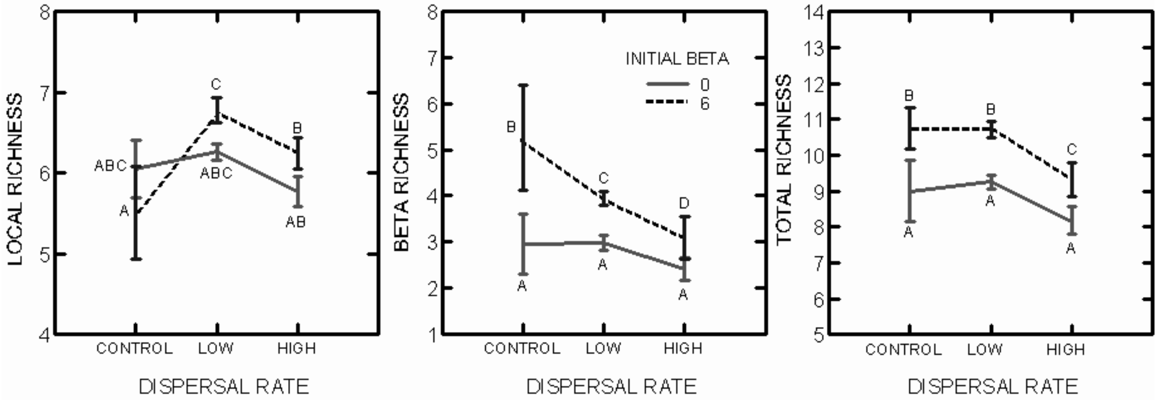

Fig. 3.3: The effects of dispersal rate and initial beta on local, beta and regional richness on day 50. Alphabet scripts refer to significant differences at P < 0.05.

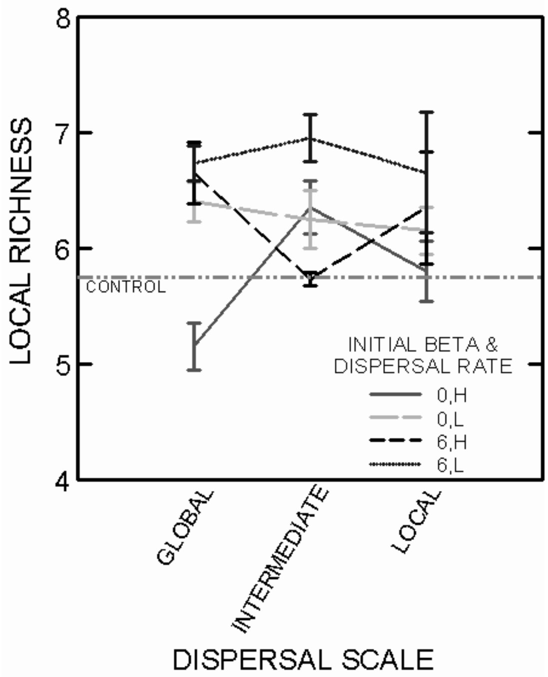

Fig. 3.4: The effect of the three-way interaction among dispersal rate, scale and initial beta on local richness on day 50.

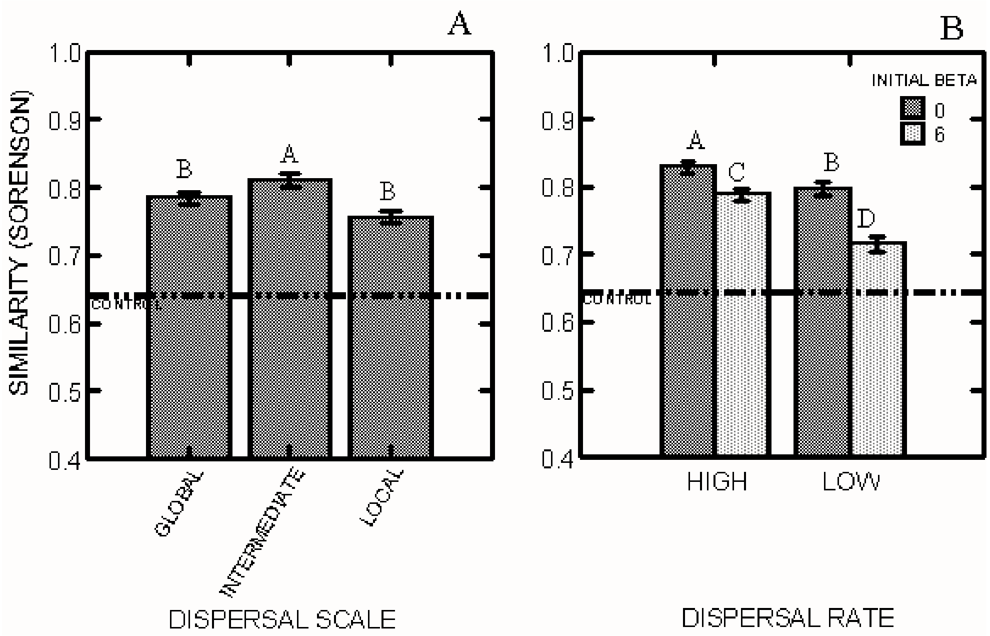

Fig. 3.5: Community similarity on day 50 as affected by A) dispersal scale; and B) both dispersal rate and initial beta, which also reveals the interaction between these two factors. Alphabet scripts refer to significant differences ($P < 0.05$).

dispersal had no effect with an initial beta of 0. With initial beta of 6, beta richness showed a monotonic decline with increasing dispersal, but again there was no relationship when initial beta was 0 (Fig. 3.3). Interestingly, despite interactions at the local and among-community (beta diversity) scales, there was no interaction between initial beta and dispersal for regional diversity (Fig. 3.3).

Dispersal scale appeared important in a three-way interaction with the other factors (Fig. 3.4). In the global dispersal scale metacommunity, with initial beta 0 and high dispersal, species richness was the lowest. However, if initial beta was 6 then richness was no different than the other dispersal rate and scale treatments. While in the intermediate dispersal scale, the treatment combination resulting in the lowest richness was high dispersal with initial beta 6.

Community similarity. Mean community similarity was significantly affected by dispersal rate ($F_{1,448} = 28.64$, $P < 0.0001$), dispersal scale ($F_{2,448} = 9.83$, $P < 0.0001$) and initial beta ($F_{1,448} = 34.69$, $P < 0.0001$) (Fig. 3.5). Contrary to the prediction, intermediate dispersal scale showed greater similarity then all other dispersal scale treatments (Fig. 3.5A). There was also a significant interaction between dispersal rate and initial beta ($F_{1,448} = 6.26$, $P < 0.013$; Fig. 3.5B). As expected, a higher dispersal rate and initial beta of 0 resulted in greater similarity (Fig. 3.5B).

Species occupancy. The occupancy of more than half of the species used in this experiment was affected by at least one treatment (Table 3.1). The dispersal rate and

Table 3.1: Results of repeated measures ANOVAs testing the effect of dispersal rate, pathway and initial beta on number of patches occupied by each species. Asterisks refer to significance level after Bonferonni correction. *P < 0.05, **P < 0.01 and ***P < 0.001 (graphs shown in Appendix C).

	Treatment			
Species	Dispersal rate	Pathway	Initial beta	Time trend[†]
Blepharisma americanum	$F_{2, 202}$ = 19.00, P < 0.0001***	$F_{2, 198}$ = 12.23, P < 0.0001***	$F_{2, 206}$ = 19.00, P < 0.0001***	Increases
Chilomonas sp.	$F_{2, 202}$ = 9.13, P = 0.0002***	$F_{2, 198}$ = 7.68, P < 0.0001***	$F_{2, 206}$ = 26.09, P < 0.0001***	Declines
Coleps sp.	$F_{2, 202}$ = 7.75, P = 0.0006**	$F_{2, 198}$ = 4.54, P = 0.0042*	$F_{2, 206}$ = 13.57, P < 0.0001***	Declines
Colpidium striatum	$F_{2, 202}$ = 11.33, P < 0.0001***	$F_{2, 198}$ = 8.06, P < 0.0001***	$F_{2, 206}$ = 0.38, P = 0.539	Unimodal
Euplotes sp.	$F_{2, 202}$ = 4.69, P = 0.0102*	$F_{2, 198}$ = 3.83, P = 0.0107*	$F_{2, 206}$ = 5.07, P = 0.0254	Declines
Lepadella sp.	$F_{2, 202}$ = 0.94, P = 0.391	$F_{2, 198}$ = 2.85, P = 0.0388	$F_{2, 206}$ = 3.55, P = 0.0774	Increases
Paramecium Aurelia	$F_{2, 202}$ = 2.01, P = 0.136	$F_{2, 198}$ = 2.13, P = 0.0976	$F_{2, 206}$ = 0.47, P = 0.493	Declines
Paramecium bursaria	$F_{2, 202}$ = 0.37, P = 0.693	$F_{2, 198}$ = 0.72, P = 0.539	$F_{2, 206}$ = 91.68, P < 0.0001***	Increases
Paramecium caudatum	$F_{2, 202}$ = 1.65, P = 0.195	$F_{2, 198}$ = 3.85, P = 0.0103*	$F_{2, 206}$ = 29.95, P < 0.0001***	Declines
Philodina sp.	$F_{2, 202}$ = 5.53, P = 0.0046*	$F_{2, 198}$ = 6.77, P = 0.0002***	$F_{2, 206}$ = 112.18, P < 0.0001***	Increases
Spirostomum sp.	$F_{2, 202}$ = 1.17, P = 0.311	$F_{2, 198}$ = 7.25, P = 0.0001***	$F_{2, 206}$ = 118.46, P < 0.0001***	Increases
Tetrahymena thermophila	$F_{2, 202}$ = 3.69, P = 0.027	$F_{2, 198}$ = 2.65, P = 0.051	$F_{2, 206}$ = 4.85, P = 0.0287	Declines
Uronema sp.	$F_{2, 202}$ = 0.62, P = 0.538	$F_{2, 198}$ = 0.93, P = 0.425	$F_{2, 206}$ = 5.41, P = 0.021	Concave

[†] Time was significant for all species repeated measures ANOVAs

initial beta results highlighted the importance of adverse species interactions, but the pathway treatment was more difficult to interpret. Of the seven species whose occupancy was significantly affected by dispersal rate, four (*Blepharisma, Colpidium, Euplotes* and *Philodina*) had higher occupancy in the presence of dispersal, and three species (*Chilomonas*, *Coleps* and *Tetrahymena*) maintained higher occupancy in the no-dispersal control (Appendix C). Of the nine species affected by initial beta, five (*Blepharisma, Coleps, Euplotes, Paramecium bursaria,* and *Philodina*) had higher occupancy when they were initialized in all local communities. However, the other four species (*Chilomonas, Paramecium caudatum, Spirostomum* and *Tetrahymena*) maintained higher occupancy, and therefore lower extinction rates, when there was initial variation in local species composition (Appendix C). Two species (*Chilomonas* and S*pirostomum*) had their lowest occupancies in the global dispersal metacommunities. Two other species (*Colpidium* and *Philodina*) had their highest occupancy at the intermediate dispersal scale (see Appendix C).

Discussion

The objective of this experiment was to examine how dispersal rate between patches in a metacommunity, dispersal scale and initial species composition influenced levels of partitioned diversity. The results appeared to be more complicated than the predictions for two reasons. First was that the relative strengths of dispersal rate, scale and initial composition on species richness could not be determined *a priori*. Second, the different species had species-specific responses to the treatments used.

A potential hypothesis would have been that better dispersers persist longer and occupy more patches in the interconnected communities because they can move to avoid superior competitors. Further, in metacommunities with initial compositional variation there may be local assemblages with open niches for allowing these dispersers to invade. Dispersal abilities (Cadotte et al. in review, see Table 3.2) were not related to species occupancy patterns (binomial probabilities > 0.05). Generally species that either negatively responded to dispersal or positively responded to initial variation were most likely to go extinct in the global dispersal scale treatment. These competitively inferior species likely find temporary refuges in the initial absence of large populations of superior competitors.

The relative effect of dispersal rate, scale and initial beta on richness depends on the spatial scale of interest. If our concern is to maximize local richness, then a low dispersal rate and intermediate dispersal scale best enhanced richness (Mouquet and Loreau 2003). However, if we are concerned with metacommunity richness, then low or no dispersal maintained the highest richness. Further, having initial compositional variation among local communities enhanced metacommunity, but not local, richness.

Few studies have explicitly examined the scale and rate of dispersal and its effects on diversity at different spatial scales (but see Forbes and Chase 2002, Cottenie et al. 2003, Cadotte and Fukami 2005). Whereas numerous studies show that dispersal generally affects local diversity (Warren 1996, Tilman 1997, Gilbert et al. 1998, Shurin 2001, Kneitel and Miller 2003, but see Pärtel et al. 1998) results are mixed on whether spatial configuration is important (Holyoak 2000, Forbes and Chase 2002, Cottenie et al. 2003, Cadotte and Fukami 2005). The large effects of dispersal rate at multiple spatial

Table 3.2: Mean time to colonize four other patches in single species metacommunity (n = 3 trials) and the corresponding dispersal rank (Cadotte et al. in review). The final two columns give the sign of the effect of dispersal rate ("+" refers to increased occupancy with dispersal) and initial beta ("+" refers to increased occupancy with initial beta of 6) (see Appendix C). "ns" refers a non-significant treatment effect.

Species	Mean dispersal time (±SD)	Dispersal rank	Dispersal rate effect	Initial beta effect
Blepharisma americanum	2.67 (0.58)	9	+	-
Chilomonas sp.	2.00 (0.00)	4.5	-	+
Coleps sp.	2.00 (0.00)	4.5	-	-
Colpidium striatum	1.00 (0.00)	2	+	ns
Euplotes sp.	2.00 (0.00)	4.5	+	-
Lepadella sp.	4.67 (0.58)	12	ns	ns
Paramecium Aurelia	2.00 (0.00)	4.5	ns	ns
Paramecium bursaria	3.00 (0.00)	10.5	ns	-
Paramecium caudatum	3.00 (0.00)	10.5	ns	+
Philodina sp.	5.33 (1.16)	13	+	-
Spirostomum sp.	2.33 (0.58)	7	ns	+
Tetrahymena thermophila	1.00 (0.00)	2	-	+
Uronema sp.	2.67 (1.16)	9	ns	ns

scales are not surprising (Forbes and Chase 2002, Cottenie and DeMeester 2004). Some studies have shown strong local community effects (Kneitel and Miller 2003) and others strong regional effects (Forbes and Chase 2002, Cadotte and Fukami 2005). Interestingly, other studies have not found strong community effects of scale of dispersal (e.g., Forbes and Chase 2002, Cadotte and Fukami 2005). However, Cottenie et al. (2003) found, in a natural metacommunity of interconnected ponds, that spatial configuration created metacommunity structure (differences among local communities). They showed that these differences could not be explained by environmental differences alone. The current results reveal that for species diversity, configuration can have important interactive effects with other processes (Fig. 3.4) or counter-intuitive effects (Fig. 3.5A).

Cottenie and DeMeester (2004) see metacommunities as the interplay between environmental variation driving divergence in composition and dispersal promoting convergence. Metacommunities are likely structured in a more complicated fashion. The configuration effects in Cottenie et al. (2003) and the current study reveal that patch spatial arrangement or scale of dispersal can serve as a source of intrinsic metacommunity structure. From the current results, I would posit that a third axis be added to Cottenie and DeMeester's scheme. Namely variation in species interactions, which is the product of stochastic compositional variation created by community assembly dynamics (e.g., Fukami 2004). Interaction variation seems to promote long-term, large-scale effects on community similarity and patterns of richness by maintaining divergence among local communities.

The role of establishment history in this experiment is surprising and important. The large difference among the global dispersal scale treatments reveals that even under high homogenizing pressure, local community compositional variation remained intact and likely resisted some species invasions (e.g., Drake et al. 1993, cf. Chase 2003). Shurin (2001) showed, in a pond system, that saturated local communities could essentially resist the invasion of new individuals. The effects of colonization history were most apparent at the beta and regional scales in this experiment. Several studies (Drake 1991, Law and Morton 1993, Price and Morin 2004) reveal that colonization history can be very important for local, closed communities. The current results reveal that these initial local differences can have profound effects even when communities remain open to immigration and at larger spatial scales (Fig. 3.3). Further, the successional and temporal dynamics, which in large part were affected by immigration, were highly impacted by the initial assembly (Mouquet et al. 2003, Fukami 2004). Most importantly, the presence of initial compositional variation determined whether these results supported or refuted an important metacommunity hypothesis. Mouquet and Loreau (2003) used a model to show that local richness should be maximized at intermediate dispersal rates, while beta and regional richness should decline. I was able to confirm this when there was initial compositional variation, but failed to support it without this variation (Fig. 3.3). With all competitors initially present, the benefits of dispersal seem to be greatly diminished.

There are number of field situations where initial community assembly is an important aspect of community temporal dynamics. Post-disturbance assembly (Brotons et al. 2005), habitat restoration (Young et al. 2001) and species invasions (Wilson et al. 2000) are all examples of local habitat assembly. Further, the trend towards widespread agricultural abandonment in Europe and Eastern North America (Flinn and Vellend 2005) means that there may be large-scale and long-term consequences to local assembly dynamics in patchy landscapes. Jacquemyn et al. (2001) showed that patch area, age and dispersal limitation were all-important for local patterns of richness in a fragmented landscape. Their study showed that long-term consequences were measurable for at least 223 years after field abandonment (the age of the oldest patches).

It is important to note that not all species benefit from dispersal (e.g., Burkey 1997, Cadotte and Fukami 2005), and in fact richness may be negatively impacted by dispersal (Mouquet and Loreau 2003; cf., Brown and Kodric-Brown 1977, Shmida and Wilson 1985). The species used in this experiment varied in their responses to immigration, no doubt driven by specific interactions with the other species in the metacommunity. Experiments also using protozoan microcosms have found that dispersal can either increase the persistence of species (Holyoak and Lawler 1996) or increase the extinction risk (Burkey 1997, Cadotte and Fukami 2005) depending on the nature and stability of the interactions.

Conclusions. Ecologists often suppose that local and regional processes are important processes structuring richness (e.g., Ricklefs 1987, Cornell and Lawton 1992). However, the current results reveal that dispersal likely has different effects on richness at different spatial scales and not as a single "regional" process. Instead, dispersal is a process at the "mesoscale" (Holt 1993), interacting with processes and community composition at a number of spatial scales. Further, assuming that dispersal generally has a positive effect on species richness ignores potential negative species-specific responses to invading competitors (Mouquet and Loreau 2003). How any specific system responds to larger-scale processes, individual species and community responses should be ascertained to determine the negative and positive impacts.

Chapter 4

The effects of resource enrichment, dispersal, and predation on local and meta-community structure [1]

Abstract Community structure is the observable outcome of numerous processes. We conducted a laboratory experiment using a microbial model system to disentangle effects of nutrient enrichment, dispersal, and predation on prey species richness and predator abundance at local and metacommunity scales. Prey species included: *Chilomonas* sp., *Colpidium striatum*, *Colpoda cucullus, C. inflata, Paramecium tetraurelia*, *P. caudatum*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, and *Uronema* sp. , and *Stentor coeruleus* was the predator used. We hypothesized that 1) increased basal resources should maintain greater species richness and higher predator abundance; 2) dispersal should maintain greater species richness; and 3) predation should reduce richness, especially in the high resource treatments relative to no-predator treatments. Our results support all three hypotheses. Further we show that dispersal affects richness at the local community scale but not at the metacommunity scale. However, predation seems to have major effects at both the local and metacommunity scale. Overall, our results show that effects of resource enrichment, dispersal, and predation were mostly additive rather than interactive, indicating that it may be sometimes easier to understand their effects than generally thought due to complex interactive effects.

Introduction

At the heart of the science of ecology is how multiple processes interact to produce extant patterns of species abundances, distributions, and diversity. Consequently, two unresolved issues in community ecology are: 1) how local and regional processes interact to produce patterns of species richness (e.g., Holt 1993; Holt et al. 1997; Loreau and Mouquet 1999; Shurin 2000; Amarasekare and Nisbet 2001; Shurin and Allen 2001; Cottenie et al. 2003; Kneitel and Miller 2003); and 2) how resource availability affects species diversity and interactions (e.g., Luckinbill 1974; Huston and DeAngelis 1994; Waide et al. 1999; Fukami and Morin 2003). We examine three fundamental community-structuring biotic processes that address these two unresolved issues: interspecific competition for resources, predation, and dispersal among local patches.

These three community-structuring processes have disparate histories, and therefore have separate theoretical underpinnings. First, competition has long been a central paradigm in ecology (e.g., Darwin 1859; Warming 1909; Gause 1934; Pianka 1966; MacArthur and Levins 1967; Tilman 1982; Chase and Leibold 2003). One

---

[1] A slightly modified version of this chapter is in press as: Cadotte, M. W., A. M. Fortner, and T. Fukami. 2006. The effects of resource enrichment, dispersal and predation on local and meta-community structure. *Oecologia*. My use o f "we" in this chapter refers my co-authors and myself. My primary contributions to this paper include: 1) development of idea and hypotheses; 2) planning experimental design, selection of species and oversaw data collection; 3) data analysis; and 4) most of the writing.

influential modern version is a simple, but powerful concept: the idea that the competitor who can survive at the lowest resource-level will likely out-compete co-existing species (i.e., *R**, Tilman 1982; Leibold 1996; Chase and Leibold 2003). In the current study we use local communities that differ in resource concentrations as a surrogate of strength of competition.

Competition therefore limits community richness while the next disparate process, the immigration of individuals in to local communities, can increase species richness by allowing species to find empty patches or resources and potentially escape dominant competitors (i.e., competition-colonization tradeoff, Holmes and Wilson 1998; Amareskare and Nisbet 2001; Mouquet and Loreau 2002; Levine and Rees 2002, Cadotte 2006a). In a metacommunity framework, immigration into local communities is dependent upon those leaving other communities. Metacommunity dispersal can reduce competition-caused extinctions in local communities (Cadotte 2006a, b), likely because extinction-prone populations are subsidized from larger, more secure populations (i.e., source-sink dynamics, Brown and Kodric-Brown 1977; Mouquet and Loreau 2002). The relative importance of these mechanisms (competition-colonization tradeoff vs. source-sink dynamics) in a closed metacommunity, with no disturbance or external colonists, will depend upon stochastic extinctions or predation-caused extinctions.

The final disparate process, predation, is often thought to have a largely positive effect on the maintenance of local richness by reducing competition among species by reducing abundances, freeing resources or opening space (Paine 1966; Holt 1977; Holt and Lawton 1994; Leibold 1996, but see Addicott 1974; Cadotte and Fukami 2005). However, different species of predators are likely to show differential effects on different prey species (e.g., McPeek 1998, Chalcraft and Resetarits 2003, Jiang and Morin 2005), with generalist predators more likely to reduce local richness than specialist predators (Jiang and Morin 2005). Negative impacts from predation in metacommunities can reduce richness at larger scales by undoing dispersal's ability to increase richness (Kneitel and Miller 2003, Cadotte and Fukami 2005).

How these processes affect communities when they are manipulated simultaneously is not intuitive. Resource manipulation may be an efficacious surrogate for intra-community competition if communities can be assumed to be at equilibrium (Tilman 1982; Waide et al. 1999). Kneitel and Miller (2003), building on the modeling work of Mouquet and Loreau (2002, 2003; Loreau et al. 2003), hypothesized that by decreasing competition (e.g., increasing resources) the effect of dispersal should be heightened, while increases in competition (lower resources) or predation rate should lessen the import of dispersal on community richness. They found that, in their inquiline communities in pitcher plants, resource manipulation had little impact on the effect of dispersal, while increasing predator abundance negated the dispersal effect.

However, enrichment can have other important interactions with predation, in the absence of dispersal. In simple tri-trophic systems, enriching three-tiered chains, can result in increased abundances of predators (e.g., Rosenzweig 1973, Oksanen et al. 1981). Wootton and Power (1993) showed that increasing basal trophic-level productivity can result in higher abundances of predators. Following this, we would expect that enrichment of systems with predators should result in no change in the bacteriovore community structure with enrichment, since the extra biomass should be captured in the predatory trophic level (Jiang and Morin 2005).

Cadotte and Fukami (2005) found that, for protist metacommunities, dispersal among local communities only had a short-term enriching effect on local richness while having long-term negative effects at larger spatial scales. In that experiment they hypothesized that predator effects may have profoundly affected those results because the predator was able to move along with prey in the dispersal treatments. More than this, a number of recent studies attempt to reconcile interactions among predation, competition and dispersal (Loreau and Mouquet 1999; Shurin and Allen 2001; Kneitel and Miller 2003), and reveal that dispersal should offset losses due to competition, but that predation (especially from a dispersing generalist predator) should counter the dispersal benefit.

In this paper we examine how predation, competition and dispersal all combine to structure local communities and generate richness patterns. We expect that 1) in the absence of predators, local communities open to dispersal will maintain higher levels of diversity; while 2) increased resources will maintain greater species richness and will enhance the effect of dispersal; and that 3) the presence of a predator will diminish or negate the effects of dispersal, and have a greater impact on high resource communities as they attain higher abundances in these communities.

The experiment described in this paper uses a microcosm approach and addresses questions brought up in a previous experiment (Cadotte and Fukami 2005). In that experiment, predation was not explicitly manipulated but it was apparent that richness patterns were differentially affected by dispersal and the presence of a generalist predator. Although microcosm experiments sacrifice natural context (Carpenter 1996), they offer many benefits (Drake et al. 1996, Cadotte et al. 2005). Microbial microcosms not only offer strict controls and replication, but also allow the researcher to observe multigenerational temporal dynamics, allowing them to be used to refine hypotheses and theories (Cadotte et al. 2005).

Methods

We used three-community metacommunities, in which the local communities were 250 ml jars filled with 100 ml of nutrient solution. Within the metacommunities were three resource levels of varying concentrations of protozoa pellets and vitamins. The three local communities, each having a different resource level, constituted an intra-metacommunity treatment. There were two other metacommunity-level treatments: 1) the presence of a predatory species; and 2) dispersal among local communities within the metacommunity. These two sets of treatments resulted in four metacommunity combinations: presence of a predator and dispersal (PD), presence of a predator only (P), dispersal with no predator (D), and a control without dispersal or predation (C). All metacommunities were replicated five times, meaning that each combination of predation and dispersal were replicated five times for each of the three resource levels. The dispersal consisted of removing 0.6 ml from all three local communities, homogenizing and redistributing among the local communities. The dispersal treatments were performed every 3.5 days (i.e., every 3rd and 7th day).

Each local community consisted of 100 ml of nutrient solution (80 ml of stock solution plus 20 ml from initial species additions), with the resource concentrations being one of three levels used in the experiment—high, medium, or low. The high resource level consisted of 1.0 g/L of protozoa pellets and 0.1 g/L of vitamins, the medium resource level consisted of 0.1 g/L of protozoa pellets and 0.01 g/L of vitamins, and the low resource level consisted of 0.01 g/L of protozoa pellets and 0.001 g/L of vitamins.

Five days prior to the initialization of local communities, the stock solution was inoculated with four bacterial species (*Bacillus cereus, B. subtilis, Proteus vulgaris, Serratia marcescens*) from stock cultures as well as bacteria from filtered prey species stock cultures -in order to introduce bacterial species that would subsequently be introduced with the prey species. Three days before initialization, microflagellates were introduced.

A total of 11 protozoan and rotifer species were used in this experiment -1 generalist predator, *Stentor coeruleus*, and 10 prey species (Table 4.1). The same local community species assemblages were used in each treatment and each replicate. The average generation time for the organisms involved is about a day. This experiment lasted eight weeks, representing about 50-60 generations of the organisms involved.

Sampling. Once a week 6 ml of community medium was removed and replaced with fresh medium of the concentration corresponding to the resource level from which it was taken. On sampling dates the excised 6 ml was used as the source for the sample.

Our sampling procedure consisted of individual-based full counts. The full counts were performed five times, in weeks 1, 2, 4, 6, and 8. From the 6 ml aliquots, we counted all individuals of each species from a 0.2 ml subsample. If species densities were too high to be accurately counted we added 2 ml of sterile solution and again counted all the individuals in a 0.2 ml subsample of the dilution. Numbers of individuals were calculated per ml.

Data analyses. Our data consisted of observations for the four metacommunity treatments (predation and dispersal) and the three intra-metacommunity treatments (resource level) across a time series. Our primary data were counts (species richness), and so we used loglinear models for analysis of this data. For local richness we modeled predator (Stentor) presence/absence, dispersal presence/absence, resource level, time (week number), and all two-way interactions. We also combined the three interacting local communities to find metacommunity species richness, by recording species presence at the metacommunity scale (i.e., present in at least one local community). We analyzed all the same variables and two-way interactions, except for resource level, in a loglinear model. We also examined class comparisons within each independent variable. We report the class effect on the model (β), as well as the percent effect ($-e^{\beta}$) on species richness. We also analyzed Simpson's diversity index (not shown) and results largely confirmed the results based on the above analysis.

There was a potential confounding influence in that resource dynamics will change in the treatments with dispersal. If the dispersal effect on nutrient level was great enough to affected species richness, then the dispersal-resource-time three-way interaction term in the loglinear model should be significant, and would merit further discussion/analysis.

We used repeated measures ANOVA to determine if dispersal and resource level had significant effects on the abundance of *Stentor*. An assumption for the repeated

Table 4.1: The 11 protozoan and rotifer species, plus the basal trophic species used in this experiment.

Species	Trophic level
Stentor coeruleus	Predator
Chilomonas sp.	Prey (Bacteriovore)
Colpidium striatum	Prey (Bacteriovore)
Colpoda cucullus	Prey (Bacteriovore)
Colpoda inflata	Prey (Bacteriovore)
Paramecium caudatum	Prey (Bacteriovore)
Paramecium tetraurelia	Prey (Bacteriovore)
Philodina sp.	Prey (Bacteriovore, Microflagellates)
Spirostomum sp.	Prey (Bacteriovore, Microflagellates)
Tetrahymena thermophila	Prey (Bacteriovore)
Uronema sp.	Prey (Bacteriovore)
Bacillus cereus	Basal (bacteria)
Bacillus subtilis	Basal (bacteria)
Proteus vulgaris	Basal (bacteria)
Serratia marcescens	Basal (bacteria)
Microflagellates	Intermediate

measures *F*-test is that the variance-covariance matrix has compound symmetry. When there is departure from compound symmetry, corrections, which modify degrees of freedom, have been proposed by Huynh-Feldt and Greenhouse-Geisser. We used these corrections in determining P-values. All statistics were done using SAS v.9.1 (SAS Institute 2003).

Results

Intra-community patterns. At the local scale, all the main effects significantly affected richness (Table 4.2 & 4.3). Local communities without Stentor averaged 50.5% more species than those with Stentor. Similarly, without dispersal, local communities showed a reduction of 36.4% in species richness compared to those with dispersal. Richness also declined with lower resources and over time (Table 4.2, 4.3, Fig. 4.1).

One interaction term (predator X week) was significant (Table 4.2). This corresponded to different temporal trajectories dependent upon the presence of *Stentor*. In the presence of *Stentor*, richness showed an exponential decline over time, while in the absence of *Stentor*, richness showed a unimodal curve (Fig. 4.1).

We also tested the three-way interaction between dispersal, resource level and time. We found that this interaction had no significant effect on species richness (χ^2 = 2.95, P = 0.9373), which leads us to conclude that resource change with dispersal had no effect on our results.

Metacommunity patterns. When we pooled all three local communities together and examined patterns at the metacommuity, the negative effects of predation were much more obvious (Fig. 4.2). At this scale, the presence of dispersal had no effect on richness (P = 0.7629), while the presence of *Stentor*, time and the *Stentor*-time interaction all significantly affected richness (Table 4.2). Without *Stentor*, metacommunity richness was on average 113.5% higher than those without *Stentor* (Table 4.3).

Species dynamics. Several species (*Chilomonas*, *Colpidium*, *Colpoda inflata*, *Paramecium caudatum*, and *Tetrahymena thermophila*) quickly went extinct or had idiosyncratic dynamics. These idiosyncratic dynamics mean that the species in question would appear a single or very few samples at different sampling dates and not in the same replicate. The rest of the species revealed more tractable dynamics. Three species (*Colpoda cucullus*, *Paramecium tetraurelia* and *Uronema*) appeared to be adversely affected by the presence of the predator, while two species (*Philodina* and *Spirosomum*) were largely unaffected by the predator.

The predator, *Stentor coeruleus*, was unaffected by communities being open to dispersal ($F_{1,96}$ = 0.08, P = 0.7745), but was significantly affected by community resource level ($F_{2,96}$ = 29.45, P < 0.0001, Fig. 4.3), with high resource patches maintaining significantly higher *Stentor* abundances after the first sampling date (Tukey's post hoc test, P<0.05 for sampling weeks 2-8). Stentor abundance also declined over time ($F_{4,96}$ = 22.86, P , 0.0001). Further, resource level and time showed a significant interaction ($F_{8,96}$ = 23.21, P < 0.0001), where high resource communities showed unimodal or logistic increases (with possible oscillations) while medium and low resource levels the *Stentor* populations showed linear declines (Fig. 4.3).

Table 4.2: Results of the loglinear model, modeling main effects and their two-way interactions on local and regional species richness. DF is the degrees of freedom and X^2 is the Chi-square statistic. Bold P-values are significant at P = 0.1.

Source	DF	X^2	P
Local Richness			
Predator	1	40.77	**<0.0001**
Dispersal	1	7.10	**0.0077**
Resource	2	90.85	**<0.0001**
Week	4	101.75	**<0.0001**
Predator X Dispersal	1	0.01	0.9415
Predator X Resource	2	0.69	0.7086
Dispersal X Resource	2	4.2	0.1222
Predator X Week	4	22.17	**0.0002**
Dispersal X Week	4	2.52	0.6411
Resource X Week	8	3.60	0.8614
Regional Richness			
Predator	1	32.59	**<0.0001**
Dispersal	1	0.09	0.7629
Week	4	62.99	**<0.0001**
Predator X Dispersal	1	0.10	0.7493
Predator X Week	4	18.60	**0.0009**
Dispersal X Week	4	0.92	0.9220

Table 4.3: Results of the loglinear model, showing within class effects on local and regional species richness. Beta is from the loglinear model, showing the effect of moving from one class state to another (e.g., from predator present to absent). % effect is the percent change in richness in the model as a result of the state change. DF is the degrees of freedom and X^2 is the Chi-square statistic. Bold P-values are significant at P = 0.1.

Variable	Condition	Beta	% effect	DF	X^2	P
Local Richness						
Predator	Absent vs. present	0.4087	50.5↑	1	3.36	**0.0669**
Dispersal	Absent vs. present	-0.4523	36.4↓	1	3.94	**0.0472**
Resource	High vs. low	0.6261	87.0↑	1	5.74	**0.0166**
	Medium vs. low	0.3532	42.4↑	1	1.62	0.2037
Week	Week 1 vs. equilibrium	0.9927	169.8↑	1	13.07	**0.0003**
	Week 2 vs. equilibrium	0.7025	101.9↑	1	6.22	**0.0126**
	Week 4 vs. equilibrium	0.3586	43.1↑	1	1.48	0.2244
	Week 6 vs. equilibrium	-0.1524	14.1↓	1	0.21	0.6462
Regional Richness						
Predator	Absent vs. present	0.7584	113.5↑	1	7.06	**0.0079**
Week	Week 1 vs. equilibrium	1.3540	287.3↑	1	21.29	**<0.0001**
	Week 2 vs. equilibrium	1.0888	197.1↑	1	13.10	**0.0003**
	Week 4 vs. equilibrium	0.3641	43.9↑	1	1.17	0.2790
	Week 6 vs. equilibrium	0.2103	23.4↑	1	0.36	0.5465

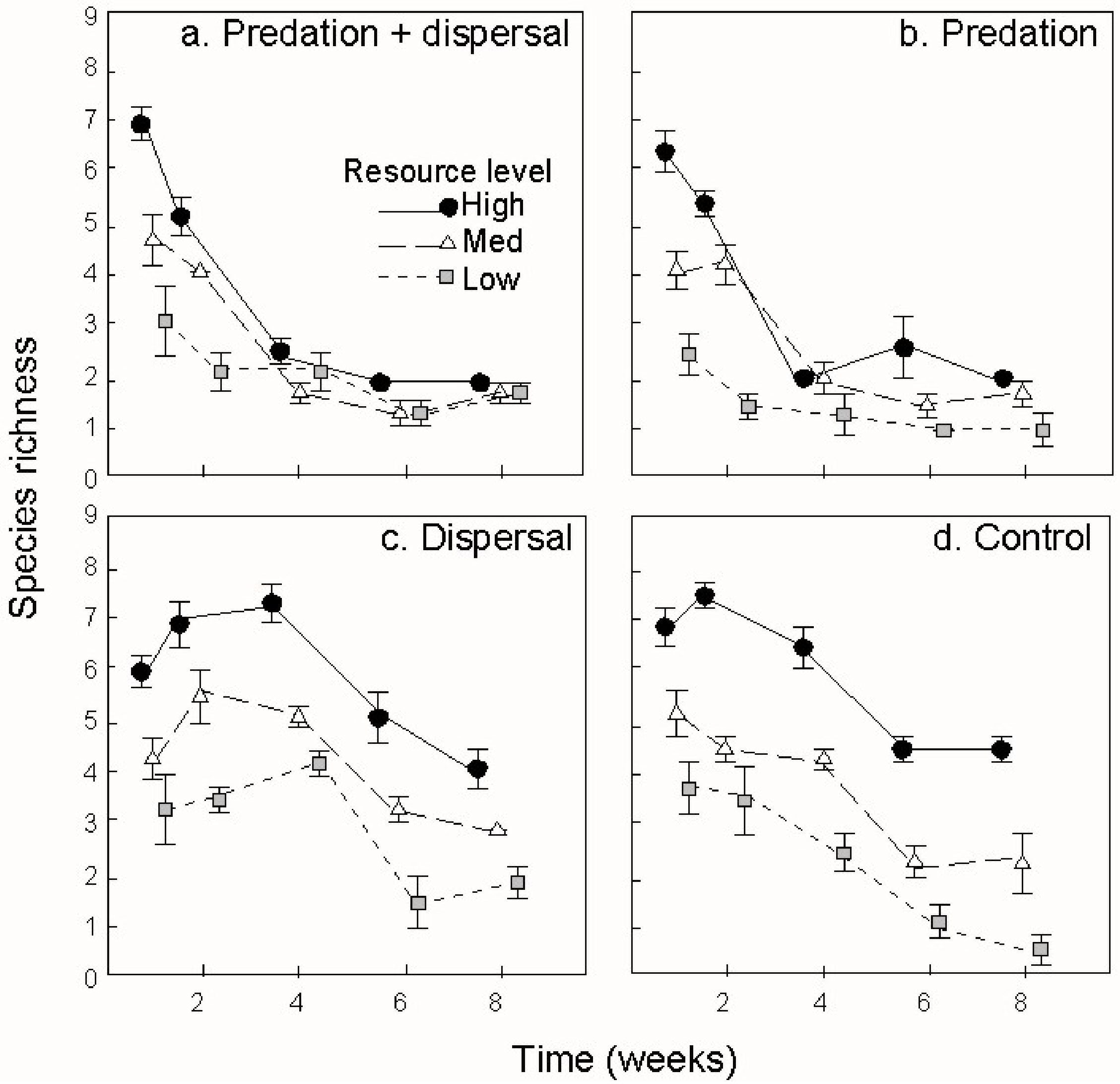

Fig. 4.1: Local prey community species richness during the 8 week study in each combination of predation/dispersal treatment (a. Predation + dispersal, b. Predation, c. Dispersal, d. Control) at high, medium, and low resource levels (means ± SE, n = 5). Prey species include: *Chilomonas* sp., *Colpidium striatum*, *Colpoda cucullus, C. inflata, Paramecium tetraurelia*, *P. caudatum*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, and *Uronema* sp.

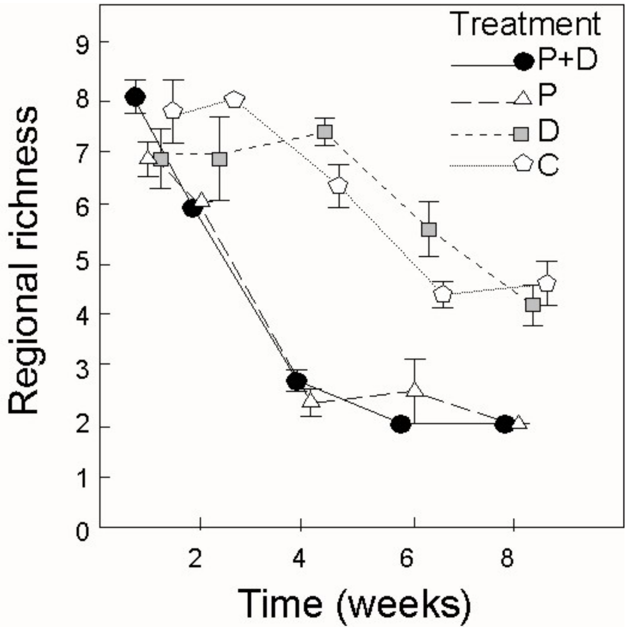

Fig. 4.2: Regional (metacommunity) species richness during the 8 week study for Predation and Dispersal (P+D), Predation (P), Dispersal (D), Control (C), (mean ± SE, n=5).

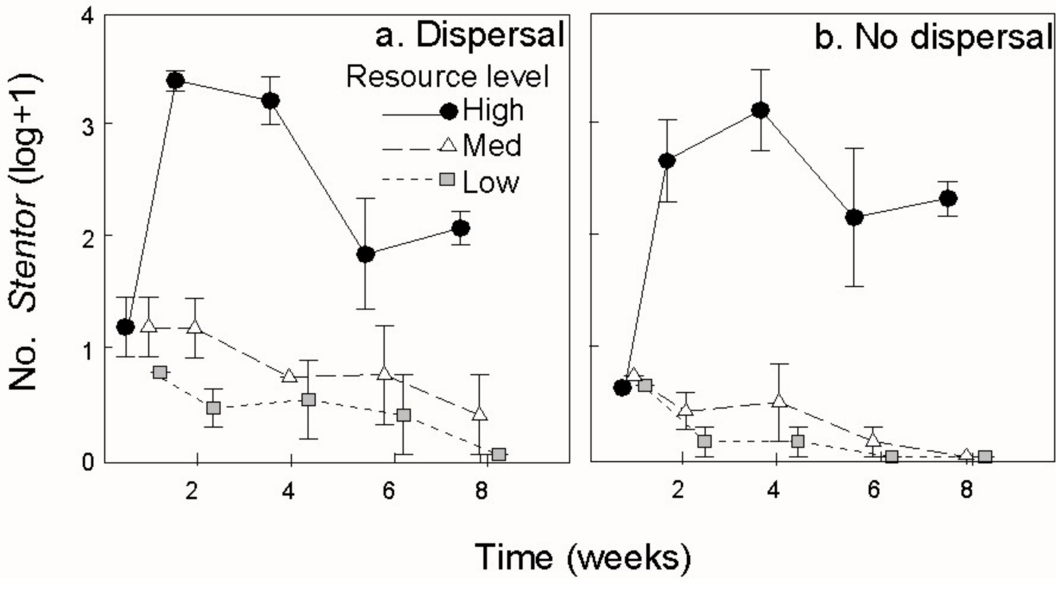

Fig. 4.3: The number of *Stentor coeruleus* (log +1) at high, medium and low resource levels, (mean ± SE, n= 5) with (a) dispersal and (b) no dispersal.

Discussion

We were interested in disentangling the effects of predation and dispersal and developed hypotheses as to the directions of their effects from the literature (Mouquet and Loreau 2002, 2003; Kneitel and Miller 2003) and in response to the findings of a previous experiment (Cadotte and Fukami 2005). We hypothesized that predation would reduce or negate the richness increasing effect of dispersal. Also, higher basal resource concentration may enhance the effect of dispersal. Therefore if we did see any effect of dispersal in the treatments with predation, it should be at high resource concentrations. Our results revealed that our predator, *Stentor coeruleus*, reduced richness to two species, regardless of resource concentration and dispersal treatment. This effect is very apparent at the metacommunity level (Fig. 4.2). Therefore predation appears to be an important community structuring mechanism regardless of spatial scale (see too Cadotte and Fukami 2005). Different predators have differential effects on prey species richness and abundance (McPeek 1998; Steiner 2001). *Stentor* is an efficacious generalist predator (Cadotte and Fukami 2005; Jiang and Morin 2005). Our results reveal some of the ecological consequences of a generalist predator.

At the local scale, dispersal had beneficial effects on richness at intermediate timescales. Even though there appeared to be some benefit of dispersal in the presence of our predator (see too Holyoak and Lawler 1996a, b), predation dramatically reduced richness compared to the no-dispersal treatment. However, at the metacommunity, dispersal had little or no effect on richness (see Cadotte 2006a for an examination of the pervasiveness of this pattern in the ecological literature). Therefore we view dispersal as an important local rather than regional structuring mechanism. The results from this study explain the patterns observed in Cadotte and Fukami (2005). In that study, dispersal appeared to have no effect at the local community, but appeared to maintain lower diversity in the metacommunity. They realized that because the strongest predator, *Stentor coeruleus* was not found in every local community that dispersal effects were confounded with predator effects. Our current results reveal that the pattern of lower regional diversity found in Cadotte and Fukami (2005) are likely the result of the regional structuring effect of *Stentor*, similar to what is shown in Fig. 4.2. Similarly, Warren (1996) found that dispersal rate had a minor effect on community structure, but was significant for individual species abundances (see too Holt et al. 2002). Warren’s (1996) experimental design also included a generalist top predator (*Amoeba proteus*) which may have been, similar to our findings and that of Kneitel and Miller (2003), an important mechanism structuring communities and reducing the effect of dispersal. Jiang and Morin (2005) examined how specialist and generalist predators structure local communities. They found that communities with the specialist predator exhibited bottom-up control of the prey community, while with the generalist, top-down processes were in control.

Shurin and Allen (2001) show that, even though dispersal can promote coexistence between competing species, inclusion of an effective, dispersing predator can potentially reduce local diversity. Their model also shows that predation, even though it reduces local diversity, may enable further invasions and maintain higher regional diversity. Our results show that the presence of a predator strongly diminishes species coexistence at both the local and metacommunity levels. Although in a more complex experimental mesocosm, Shurin (2001) found that dispersal provided a rescue effect for zooplankton, when without dispersal, predation drove many to extinction. Shurin (2001) also showed that the presence of predators did facilitate subsequent invasions by other zooplankton. It is difficult to say how our findings would hold given an open species pool.

Our view of predation is like that of Shurin and Allen (2001), where the predator is a member of the community and therefore influenced by dispersal. In a sense our design is not truly factorial, because predator dynamics can change with dispersal. This reality may limit our understanding of how dispersal and predation structure prey communities as independent processes. However we feel that the current results are pertinent to factors structuring communities and to conservation issues concerning fragmentation and habitat connectivity.

Several authors have noted that predator abundances are often positively affected by resource enrichment, perhaps more than other trophic levels below the predator (e.g., Leibold 1996; Bohannan and Lenski 1997, 1999; Kaunzinger and Morin 1998; Jiang and Morin 2005). Enrichment is thought to have a number of other consequences for community structure, beyond relaxing competition. Enrichment can destabilize predator-prey interactions, increasing the probability that one or both species go extinct (Luckinbill 1974). Conversely, enrichment is thought to support longer food chains, with lower probability of top predator extinction (e.g., Leibold 1996). Our results show that, over the course of the experiment, predator population abundances were enhanced by resource enrichment. Jiang and Morin (2005) show that increases in generalist predator abundance with increasing nutrients is a logical consequence of increased reproduction in prey populations. However, they point out that specialists are unlikely to similarly benefit because of shifts in prey composition or size.

Conclusions. Dispersal and predation are known to affect species diversity in sometimes interactive or negating ways (Knietel and Miller 2003, Leibold et al. 2004). These effects can be difficult to understand as universal processes. However, by examining these effects at different spatial and temporal scales, it becomes possible to dissect the relative effects of predation, competition and dispersal. We show that 1) increased resources supported higher prey diversity; 2) increased resources supported higher predator abundances; 3) dispersal increased local richness both in the presence and absence of the predator, but the negative impact of predation on richness was much stronger than the positive dispersal effect; 4) dispersal enhances local richness, and not metacommunity richness; and 5) predation structures communities at multiple spatial scales. These results show that although competition, predation and dispersal have differing effects on the maintenance of species richness, they actually may not have interactive effects, rather they appear additive, at least when examining dispersal as a binary factor (as opposed to a continually varying factor, e.g., Mouquet and Loreau 2002). In such cases, it may be sometimes easier to understand their effects than generally thought due to complex interactive effects.

Chapter 5

On testing the competition-colonization tradeoff in a multispecies assemblage[1]

Abstract The competition-colonization tradeoff has long been considered an important mechanism explaining species coexistence in spatially-structured environments, yet data supporting it remain ambiguous. Most competition-colonization research examines plants and the dispersal-linked traits of their seeds. However colonization is more than just dispersal, since a species ability to rapidly grow is also an important component of colonization. We tested for the presence of competition-colonization tradeoffs with a commonly used artificial animal assemblage, consisting of protozoan and rotifer species, where colonization was a species ability to establish populations in patches. By ranking species according to their colonization abilities and their pair-wise competitive interactions, we show that these species strongly exhibit competition-colonization tradeoffs. These results reveal that the competition-colonization tradeoff exists within animal assemblages, and that even in a laboratory setting, species could not overcome evolutionary constraints that cause a species to either be a good competitor or colonizer, but not both.

Introduction

When it comes to mechanisms explaining species coexistence, the competition-colonization tradeoff has long been considered one of the most important in spatially-structured environments (Levins and Culver 1971). This tradeoff predicts that better competitors are inferior colonizers and vise versa (Fig. 5.1). Recently however, significant doubt has been raised questioning the pervasiveness of these tradeoffs (e.g., Jakobsson and Eriksson 2003).

The source of this doubt comes from the fact that many field studies fail to detect evidence for this competition-colonization tradeoff (e.g., Harrison et al. 1995, Turnbull et al. 1999, Yu and Wilson 2001, Jakobsson and Eriksson 2003), where spatial heterogeneity may be overwhelming tradeoff effects (Levine and Rees 2002) or they simply do not exist in the form researchers think they do. Most work done on competition-colonization tradeoffs has focused on plants, where seed attributes supposedly reveal the evolutionary outcome of this tradeoff in the form of a tradeoff between seed size and seed number (Rees 1995, Jakobsson and Erikkson 2000). Despite the presence of these seed characteristics, Jakobsson and Erikkson (2003) failed to find support for the existence of a competition-colonization tradeoff in 15 wind-dispersed Asteraceae species. They concluded that doubt must be cast on models that assume this tradeoff. This is a controversial conclusion as numerous theoretical studies have revealed

---

[1] A slightly modified version of this chapter is in review as: Cadotte, M. W., D. V. Mai, S. Jantz, M. Keele and J. A. Drake. On testing the competition-colonization tradeoff in a multispecies assemblage. *American Naturalist*.. My use o f "we" in this chapter refers my co-authors and myself. My primary contributions to this paper include: 1) development of idea and hypotheses; 2) planning experimental design, selection of species and oversaw data collection; 3) data analysis; and 4) most of the writing.

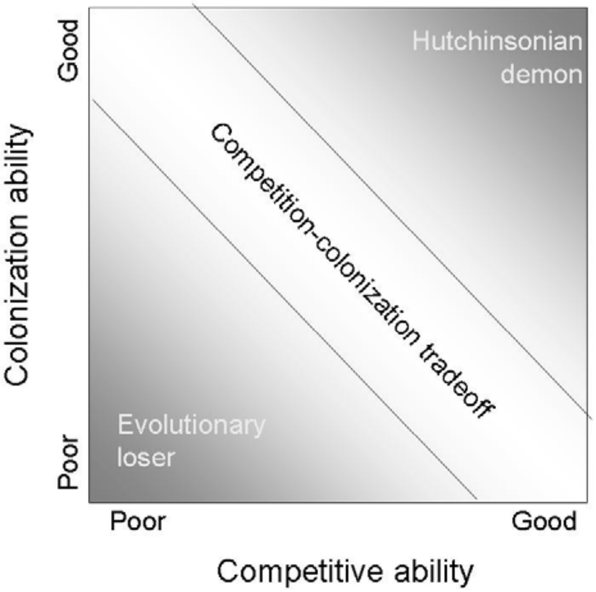

Figure 5.1: Hypothesized relationships between competitive and colonization abilities. If a tradeoff exists, then species should fall along the diagonal line.

the potential importance of and under what conditions this tradeoff ought to affect patterns of coexistence (e.g., Levins and Culver 1971, Hastings 1980, Yu and Wilson 2001, Amarasekare et al. 2004). Furthermore, several authors believe that competition-colonization tradeoffs are an important key for understanding patterns of coexistence at larger spatial scales (Amarasekare 2003, Kneitel and Chase 2004).

It seems then that there is a fundamental disconnect between empirical findings and theoretical assumptions. However, we contend that empirical studies are really measuring dispersal and not colonization, *per se*. Dispersal describes the movement of individuals or propagules, while colonization also includes the ability to overcome Allee effects and successfully establish a population. Obviously, dispersal is important for establishing a population and that by increasing the number of propagules likely increases chances of establishing a population (Lockwood et al. 2005, Warren et al. 2006).

We utilize an artificial species assemblage, often used in aquatic microcosm experiments (e.g., Warren 1996, Cadotte and Fukami 2005, Cadotte 2006b), to examine the competition-colonization tradeoff. This assemblage is referred to as “artificial” because these organisms have been collected at different times and places and have been in isolation for at least 1000 generations, and are placed together in controlled habitats. As a result these species are not likely to have a strong evolutionary pressure maintaining relative competitive and colonization differences. These species could conceivably be classified in to one of three groups: those showing a tradeoff; ‘Hutchinsonian demons’, with superior competitive and dispersal abilities (Kneitel and Chase 2004); or else ‘ecological losers’ being poor competitors and dispersers (see Fig. 5.1). If competition-colonization tradeoffs in these species are based upon a real tradeoff between the ability

Table 5.1: Mean colonization time in weeks, the associated colonization rank and the competition rank for each species used in this experiment.

Species	Colonization time	Colonization rank	Competition rank
Blepharisma americanum	2.67	5.5	9.9
Chilomonas sp.	1.33	11	3.3
Coleps sp.	2.00	9	7.2
Colpidium striatum	1.00	12.5	3.3
Euplotes sp.	2.00	9	7.3
Lepadella sp.^{r}	4.67	2	8.7
Paramecium aurelia	2.00	9	9.2
Paramecium bursaria	3.00	3.5	9.4
Paramecium caudatum	3.00	3.5	5.6
Philodina sp.^{r}	5.33	1	11.8
Spirostomum sp.	2.33	7	8
Tetrahymena thermophila	1.00	12.5	1.8
Uronema sp.	2.67	5.5	5.3

Notes: Rotifers are marked with ^{r}. All other species are protozoa.

to compete vs. colonization ability then we expect to see this tradeoff maintained despite isolation.

Thirteen species were used in the two experiments below, and they are listed in Table 5.1. Several labs use these same or closely related organisms in experiments investigating the role of dispersal in regulating coexistence and species richness (e.g., Holyoak and Lawler 1996, Warren 1996, Holt et al. 2004, Holyoak 2000, Cadotte and Fukami 2005, Cadotte 2006b). Yet no study has examined if there is in fact competition-colonization tradeoffs exhibited by these organisms.

Methods

It is important to note that, although laboratory microcosms lack naturalness important for understanding ecological processes, they do offer some invaluable benefits (see Cadotte et al. 2005). Essentially they allow researchers to control and manipulate variables as well as provide truly multigenerational data, something that is often essential for testing ecological theory (Cadotte et al. 2005, Hastings 2004), an in our case both colonization and the outcome of competition are multigenerational processes.

We ran two separate experiments, one to determine the relative colonization abilities and a second to determine the relative competitive abilities of the organisms involved. In both experiments we used aquatic microfauna (Table 5.1). Resource patches consisted of a nutrient solution consisting of 0.55 g/L of protozoa pellets (Carolina Biological Supply Company), 0.05 g/L powdered vitamins, and a single sterilized wheat seed as a source of slow-release carbon in commercially available spring water (Crystal Springs). Six days prior to the initialization of local communities, the stock solution was inoculated with four bacterial species (*Bacillus cereus*, *B. subtilis*, *Proteus vulgaris*, *Serratia marcescens*) from stock cultures Four days before initialization, microflagellates and associated unidentified bacteria were introduced.

It is important to note that these organisms interact in complicated ways. They do not all compete for a single resource in a single way. Instead they may potentially utilize resources in species-specific ways, such that applying resource competition theory can lead to ambiguous results or interpretations (e.g., Fox 2002). It is apparent that with species supplementing their bacteria diets with other ciliates, decomposing material, direct resource utilization, and photosynthesis, and there exists much potential for coexistence and niche partitioning. This could result in a decoupling of the competition-colonization tradeoff, as competition may depend more on a species niche requirements rather than competition for a limiting resource. Regardless, it has been shown that negative interactions do limit the coexistence of these species to about five species (e.g., Cadotte 2006b).

Experiment 1: colonization ability. We constructed a five-patch system, where local patches were 125 ml nalgene bottles filled will 100 ml of the above-described nutrient solution. These bottles had two 3/16" holes drilled into opposing sides and were tapped. Threaded 3/16" barbed nylon tube fittings (Small Parts Inc., Miami lakes, FL) were then twisted in to the holes and secured with pure silicone caulk. Dispersal corridors were 12.5 cm of clear Nalgene 3/16" PVC tubing. This entire landscape apparatus was completely autoclavable.

In this five-patch system, the patches were link serially, so that community A was linked to B, B to C, C to D, D to E, and E back to A. Between 25-60 individuals of a single species was introduced in to community A. All five communities were sampled weekly for species presence by removing 5 ml of solution, which was replaced with 5 ml of sterile solution. We consider an observed occurrence of individuals to mean the patch was colonized. Even if a single individual was observed in the 5 ml sample, the population would consist of approximately 20 individuals, yet none of our observations consisted of a single individual in the 5 ml aliquot. We typically observed tens to hundreds of individuals.

During sampling, tube clamps closed dispersal corridors so that the displaced solution did not cause the movement of solution with individuals among communities. This was repeated three times for each of the 13 species. This experiment ran for a total of eights weeks, enough time for all communities to be colonized.

Experiment 2: competitive ability. In isolated glass jars with 50 ml of nutrient solution each species was introduced with one of the other 12 species. This was done for all 78 two-species combinations, and was replicated three times.

Again species presence/absence was sampled weekly by removing 5 ml and replacing it with a 5 ml sterile aliquot. This experiment was again run for eight weeks, but for purposes of this study, competitiveness was assessed with the results from the last sampling period.

Data analysis. In order to assess relative performance of these species we ranked their abilities. For colonization, we ranked the species by the mean number of weeks to occupy all five patches. Competitive ability was also rank-based, but was based on two measures. First we ranked species by the mean number of competition trials in which the species was still present at week eight. We also ranked species by the mean number of extinctions caused by that species by week eight. In both cases, smaller mean values were given smaller ranks. We then calculated the mean rank. Of course competition could have been measured a number of different ways –most notably using abundance measures relative to control abundances. Abundance measures would have provided finer-scale measurements as two species could both persist while still having detectable competitive effects. However, we were constrained by the amount of time needed to sample each trial, and therefore used persistence and extinctions-caused as surrogates for competitive ability.

Lower values for both ranks correspond to poorer colonization or competitive abilities. We then simply plotted and used a rank-based correlation to examine if species corresponded to the relationship hypothesize in Fig. 5.1.

Results

Experiment 1: colonization ability. By the end of this experiment (week 8) all species had colonized all empty patches. There was substantial among-species variation in colonization rate of patches (Fig. 5.2). The best colonizers were able to colonize all patches within 1 week, while the poorest colonizers took 5 weeks or more (Fig. 5.2). The mean time to colonize all patches and their relative ranks are given in Table 5.1.

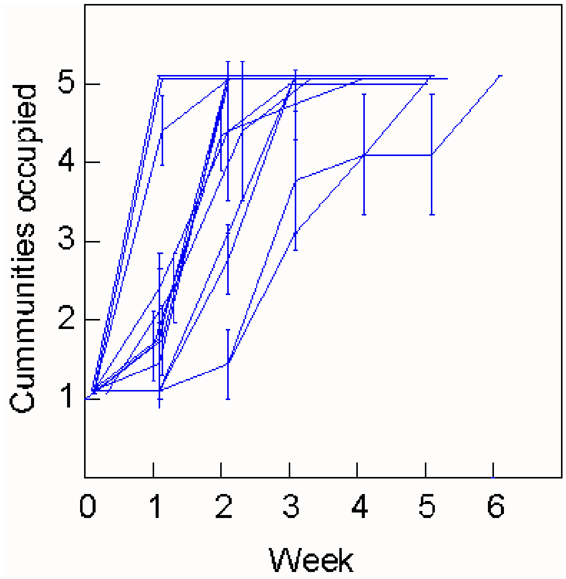

Figure 5.2: Colonization rates for individual species. Each line represents the mean colonization rate for an individual species. There is a continuum between those that colonized all patches within a week to those that took more than five weeks.

Experiment 2: competitive ability

By week 8, 10 species went extinct in at least one trial, and 11 species caused at least one extinction. There was a positive correlation between the number of extinctions caused, and the number of trials a species survived in ($r = 0.317$, $P = 0.049$). However, there was considerable scatter (Fig. 5.3), which is why we decided to combine these two variables in to a singular competition rank (Table 5.1).

Competition-colonization tradeoff

The two ranks, colonization and competition, were highly negatively correlated with one another ($r = -0.735$, Fig. 5.4). This figure conforms very well to the expectation highlighted in Fig. 5.1.

Discussion

From these results we can conclude that the poorest competitors were the best at colonizing new populations, and vice versa. Most of the previous competition-colonization tradeoff research has focused on plant communities in field studies, and some of this research has failed to detect competition-colonization tradeoffs (e.g., Levine and Rees 2002, Jakobsson and Eriksson 2003). Environmental heterogeneity, as with most evolutionarily-derived mechanisms, likely reduces the strength of this tradeoff. Although detection of the competition-colonization tradeoff signal is reduced, it does not mean that processes such as this tradeoff are not ecologically important, especially over long periods of time or over large spatial scales (Amarasekare 2003, Kneitel and Chase 2004). We feel that these results are significant for three reasons. First, as mentioned, most work on this tradeoff has been done with plants. Further, many studies focus on seed traits (e.g., Rees 1995) to detect dispersal ability, which does not actually measure colonization because, as pointed out above, colonization includes the ability to rapidly form larger populations. The current study is the first we know of that finds a competition-colonization tradeoff in an animal assemblage and measures colonization of empty patches rather than individual dispersal ability.

Second, these species reveal potential evolutionary constraints. Constraints are the basis of any tradeoff, as no single species should be superior local competitors and superior colonizers. The species used in this experiment have various origins. Some were ordered from Carolina Biological Supply Company (Burlington, NC, USA), some were obtained from other labs, and others were obtained from ponds around Knoxville, TN. This, accompanied by the fact that these species have been cultured in isolation for at least 1000 generations, means that any observed tradeoff is not the product of recent evolutionary interactions among these species. Rather, this tradeoff seems to be the product of robust traits, not subject to short-term releases from competitive selection pressures. However we can only speculate, albeit with circumstantial evidence, on the currency of this tradeoff. It seems that energetics play a major role in this tradeoff. Superior colonizers appear to move faster and for longer periods of time while superior competitors move intermittently and for shorter durations of time (MWC personal observations). The colonizers appear to quickly find and colonize open patches while the

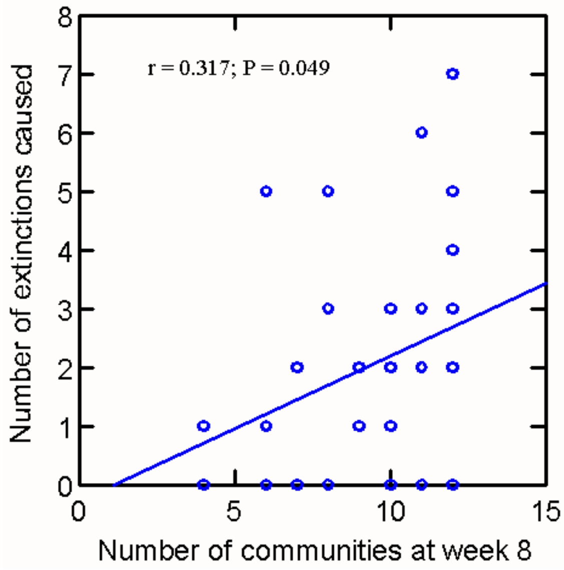

Figure 5.3: The relationship between the number of extinctions caused by a species and the number of trials in which it persisted.

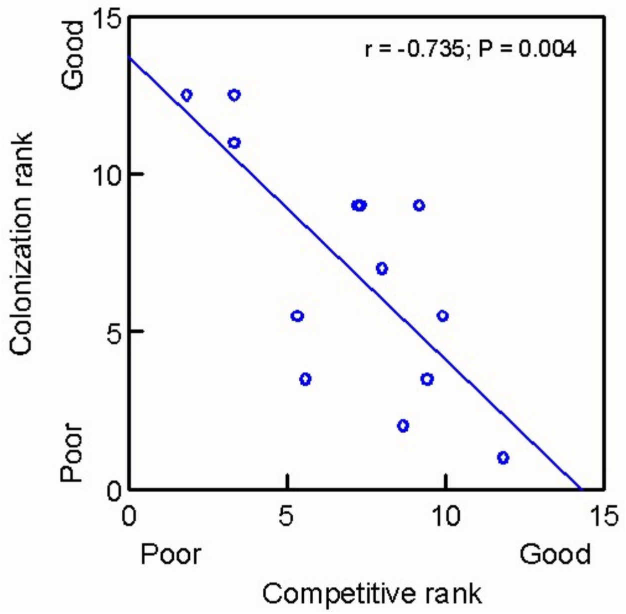

Figure 5.4: The relationship between competitive and dispersal abilities, which support a competition-colonization tradeoff.

competitors use less available resources or resources more thoroughly than the colonizers.

Finally, as mentioned in the introduction, a number of laboratories use these organisms to test ecological hypotheses and theories, including the role of space and species movement and metacommunity dynamics (e.g., Holyoak and Lawler 1996, Warren 1996, Holt et al. 2004, Holyoak 2000, Cadotte and Fukami 2005, Cadotte 2006b). Yet, even in these well-studied species, the presence of competition-colonization tradeoffs has not been observed nor tested for. In a recent paper by Cadotte (2006b), dispersal rate and patch connectivity was manipulated, and competition-colonization tradeoffs were hypothesized as an important mechanism affecting the results. The current results do reveal that the dominant species in Cadotte's (2006b) no-dispersal control are the superior competitors/inferior colonizers. However, some dispersal treatments enhanced richness, and the species benefiting most from these treatments are those that are intermediate in the trade-off. The superior colonizers still eventually lost out, likely because there were no disturbances in Cadotte's (2006b) experimental design. We would hypothesize that the inferior competitors/superior colonizers would benefit from non-equilibrial conditions imposed by local disturbances, much like weedy species in an agricultural landscape.

Conclusion. While the idea that competition-colonization tradeoffs are an important tool in explaining species coexistence at larger spatial scales (i.e., Amarasekare 2003, Kneitel and Chase 2004), we feel that studies thus far actually measure dispersal and not colonization. We here show that, when measuring colonization, the competition-colonization appears to be potentially robust. Further, most studies of this tradeoff use plants, we show its existence in an animal system.

Chapter 6

Competition-colonization tradeoffs and the intermediate disturbance hypothesis

---

Abstract The competition-colonization tradeoff has long been a mechanism explaining patterns of species coexistence and diversity in non-equilibrium systems. It is the basis of the intermediate disturbance hypothesis (IDH) for local communities – specifically that diversity should be maximized at intermediate disturbance frequencies, yet only a fraction of empirical studies support IDH predictions. Similarly, this tradeoff is the basis of coexistence at larger spatial scales. I show, with a simple simulation and a microbial experimental system, that the relative distribution of species along a tradeoff gradient can alter how intra-patch diversity varies with disturbance frequency. When species are regularly spaced along a competition-colonization tradeoff gradient, increasing disturbance frequency produces the IDH pattern. However, when species are skewed towards many colonists, diversity increases with increasing disturbance, and if species are skewed towards late-successional habits, diversity declines with disturbance. Yet, diversity at scales larger than the patch appears insensitive to the tradeoff distribution. Intermediate disturbance frequencies produce the greatest diversity in patch successional stage, thus benefiting the maximum number of species.

Introduction

Disturbance has a long and recurring role as a potential explanation for the coexistence of species and the maintenance of patterns of species diversity (Levin and Paine 1974, Slatkin 1974, Petraitis et al. 1989, Shea et al. 2004) often because disturbance resets local successional trajectories preventing early-successional species from going extinct at regional scales (Denslow 1980, Caswell and Cohen 1981, Pickett and White 1985, Ellner and Fussman 2003). A fundamental aspect of disturbance-mediated coexistence in local patches is the hypothesis that species diversity is maximal at intermediate disturbance frequencies (Connell 1978, Sousa 1979, 1984, Petraitis et al. 1989). Yet, only a fraction of empirical tests have supported the intermediate disturbance hypothesis (IDH), with results from some systems showing distinctly differing patterns, such as monotonic increases and declines with increasing disturbance intensity or frequency (Mackey and Currie 2001). These discouraging results have lead researchers to look for concurrent ecological processes that maybe obfuscating the IDH, such as habitat productivity (Kondoh 2001, Scholes et al. 2005, Cardinale et al. 2006), complications on species interactions (Roxburgh et al. 2004, Shea et al. 2004), and characteristics of the disturbances (McCabe and Gotelli 2000, Hastings 2003).

Yet the fundamental, and seldom criticized, assumption of the classic formulation of the IDH is that species exhibit competition-colonization tradeoffs, such that the first colonists are inferior competitors against later colonizing species (Connell 1978, Petraitis et al. 1989, Dial and Roughgarden 1998, Amarasekare 2003) which is related to the more general notion that this tradeoff is necessary for spatial coexistence (Slatkin 1974, Hastings 1980, Pacala and Rees 1998, c.f. Casagrandi and Gatto 2002). The verbal modal of the IDH assumes a uniform gradient from the best colonists to the best competitors, such that very few species immediately invade newly opened patches, while very few species ultimately limit all others over long time scales (Connell 1978). However, the distribution of species along the competition-colonization tradeoff continuum ought to depend upon evolutionary pressure from historical disturbance frequency. In frequently-disturbed systems there should be a skew towards a greater number of colonists versus competitors (Pianka 1970, Denslow 1980, Loehle 2000). Similarly, in low disturbance frequency systems, the tradeoff continuum should be skewed towards species that exist in later successional stages (Pianka 1970, Denslow 1980, Loehle 2000). Dynamics from invading *Spartina alterniflora* populations reveal that this tradeoff continuum varies within populations, such that selection on the invading edge has resulted in individuals there becoming faster growing and reproducing while individuals surrounded by high densities of conspecifics are slower-growing and longer lived (Davis 2005). Further, in a broad study of tree species, Loehle (2000), showed how life history evolution can result from differing disturbance regimes. He showed that decreased disturbance frequency can result in larger, longer-lived, clonal, and short-dispersing species that equate to K-selected species (Loehle 2000).

Given that species vary how resources are partitioned to reproduction, growth, life span and dispersal under differing regimes of density-independent mortality, historical disturbance trends may influence the current distribution of species along a competition-colonization gradient. Unclear is how sensitive diversity-disturbance patterns are to the distribution of species along competition-colonization tradeoff gradient.

Yet the local community scale is but one scale at which species coexist and pertinent ecological processes operate (Knietel and Chase 2004, Holyoak et al. 2005), and one can parse diversity patterns and relevant processes in to local, beta (or average among patch differences), and regional (which contains the entire species pool) (Lande 1996, Loreau 2000). Other ecological processes have been shown to have differential effects at different spatial scales (Chase and Leibold 2002, Fukami 2004) as has disturbance (Ostman et al. 2006). Denslow (1980) viewed disturbances as a coexistence mechanism at larger spatial scales, yet too high or too low a disturbance frequency should ultimately limit coexistence even at larger scales. Again the competition-colonization tradeoff is the primary mechanism promoting coexistence at larger spatial scales (Slatkin 1974, Hastings 1980, Caswell and Cohen 1991, Pacala and Rees 1998, Amarasekare 2003, Kneitel and Chase 2004), and as disturbance frequency increases the relative occupancy of colonizing or early successional species increases. Therefore, given the role of competition-colonization tradeoffs for spatial coexistence, is the IDH a functioning hypothesis for patterns of diversity at larger spatial extents?

I here use a simple simulation to examine if relative distribution of species along a competition-colonization tradeoff affects diversity-disturbance relations. I then use an aquatic microcosm species assemblage known to exhibit competition-colonization tradeoffs (Cadotte et al. in review), to test whether a non-uniform competition-colonization gradient (in this case a competition-skewed one) confirms simulation predictions that richness is not maximized at intermediate disturbances (but rather declines with increasing disturbance frequency). Aquatic microorganisms have rapid life cycles and in natural systems, experience periodic disturbances (drying and seasonality) at an extremely low frequency relative to generation time, meaning that aquatic microorganisms ought to show a competitor-skewed tradeoff gradient, relative to one another.

Methods

Simulation. I use the general logic of a seed rain patch occupancy model (e.g., Gotelli 1991) in a numerical simulation of 20 potentially coexisting species on ten patches in a metacommunity with local disturbances. This simulation manipulates the colonization (c_i) and competitive ability (i) of each species and varies the disturbance frequency (D). Whereas classic metapopulation models assume identical patches, here I include successional trajectories. Succession in this system mimics facilitation (Connell and Slatyer 1977, Caswell and Cohen 1991), in that early-successional species are the first to enter a patch after a disturbance and late-successional species enter local patches after early-successional species. I assume that the competitive hierarchy is itself unaffected by disturbance either through evolution or resource dynamics (Chesson and Huntly 1997) although there is some evidence that partial biomass removal may result in alterations to competitive hierarchies (Suding and Goldberg 2001). The simulation assumes “seed rain” dispersal (Gotelli 1991), competitive exclusion in one time step and deterministic colonization, and does not assume that only a single species can exist on any single patch. I measure local richness (S) at time t:

$$S_t = \sum_{t}^{c=1} n_{ci} - \sum_{i-1}^{1} n_{c \le t,i} \ . \qquad \text{Eq(1)}$$

Here each species (n) is identified by its position in the competitive hierarchy, i, and, c, which is a measure of the time step it colonizes an empty patch in. Species n replaces all species $c \le i$ (see Table 6.1)..

I hypothesized that the relative distribution of species along a competition-colonization tradeoff can fundamentally alter the richness-disturbance pattern. I explicitly examine three competition-colonization tradeoff distributions among the 20 species. These scenarios are termed: 1) gradient, 2) colonists, and 3) competitors. In the first case, gradient, there is a regular gradient from colonists/poor competitors to good competitors/poor colonizers (see Table 6.1 for trait distributions). In this scenario species have the ability to colonize a patch in successive times steps, such that species 1 colonizes a new patch in time step 1, species 2 in time step 2, and so on, with species 20 colonizing in time step 20 (Table 6.1). Further, the first six colonists do not competitively replace other species, and the poorest colonizers displace most other species (Table 6.1).

The second scenario, colonists, is skewed toward rapid colonization of empty patches, and less competitive exclusion during early succession. Here species 1 colonizes in the first time step, species 2-8 colonize in time step 2, and successive species colonize in successive time steps, so that species 20 colonizes in time step 14 (Table 6.1).

In the third scenario, competitors, succession begins earlier and competitive species dominate, quickly replacing colonizers. Further, in this scenario, a greater proportion of species persist at long time intervals. Here species 4 competitively replaces species 1, and so on, until species 15 which replaces 1-12. Species 13-20 coexist (Table 6.1), representing evolved niche partitioning in a late-successional community.

Table 6.1: The two traits, colonization (c) and competitive ability (i) from Eq(1), defining the 20 species used in the disturbance simulations. Species' traits were distributed according to three scenarios: 1) species exhibited a uniform gradient where the best colonizers were the poorest competitors and vice versa; 2) species were colonist-skewed such that the first eight species colonized empty patches by the second time step and subsequent competitors colonized faster; and 3) species were skewed towards competitive coexistence, where the first colonists are rapidly replaced by competitors, but more dominant competitors coexist in the long term.

Species	Gradient (c, i)	Colonist (c, i)	Competitive (c, i)
1	1,0	1,0	1,0
2	2,0	2,0	2,0
3	3,0	2,0	3,0
4	4,0	2,0	4,1
5	5,0	2,0	5,2
6	6,0	2,0	6,3
7	7,1	2,0	7,4
8	8,2	2,0	8,5
9	9,3	3,1	9,6
10	10,4	4,2	10,7
11	11,5	5,3	11,8
12	12,6	6,4	12,9
13	13,7	7,5	13,10
14	14,8	8,6	14,11
15	15,9	9,8	15,12
16	16,10	10,10	16,12
17	17,12	11,12	17,12
18	18,14	12,14	18,12
19	19,16	13,16	19,12
20	20,18	14,18	20,12

In order to examine how species richness is affected by disturbance, I sampled species richness at the three spatial scales at time step 21, across 16 disturbance frequencies along a gradient in a ten-patch landscape. Here disturbance is simply the local extinction of all species on a local patch, which is then open to recolonization in the next time step. Each disturbance regime differed in the frequency of local patch disturbance, over 20 time steps. Frequencies ranged from 0.0 to 1.5 disturbances in the ten-patch system per time step, increasing in 0.1 increments. For example, a disturbance frequency of 0.1 meant that there was a single patch disturbance at time 10 and 20. I then measured mean local richness as well as beta and regional richness.

Microcosm experiment design. Local patches were 125 ml Nalgene narrow-mouth square bottles with two or four 3/16" holes drilled into opposing sides and tapped. Threaded 3/16" barbed nylon tube fittings (Small Parts Inc., Miami Lakes, FL) were then twisted into the holes and secured with silicone caulk. Dispersal corridors were clear Nalgene 3/16" tubing. Tube clamps were placed on every tube exiting the local communities, and when closed most movement of fluid and organisms was blocked. Local patches were arranged into "landscapes" by connecting local patches via dispersal corridors. Patches were arranged in parallel, which represents a distance dispersal gradient among patches (see Cadotte 2006b).

Biological communities. Each local patch consisted of 100 ml of sterilized nutrient medium with 0.55 g/l of protozoa pellets (Carolina Biological Supply Company, Burlington, NC), 0.05 g/l powdered vitamins, and two sterilized wheat seeds as a source of slowly released nutrients in spring water (Crystal Springs, Flowery Branch, GA). Six days prior to the initialization of local communities, the stock solution was inoculated with bacteria (*Bacillus cereus*, *B. subtilis*, *Proteus vulgaris*, *Serratia marcescens*) from stock cultures and with unidentified bacteria from filtered protozoan species stock cultures. Four days before initialization, microflagellates and further associated unidentified bacteria were introduced, which were assumed to have a ubiquitous distribution throughout the experiment. The above procedure was repeated each day for 4 days with the first replicate of each of the 11 treatments being initiated on the first day, and so on.

I used a total of 13 protozoan and rotifer species: *Blepharisma americanum*, *Chilomonas* sp., *Coleps* sp., *Colpidium striatum*, *Euplotes* sp., *Lepadella* sp., *Paramecium aurelia*, *P. bursaria*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, *Uronema* sp., and an undetermined rotifer species. Three species (*Philodina, Lepadella* and *Euplotes*) were cultured from ponds in and around Knoxville, while the rest were obtained from other laboratories and periodically restocked with individuals ordered from Carolina Biological Supply. Initial number of individuals ranged from 25 to 100 per 100 ml to reduce any strong interactions during the initial phase of the experiment.

The species are protozoan flagellates or ciliates, or metazoan rotifers, all of which naturally inhabit still and stagnant ponds. They range in size from 25-1000 μm in length. Species were quite variable in their dietary habits. Further, from a previous study these species are known to display competition-colonization tradeoffs in this experimental system (Cadotte et al. in review).

Disturbance treatments. A disturbance was simply resetting the successional trajectory of a patch to an empty state by closing tube clamps and replacing a randomly selected local patch with a new patch consisting of bacterialized medium only. Therefore, local post-disturbance occupancy is entirely dependent upon a species' colonization ability. Disturbance treatments manipulated the number and timing of disturbances over the span of eight weeks (Table 6.2). The current results only consider the outcome at the end of the experiment and use the number of disturbances per week as the independent variable, referred to as "disturbance frequency".

Sampling. Twice a week, all clamps were closed and 5 ml of medium was removed from each local community and replaced with fresh nutrient medium. Once per week the extracted 5 ml was used to record presence/absence of species. (In a previous study, Cadotte and Fukami (2005) found that diversity indices incorporating local abundance did not change conclusions drawn from richness observations.) Up to the entire 5 ml aliquot was scanned for the presence of species.

Statistical analyses. Species richness at local, beta and regional scales were individually regressed against the log-transformed number of disturbances per week, in both a linear and non-linear (quadratic) model. If both models revealed a significant relationship, they were compared using Akaike's information criteria (AIC). Confirmation of a unimodal relationship was done with the MOS test which determines whether maximal richness was at intermediate disturbance frequencies by creating

Table 6.2: Disturbance treatments used in the microcosm experiment.

Treatment	No. of patches removed	Frequency (per week)	Disturbances per week	Total No. of disturbances
Control	0	0	0	0
One disturbance on week 4	1	0.25	0.25	1
One disturbance every 3rd week	1	0.33	0.33	2
One disturbance every 2nd week	1	0.5	0.5	3
One disturbance per week	1	1	1	7
Two disturbances once every 2nd week	2	0.5	1	7
Two disturbances per week	2	1	2	14
One disturbance twice per week	1	2	2	15
Three disturbances per week	3	1	3	21
Two disturbances twice per week	2	2	4	28
Three disturbances twice per week	3	2	6	42

constrained regression models in which the null hypothesis is that the maximal dependent values are found at either the minimum or maximum values in the independent variable (Mitchell-Olds and Shaw 1987, Fukami and Morin 2003).

In order to determine how individual species responding to increasing disturbance frequency, individual species occupancies were examined using loglinear models. Species with increasing occupancies are the colonists, benefiting from increasing the number of open patches. Those decreasing were the competitors, or those that exclude colonists and need longer time spans to colonize but remain part of local communities for long time periods once established.

Results

Simulation. Using a simple simulation of deterministic colonization times and competitive interactions, across differing frequency of local disturbances, I show that how species are distributed along competition-colonization tradeoff gradient can affect how local diversity changes with increasing disturbance frequency (Fig. 6.1). When 20 simulated species are uniformly distributed along a competition-colonization tradeoff gradient, the mean local diversity confirms the IDH (Fig. 6.1a). However, if species are colonist-skewed by having greater numbers of rapid colonizers, then diversity is positively related to disturbance frequency (Fig. 6.1a). If species are competition-skewed, that is the first colonists are rapidly replaced and a larger number of species coexist over the long term –indicative greater niche specialization, then a negative relationship is observed (Fig. 6.1a). These results reveal that the evolutionary response of species to differing disturbance regimes ought to fundamentally change how local diversity changes across a disturbance gradient. Richness at the beta and regional scales both support the IDH, with maximal values at intermediate disturbance frequencies.

Microcosm experiment. The relationship between local community richness and disturbance frequency in the microcosm experiment is best described as a negative linear relationship ($F_{1,42} = 30.182$, $P < 0.001$, $R^2 = 0.42$, AIC = -7.25) compared to a unimodal or quadratic relationship ($F_{2,41} = 16.680$, $P < 0.001$, $R^2 = 0.45$, AIC = -6.41) (Fig. 6.2a). I also employed the MOS test and maximal richness was found at a disturbance frequency of 0.0097 patches disturbed each week, which is indistinguishable from a disturbance frequency of 0 ($P > 0.05$). Thus this experimental system appears to both refute the classic IDH, while confirming the expectations from a competitor-skewed system.

However, at both the beta ($F_{1,40} = 3.330$, $P = 0.076$, $R^2 = 0.08$, AIC = -4.95 for the linear model, and $F_{2,39} = 10.345$, $P < 0.001$, $R^2 = 0.35$, AIC = -17.48 for the quadratic) and regional scales($F_{1,41} = 27.634$, $P < 0.001$, $R^2 = 0.40$, AIC = 21.88 for the linear model, and $F_{2,40} = 30.936$, $P < 0.001$, $R^2 = 0.61$, AIC = 5.83 for the quadratic), the unimodal model better described the relationship between diversity and disturbance frequency (Fig. 6.2b & c). The MOS test indicated that maximal beta richness was found at 1.28 disturbances per week, and is best described by a unmodal relationship ($P < 0.01$). Similarly, regional richness was maximized at 0.81 disturbances per week and best described by a unimodal relationship ($P < 0.01$) These results indicate that the IDH is a

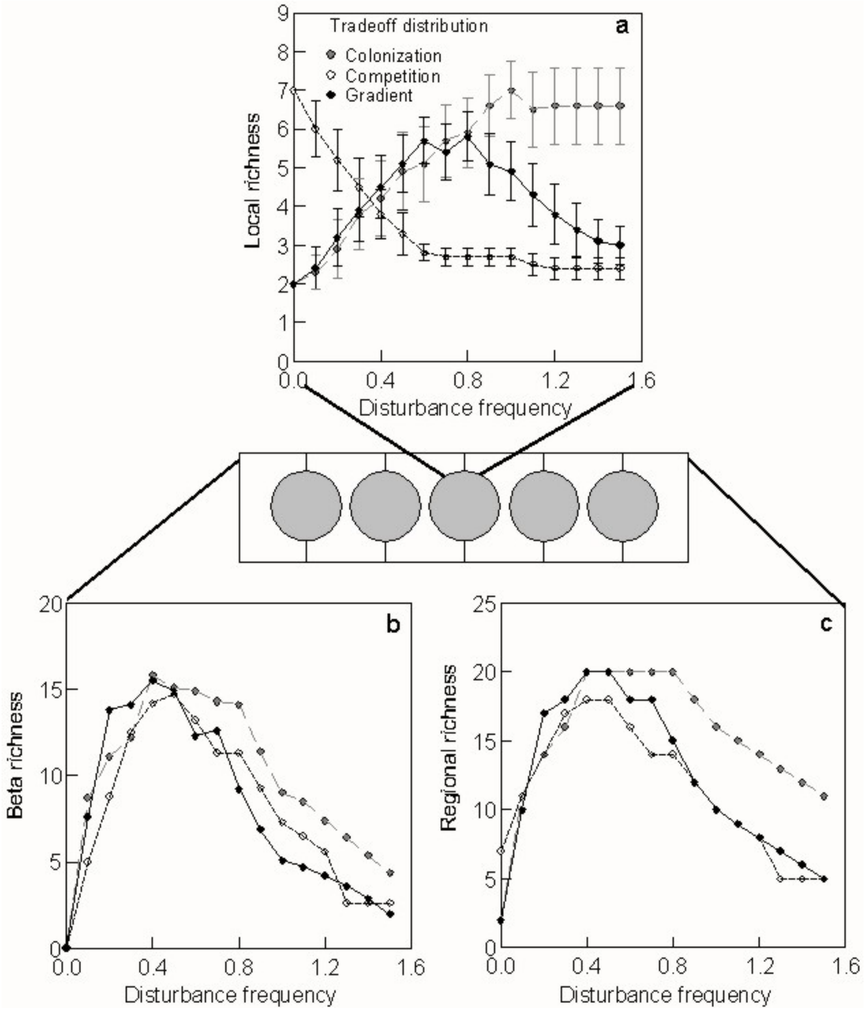

Figure 6.1: At the (a) local, intra-patch, scale, disturbance frequency (here defined as number of disturbances per patch per time step) can produce unimodal or linear (increasing and decreasing) richness patterns dependent upon the distribution of species along a competition-colonization tradeoff gradient. I used three such distributions: Colonization, in which species were skewed towards rapid colonization; Competition, in which species were skewed towards competitive interactions; and Gradient, where species were evenly spaced along the competition-colonization tradeoff. However, patterns of diversity confirm the IDH at (b) beta and (c) regional scales regardless of species tradeoffs. The patchy system shown was the setup used in the microcosm experiment.

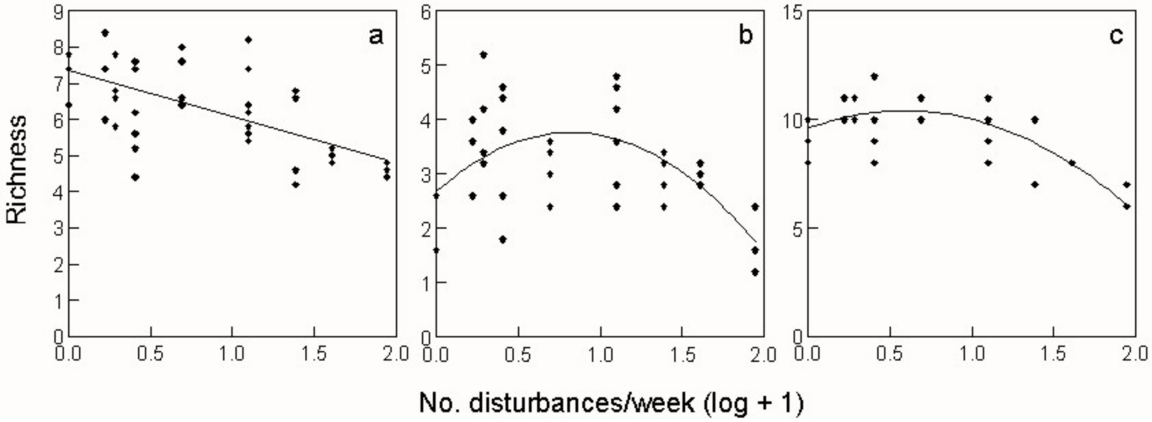

Figure 6.2: Results of the microcosm experiment showing that (a) local richness linearly declines with increasing disturbance frequency, while richness at (b) beta and (c) regional scales conforms to the IDH.

robust descriptor of diversity patterns at these scales, despite the lack of IDH support at the local scale.

From the control for this experiment and in previous experiments (e.g., Cadotte 2006, Cadotte et al. 2006), I've shown that an average of 5-7 of these species coexist over long timescales, and these same seven species showed significant declines in number of patches occupied with increasing disturbance frequency (Fig. 6.3). These seven are members of competitively-structured communities, and do not colonize empty patches rapidly. Further, only four species showed occupancy increases with increasing disturbance frequency (Fig. 6.3b, d, g, k). Here two of these relationships are non-significant but the pattern exhibited by *Copidium striatum* (Fig. 6.3d) shows significantly greater occupancy at all disturbance treatments compared to the no-disturbance control, and *Tetrahymena pyriformis* (Fig. 6.3k) is only found in extremely high disturbance treatments.

Discussion

Competition-colonization tradeoffs and local diversity-disturbance relationships. In a previous publication using these exact species, Cadotte et al. (in review), show that these species show competition-colonization tradeoffs (Fig. 6.4). The four species that increase occupancy with increasing disturbance frquency (Fig. 6.3) are the best colonists and poor competitors while the seven species that decline (Fig. 6.3) are superior competitors and generally inferior colonizers. As expected from the simulation and experiments (Figs. 6.1 & 6.2), these are indeed skewed toward the competitive end of the competition-colonization tradeoff.

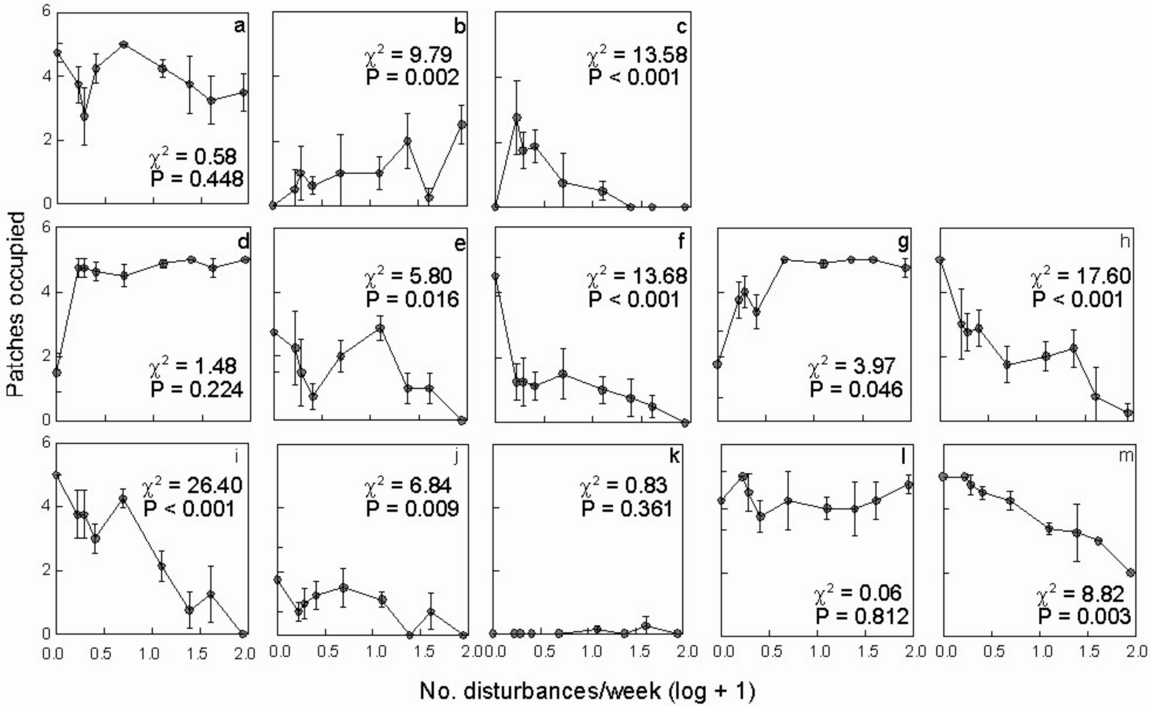

Figure 6.3: Patch occupancy patterns for each of 13 species across increasing disturbance frequencies. a) *Blepharisma americanum*, b) *Chilomonas* sp., c) *Coleps* sp., d) *Colpidium striatum*, e) *Euplotes* sp., f) *Lepadella* sp., g) *Paramecium aurelia*, h) *P. bursaria*, i) *Philodina* sp., j) *Spirostomum* sp., k) *Tetrahymena pyriformis*, l) *Uronema* sp., and m) unidentified rotifer. Results of loglinear models are indicated in each panel.

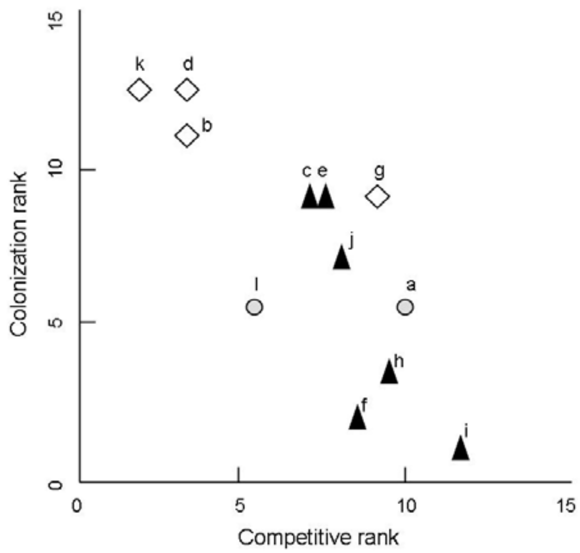

Figure 6.4: The species used in this experiment reveal a general tradeoff between relative competitive and colonization ability (from Cadotte et al. in review). Open diamonds are species that increased in occupancy with increasing disturbance frequency, black triangles are those that declined, and shaded circles are species that showed no respond to disturbance. Letters refer to species in Figure 6.3.

The notion that species vary in their colonization and competitive abilities or the successional stages at which they thrive is essential for spatial coexistence in spatial systems facing localized disturbance (Slatkin 1974, Hastings 1980, Pacala and Rees 1998, Amarasekare 2003, Kneitel and Chase 2004). Coexistence in these systems is regional rather than local, so that even though species exclusion is observed locally, regionally, there are patches at different successional stages (Denslow 1980, Caswell and Cohen 1991, Ellner and Fussman 2003). Therefore, too high a disturbance frequency ought to increase the regional occupancy of colonizing and early successional species, while too low a disturbance frequency results in high regional occupancy of late successional species.

Several models examining patch occupancy and localized disturbances have found that the occupancy of late-successional species (or dominant competitors) declines with increasing disturbance frequency, while the reverse is true for colonizing species (Hastings 1980, Caswell and Cohen 1991, Amarasekare and Possingham 2001). Further, in an examination of native versus exotic plant responses to disturbances, Allcock and Hik (2003) showed that exotics, which tend to be weedy, increased with disturbance frequency. They also showed that the natives tend to decline with disturbances (Allcock and Hik 2003). Their explanation is an evolutionary one. Successful exotics tend to be adapted to ruderal, ephemeral habitats and thus exhibit traits often associated with “r-selected” species, while the majority of native plants tend to be adapted to habitats with low disturbance regimes (at least in a pre-human settlement regime) and thus exhibit relatively “K-selected” traits (Allcock and Hik 2003).

Hastings (1980) showed that when competition-colonization tradeoffs are present, differing disturbance rates result in different species composition –which is a logical result of the models and of the current study. The reason is that species traits responsible to regional coexistence and disturbances are both temporally scaled. Hence if the disturbance frequency is less than the rate at which local habitats are colonized ($c_i > D$), species *i* will not be able to colonize patches fast enough to persist regionally. While, when $c_i << D$, superior competitors are likely to enter, replacing colonist species.

Studies assuming strict competition-colonization tradeoffs usually show that maximal diversity results from intermediate disturbance rates (e.g., Caswell and Cohen 1991, Barradas et al. 1996). However, as mentioned previously, the majority of empirical studies actually fail to support the IDH, and instead often show either monotonically increasing or declining diversity-disturbance relationships (Mackey and Currie 2001). The present study is the first to show that local, non-unimodal diversity-disturbance relationships are possible, while still assuming competition-colonization tradeoffs.

It can be concluded then, that local diversity-disturbance patterns are produced by species having competition-colonization tradeoffs, but that the relative position of species along this tradeoff gradient is itself dependent upon evolution under historical disturbance regimes (Pianka 1970, Loehle 2000). When testing the IDH or any diversity-disturbance relationship, researchers need to also use methods to estimate relative competitive and colonization abilities of species.

IDH at scales above the local patch. In what is likely the first modeling examination of the IDH at larger scales, Caswell and Cohen (1991), again, using a model that incorporates competition-colonization tradeoffs, also show that beta diversity appears unimodally related dispersal rate under a number of different models, though they failed to discuss the biological reasons why. In the current paper, both the simulation and experimental results support the IDH at scales above the local patch. These results support the IDH regardless of the distribution of species along a competition-colonization gradient.

The reason for the robustness of the IDH at the beta and regional scales is that local disturbances create a successional mosaic at a larger scale, where certain species are favored at certain successional stages (Denslow 1980, Ellner and Fussman 2003). Species adapted to differing temporal niches reach their greatest abundances at different times since the disturbance, meaning that too low a disturbance frequency favors late successional species, and too high favors early successional species across all patches. Buckling et al. (2000) showed that niche differences among species were key to supporting the IDH. At intermediate disturbance frequencies, the greatest diversity of successional stages is obtained, thereby resulting in the greatest dissimilarity among patches (i.e., greatest beta values).

Limitations and implications. There are two general limitations of the current. First, in order for the above explanation of different local diversity-disturbance relationships to be applicable to natural systems, the competition-colonization tradeoff must be a pervasive phenomenon. Recently however, significant doubt has been raised questioning the pervasiveness of these tradeoffs (e.g., Jakobsson and Eriksson 2003). Yet most work done on competition-colonization tradeoffs has focused on plants, where seed attributes supposedly reveal the evolutionary outcome of this tradeoff in the form of a tradeoff between seed size and seed number. Cadotte et al. (in review) argued that many studies purporting to test for competition-colonization tradeoffs actually measure dispersal-linked traits and not colonization *per se*. No doubt dispersal is an important component of colonization, but colonization also includes a species ability to overcome Allee effects and establish a population (see Cadotte et al. in review). Therefore, there is not adequate information to judge how widespread this tradeoff is.

Secondly, the current results apply to a specific type of disturbance, namely the complete removal of all local biomass, resulting in complete local extinctions. There are numerous qualities of disturbances, such as their cause, intensity, frequency, regularity, etc. (Pickett and White 1985). There numerous other studies that examine the effects of disturbances of various intensities below complete biomass removal (e.g., Buckling et al. 2000, McCabe and Gotelli 2000) and for these studies, a tradeoff between disturbance resistance and competitive ability may be important (Petraitis et al. 1989, Chesson and Huntly 1997). Unresolved then, is the role that within-patch dynamics play in disturbance-diversity relationships –such as with disturbance resistance.

Despite these limitations, these results reveal several potentially important consequences for the IDH. First, rather than search for other processes that may potentially explain failures of the IDH, simply understanding how species conform to the fundamental assumption of the IDH (competition-colonization tradeoff) could alter expectations of diversity's response to disturbance. Secondly, evolutionary responses to indigenous disturbance frequencies ought to profoundly effect how species are distributed along a competition-colonization tradeoff gradient, thus making the IDH contingent upon evolution. Thirdly, regardless of these evolutionary responses and the local diversity response to disturbance frequency, the IDH should be robust at larger spatial scales.

Chapter 7

Act locally, think regionally: incorporating ecological scale into conservation thinking.

Abstract Many ecologists and conservation biologists recommend that conservation efforts be directed at the community-level as the best way to conserve both biodiversity as well specific taxonomic groups. Therefore understanding community ecology is necessary for conservation biologists. Managing ecological communities is something that can only be done at small spatial scales, such as species removals, additions, restoration and prescribed burns. However, the mechanisms structuring communities are multifaceted and current advances in community ecology explicitly consider processes operating at different spatial scales. Of fundamental importance to this shift to larger scales is the notion of the metacommunity, in which species diversity and coexistence patterns require scales larger than single communities. These processes, which all rely on dispersal, include patch dynamics, species sorting, mass effects, source-sink dynamics and potentially neutral dynamics. I review five recent advances that incorporate spatial and metacommunity ecology, including extending metapopulation dynamics to communities, the role of dispersal on diversity, invasions and community saturation, invasive species dynamics across scales, and neutral dynamics and spatial coexistence. By incorporating ecological processes operating across different scales, conservation managers can better plan outcomes of specific actions. This spatial approach may help guide action on fragmentation and corridors, species invasions, conserving diversity and manipulating habitat heterogeneity. Even though effective community management occurs at relatively small scales, by understanding spatially-explicit processes, conservation plans may potentially be designed for greater impacts across numerous scales of organization.

Introduction

“we must study communities because understanding them is crucial to dealing with many key conservation and environmental issues” Simberloff (2004) Pg. 787.

Recently, Simberloff (2004), commenting on Lawton’s (1999) criticism of the search for general laws in ecology, made the argument that community ecology is quintessential if we are to overcome, or at least ameliorate current conservation problems (see opening quote). Lawton’s (1999) primary criticism was that community ecology was too “local” in its purview, and therefore overwhelmed by the vagaries of environmental and temporal stochasticity. Both Simberloff (2004) and Lawton (1999) contain pertinent criticisms of community ecology as well as important recommendations, however, current advances in community ecology explicitly considers processes operating at different spatial scales, and therefore the concern that community ecology is too “local” ignores many recent advances. Further, I would argue that the incorporation of ecological scale into community ecology makes this field of study even more critical to conservation and environmental issues.

Ecologists' understanding of the processes driving patterns in community ecology is undergoing a fundamental change. Historically, ecologists tried to understand how communities were assembled by local interactions among species, between species and the abiotic environment, and historical effects (e.g., MacArthur 1958, Hutchinson 1959, Tilman 1982, Drake 1991), perhaps with limited success as pointed out by Lawton (1999) and Simberloff (2004). Yet ecologists are increasingly coming to view communities as the product of numerous processes operating across multiple spatial scales (e.g., Allen and Starr 1982, Ricklefs 1987, Wilson 1992, Holt 1993, Zobel 1997, Peterson and Parker 1998, Whittaker et al. 2001, Leibold et al. 2004, Holyoak et al. 2005).

The realization that dispersal was a fundamental ecological process made explicit the need to incorporate spatial scale into ecological understanding. Dispersal has had continued success as a potential explanation for community and biogeography patterns – at least as it affects local community composition (e.g., Gleason 1917, MacArthur and Wilson 1967, Levins 1969, Levins and Culver 1971, Horn and MacArthur 1972, Brown and Kodric-Brown 1977, Hastings 1980, Terborgh and Faaborg 1980, Cornell 1985, 1993, Shmida and Wilson 1985, Cornell and Lawton 1992, Rees 1995, Zobel 1997, Chesson 2000). MacAurthur and Wilson (1967) perhaps changed ecologists' understanding of the role of dispersal more than any other publication. They explicitly examined the role of dispersal and colonization in regulating island diversity.

The core concept of this review is that different ecological processes potentially have differing effects at different levels of organization. The world is not a uniform homogeneous place. To quote Robert MacArthur:

> "A real environment has a hierarchical structure. That is to say, it is like a checkerboard of habitats, each square of which has, on close examination, its own checkerboard structure of component subhabitats. And even the tiny square of these component checkerboards are revealed as themselves checkerboards, and so on." (MacArthur 1972: 186)

Thus, our conservation efforts should likewise explicitly view the world as structured. If Simberloff's (1988, 2004) view that traditional community ecology has much to offer conservation, then modern, spatially-informed community ecology likely has even more to offer.

What ecologists mean when they use the term "scale" can vary greatly and this can lead to confusion (e.g., Allen 1998, Whittaker et al. 2001). What I do not mean by scale is measures of grain and extent. These types of measures, important for landscape ecologists, are useful as quantifying metrics, in statistical analyses and for examining scale-specific patterns. Related to this conception of scale was thinking about ecological processes across a hierarchy of scales (Allen and Starr 1982, O'Neill et al. 1986, Kolasa 1989). This paradigm devised metrics and theory that predicted how processes created pattern across a gradient of scales. One of the first predictions from this group was that processes higher in the hierarchy should be slower than lower ones (Allen and Starr 1982, O'Neill et al. 1986). Intuitively, processes like extinction must occur more rapidly in local patches than extinction across an entire range, yet as we will see in section 4, processes like species invasions may actually be more rapid at larger scales! The hierarchical view of ecological processes has important conservation implications in its own right. For example, predators and prey may perceive heterogeneity at different spatial grains, such that manipulating small-scale heterogeneity may indirectly benefit predators by enhancing prey populations but that heterogeneity has no direct impact on how predators "perceive" the environment (Kotliar and Wiens 1990, Kolasa and Waltho 1998, Cadotte and Fukami 2005).

What I am considering in this review is the notion of ecological processes that operate at different levels of organization and explanations of species coexistence that are scale-explicit. The idea that making observations at different scales could inform our understanding of mechanism that structure communities first come to prominence in the 1980's when ecologists examined local community saturation as a product of patterns of regional richness (Terborgh and Faaborg 1980, Cornell 1985, Ricklefs 1987) These ecologists explicitly defined process-dependent scales, and the local scale is that scale of organization in which species are likely to interact, while the regional scale is that which includes all the species that could potentially colonize the local community(ies) of interest (Table 7.1, see also Srivastava 1999).

More recently some ecologists, using the terminology of Whittaker (1972), support the notion that there are three hierarchal levels of organization that reveal the impact of ecological processes (Lande 1996, Loreau 2000, Veech et al. 2002). These three levels are referred to as alpha (α or local), gamma (γ or regional), and intermediary scale, beta (β) (see Table 1). β, as formulated by Whittaker (1960, 1972) is multiplicative measure of community similarity and envisioned as a measure of the impact of environmental changes across a gradient, while the recent resurrection uses β as an additive portion of total diversity such that $\alpha + \beta = \gamma$ (see Lande 1996, Loreau 2000, Veech et al. 2002). By dividing patterns of diversity into these scales, one could look for ecological or evolutionary processes driving spatially explicit patterns.

The purpose of this review is to highlight how spatially-explicit processes that structure communities can be used in conservation thinking. Most conservation activities directly affect local communities (e.g., species introductions, removals, prescribed burns, etc.), but by incorporating a spatial view of ecology, we can understand how these activities have consequences at other scales –hence the title "act locally, think regionally". Further, by understanding spatially-explicit processes, conservation plans may potentially be designed for greater impacts across numerous scales of organization. This paper will focus primarily on community and habitat level conservation measures and includes scenarios of species removals, introductions and reserve design, and I consider seven scenarios where conservation efforts and thinking about scale could be important.

Table 7.1: Ecological scales at which ecological processes occur and measures of species diversity are made.

Scale	Synonyms	Definition	Measures
Local	Alpha, α, community	Scale of organization in which species are likely to interact. Here individuals are observable.	Species richness or diversity indices that incorporate abundance (e.g., Simpson's index, Shannon-Weiner index, etc.).
Among	Beta, β, (dis)similarity	A measure of species differences among local sites. Can be measured multiplicatively, as in measures of similarity or alternatively, can be measured additively as average difference among local sites.	Multiplicatively, such as $\beta = \gamma / \alpha$, measures of species turnover, or similarity measures. Alternatively, can be measured additively as $\alpha + \beta = \gamma$.
Regional	Gamma, γ, species pool, landscape, metacommunity	Scale which includes all the species that could potentially colonize the local communities.	Species richness much more feasible than diversity indices since abundance data is difficult to assess at this scale. Regional species lists or large surveys required.
Metapopulation	Patchy population, large-scale population dynamics	Populations occupy discrete patches that individually undergo extinction and recolonizations. Metapopulations consititutes a dynamic view of population dynamics in space.	Static occupancy patterns as well as multiple samplings that record extinctions and colonizations. Population viability analysis (e.g., Wootton and Bell 1992) a key application of metapopulation theory.
Metacommunity	Region, landscape, species pool, multispecies metapopulation	a) An extension of metapopulation theory, such that multiple species interact across discrete patches. Here predator-prey or competitor coexistence is a spatial process. Or: b) A term for ecological processes that happen a scales larger than individual-individual interactions. Does not require discrete patches. For example, Hubbell (2001) viewed the metacommunity as all the species that could potentially disperse into local sites.	Occupancy patterns, multivariate compositional measures, interaction persistence (e.g., predator-prey interactions), and co-occurrence patterns.
Continental to global	National, biogeographic, latitudinal gradients	Extremely large scales where broad climatic and evolutionary processes dominate (Willis and Whittaker 2002).	Species inventories, proxy measures of diversity (e.g., primary production, key taxonomic groups, etc.), and perhaps paleontological patterns.

1. *Metapopulations extended to the community.*

From the pioneering work of Levins (1969) and later, Hanski (1981, 1982), ecologist's now view populations as spatially structured entities and that population persistence may depend upon local extinction rates coupled with the migration of individuals among patches (Hanski and Simberloff 1997). The classic metapopulation model, described by Levins (1969) and reformulated by Hanski (1981, 1982), simply attributes the number of local patches occupied (*P*) by a species as the product of its ability to colonize (*i*) patches versus local extinction rates (*e*):

$$\frac{dp_i}{dt} = c_i p_i (1 - p_i) - e_i p_i (1 - p_i). \qquad \text{Eq(1)}$$

Figure 7.1 shows how colonization and extinction terms vary with the number of patches occupied. Thus, local populations can often be impermanent, and dependent upon dynamics across a larger spatial scale.

Though the metapopulation perspective may be attributed to population dynamics too liberally sometimes, there are numerous examples of populations showing metapopulation dynamics (Harrison and Taylor 1997). Further, there are several key examples where viewing populations as metapopulations was key for obtaining conservation relevant information (see Hanski and Simberloff 1997). A metapopulation view has had two other key conservation implications. First, conservation biologist's now often think about species conservation in terms of larger spatial scales and the role of multiple habitat patches instead of single patches (Hanski and Simberloff 1997). Secondly, is that human-caused habitat fragmentation is forcing populations into metapopulation situations, and conservation plans now incorporate dynamics associated with fragmented populations (Fahrig and Merriam 1994, Harrison 1994).

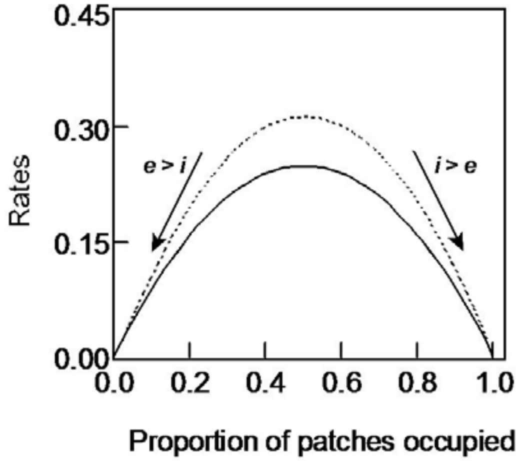

Figure 7.1: Graphical representation of Hanski's (1981) metapopulation model. Colonization ($iP(1-P)$) and extinction ($eP(1-P)$) rates are maximized at an intermediate number of patches occupied. If $i > e$, the metapopulation eventually occupies all patches, and if $e > i$, the metapopulation moves towards extinction.

However, as pointed out at the start of this review, and by Simberloff (2004), communities are an important, perhaps THE important conservation unit. Therefore, should species interactions be included into this multi-patch framework? Numerous theoretical models have revealed that competitive interactions and predator-prey interactions could be stabilized and coexistence promoted (especially when coexistence is not possible at a local patch scale) when species occur over discrete habitat patches (Holt 1997, see review by Hoopes et al. 2005). Furthermore, classic ecology experiments have shown that coexistence is promoted despite negative interspecific interactions when species are allowed to migrate and colonize multiple patches (Nicholson and Bailey 1935, Gause 1935, Huffaker 1958, Holyoak and Lawler 1996). Therefore managing any single species may require understanding how a competitor or predator interacts with the target species across space. For example, having a prey refuge –or predator-free areas- may be critical for the prolonged existence of both predator and prey.

Thinking about interacting metapopulations of two species seems tractable, but what happens when we are truly interested in whole communities? Just like the metapopulation perspective represented a paradigm shift for population ecologists (Hanski and Simberloff 1997), the metacommunity perspective is a paradigm shift for community ecologists (Leibold et al. 2004, Holyoak et al. 2005). Since the term "metacommunity" was coined in 1992 (Wilson 1992), publications using "metacommunity" as a keyword have increased exponentially (Fig. 7.2). The general definition of a metacommunity is a set of local communities linked by dispersal of potentially interacting species (Wilson 1992, Leibold et al. 2004). Whereas the metapopulation approach focused on population dynamics and persistence, the metacommunity approach focuses on species coexistence and patterns of species

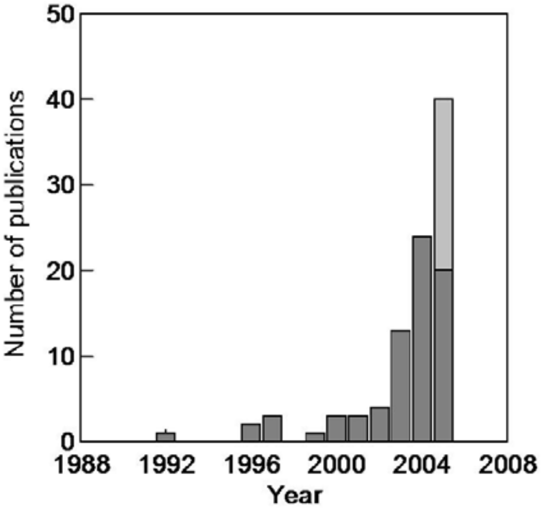

Figure 7.2: Number of citations using the term "metacommunity". Dark grey indicates publications in refereed journals, and light grey refers to chapters in Holyoak et al. 2005.

diversity, and unlike metapopulation theory, may not necessarily assume discrete patches (Table 7.1). This approach examines traditional local-scale interactions (i.e., competition and predation) across scales, and thus explicitly links processes regulating species diversity across spatial scales (Liebold et al. 2004). For example, we can add multispecies competition to Eq(1) (e.g., see Hoopes et al. 2005).

Metacommunity theory can be parsed into four main processes (reviewed in Leibold et al. 2004), and the first three will be considered here, and the fourth (neutral dynamics) will be the topic of section 5, below. The first process, patch dynamics, is a direct outgrowth of metapopulation theory, and essentially examines predator-prey or competitor-competitor dynamics as a series of extinctions and colonizations, such that coexistence occurs at larger spatial scales. Here, as with the traditional metapopulation approach, local populations are impermanent, and so species interactions should not be viewed as local dynamics, which may appear unstable, but rather as part of a larger dynamic (Holt 1997, Nee 1997).

Whereas patch dynamics assumes that there are no substantial or biologically important differences among local patches, the second process, species sorting, explicitly uses patch heterogeneity as a basis of coexistence (Amarasekare and Nisbet 2001, Cottenie et al. 2003, Cottenie and DeMeester 2004, Mouquet et al. 2006). As the environment changes species assemblages may track these changes, granted that the appropriate species are part of the metacommunity and thus can disperse into local communities. Again, we see that local coexistence may be limited by localized environmental conditions, but regional coexistence is possible in heterogeneous systems.

The third process, mass effects, combines the first two. Here local species diversity is enhanced because of immigrants entering from other patches (Brown and Kodric-Brown 1977, Shmida and Wilson 1985). Populations in patches with unfavorable local conditions will experience negative growth rates but are supplemented by immigrants from better patches with positive growth rates, allowing them to persist. For the community, this means that in any given patch a number of declining species are supplemented, thus local diversity is increased. However, if all patches are identical, then the best adapted to those conditions will likely come to dominate all patches in the metacommunity (Amarasekare and Nisbet 2001, Mouquet et al. 2006). Similarly, if patches are too different then species will simply sort according to local conditions (Mouquet et al. 2006).

Metacommunity dynamics has, at least, a heuristic value for conservation of species diversity. To maximize local diversity in a fragmented landscape (if that is the conservation goal), maintaining patch heterogeneity may serve to promote local diversity while also promoting regional coexistence (see too section 5). Also, by investigating population growth rates with the patches of a fragmented landscape could allow managers to determine which patches are sources and which are sinks, helping to develop differing conservation plans.

2. *Dispersal: predicting increases in diversity*.

A question of fundamental importance to conservation is whether or not local communities are saturated. Of course existing species can be replaced if the immigrants are superior competitors. Classical ecology thinking supposes that there are a finite number of niches and no two species can coexist while occupying the same niche (e.g., Grinnell 1917, 1925, Gause 1934, Hutchinson 1959 –see Chase and Leibold 2003), and so as more species colonize a local habitat, the greater the likelihood that future colonists will be excluded (Tilman 1997, Shea and Chesson 2002). Conservation biologists and managers undertake reintroduction effects, population stocking and build migration corridors, all of which add individuals and species to local habitats. These types of activities implicitly assume that communities are not saturated and that other processes, especially dispersal limitation, restricts the number of species within a habitat. In order for systems to be dispersal limited species generally undergo stochastic local extinctions more or as frequently as species can colonize the habitat. Therefore any large influx of species should result in increased diversity. For example, the biotic interchange resulting from the construction of the Panama Canal in 1914 has significantly increased the diversity of fishes in the Rio Chagres and Rio Grande without any resultant extinction of species (Smith and Shurin 2006). How well can conservation biologists use community invasibility to maximize species richness? Well, as with the answer for most things in ecology, it depends, and in this case it depends on dispersal rate and on the scale of interest (Fig. 7.3). We may want to promote immigration of individuals into local communities, but will likely have consequences at other spatial scales.

First and foremost, we need to explore how local community diversity can be affected by dispersal (e.g., Loreau and Mouquet 1999). This is the scale at which conservation efforts are levied, this is where we release individuals or build connecting corridors to. In a recent meta-analysis, I (Cadotte 2006a) combined the results of 50 experiments that manipulated dispersal into communities and from these experiments dispersal generally increased diversity. More than 72% of experiments found increases in local diversity, with many showing quite large diversity increases.

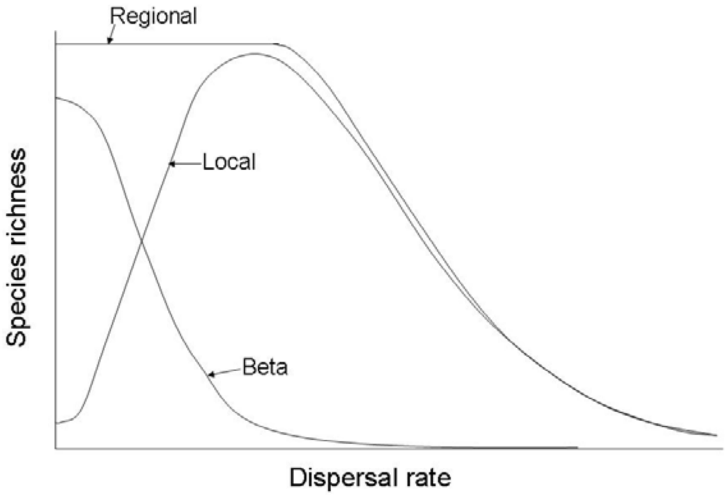

Figure 7.3: The hypothesized interaction between dispersal rate and species diversity at different spatial scales (Adapted from Mouquet and Loreau 2003).

However, dispersal is often more than an all or nothing process: species vary in their dispersal abilities, and local communities vary in their levels of isolation and connectedness (MacArthur and Wilson 1967, Cottenie et al. 2004). Mouquet and Loreau (2003) modeled competitive differences and stochastic extinctions within local communities, and showed that intermediate dispersal rates maintain the greatest local diversity (Fig. 7.3). The reason is that too low a dispersal rate means that both stochastic extinctions and negative interactions cause local populations to go extinct without rescue, while at high rates dominant competitors are introduced into all local communities. In the same meta-analysis, I also examined this hypothesis –that there is a modal relationship between local diversity and dispersal rate (Cadotte 2006a). The difficulty in testing this hypothesis is that different studies had idiosyncratic methods for varying dispersal rate. Given this, we need to use standardized measures of dispersal rate (*D*), which I did by using the following formulation:

$$D = \left(\frac{n}{t}\right) \Big/ \rho \quad , \qquad \text{eq(3)}$$

where *n* is the number of individuals introduced per generation time (*t*), and ρ is a measure of the number of resident individuals per unit area (or volume). Therefore the relative magnitude of dispersal rate should be viewed as a consequence of local density and on a generational time scale (see Cadotte 2006a). Using this standardization, I was able to support the hypothesis of a unimodal relationship for animal studies and not plant ones (Cadotte 2006a). However studies that explicitly manipulate dispersal rate are only just beginning (Forbes and Chase 2002, Brown and Fridley 2003, Cadotte 2006b, Matthiessen and Hillebrand 2006), and thus more work is required. Regardless, tentative evidence suggests that rate may be an important determinant in immigration's effort on local diversity, and thus conservation managers should try to determine what high and low dispersal should be based upon resident densities and generational time.

Despite the potential positive effect of dispersal on local diversity, is equally potential negative effect of dispersal on diversity at larger scales. By promoting the movement of organisms among local patches, there is risk that dominant competitors will exclude the same species at all locations thus homogenizing local patches. Even though Mouquet and Loreau (2003) showed positive effects associated with dispersal on local communities, the same model reveal the increasing dispersal reduced beta diversity, as a result of greater similarity, and eventually reduced regional diversity (Fig. 7.3). Again, looking to the meta-analysis (Cadotte 2006a), even though there were very few experiments that adequately examined the role of dispersal on regional diversity, those studies that did examine it tend to find declines in regional diversity as a result of dispersal among local patches.

These scale-dependent effects of dispersal have important conservation implications because the perspective of conservation managers in regard to migration depends upon their scale of concern. For example, if managers are interested in maintaining maximal diversity over a fragmented landscape, then perhaps restricting, or at least not enhancing, dispersal would best ensure regional diversity. However, if the concern is a single local community, then enhancing immigration may be the best option. It is important to point out that richness is but one conservation priority, and other priorities may require a strategy to limit diversity increases –such as with locally endemic or unique communities.

There is a long-running debate in conservation ecology as to the benefit of using corridors to link habitats (e.g., Noss 1987, Simberloff and Cox 1987), with one side arguing that there may be negative consequences, such as the spread of disease, fire and invaders, associated with corridors (Simberloff and Cox 1987, Procheş et al. 2005), and the other side arguing that the benefits, such as reduced extinction rates and inbreeding depression, are real and possibly offer greater benefits than hypothesized risks (Noss 1987, Tewksbury et al. 2002, Levey et al. 2005). I would argue, given that different effects can be observed at different scales, that this is a debate about the scale of effects, rather than the nature of effects. For example, having five dominant competitors or invaders moving through corridors will likely increase local diversity, but if they happen to replace one or two relatively rare species in each local patch, then, given a large number of patches, the consequences of these local diversity increases could be catastrophic at larger scales. Unfortunately, as was true 20 years ago (Simberloff and Cox 1987, Simberloff 1988), there is still a dearth of experiments assessing the effects of corridors, especially at larger scales. The most sophisticated corridor experiments (e.g., Tewksbury et al. 2002, Levey et al. 2005) definitely show positive patch-level effects associated with corridors, yet these experiments only examine the role of corridors linking two patches, and thus evaluating corridor effects at larger scales is so far impossible.

3. *Community saturation and invasions: it depends on the region*.

The hypothesis that diverse local communities should limit future immigrants is crucially important to predicting where non-indigenous invaders will spread to. This prediction, pertaining to invaders, was first articulated by Charles Elton (1958), and is still a vibrant hypothesis (e.g., Shurin 2000, Dukes 2001).

Looking across large regions, whether local communities are in fact saturated can be discerned by plotting local richness against regional richness (Ricklefs 1987, Cornell and Lawton 1992, Cornell and Karlson 1997, Srivastava 1999). If local richness increases as a linear function of regional richness, then these communities can be said to be dependent upon immigration from the regional species pool, and therefore not saturated by local interactions independent of species pool size (Fig. 7.4). However, if local richness is not dependent upon regional richness, than local communities are likely to be saturated. Results generally seem to fail to support the idea that local communities are saturated (e.g., Caley and Schluter 1997). However, the use of local-regional plots can be more difficult than at first glance (see Srivastava 1999, Russell et al. 2006). To test for saturation one needs to carefully define and measure local and regional richness,

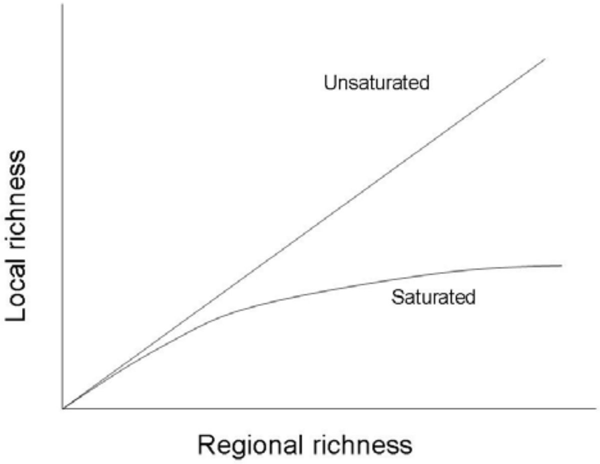

Figure 7.4: The relationship between local and regional richness given saturated and unsaturated local community models.

environmental differences among local habitats, and find regions that differ in richness but not other major ecological processes –such as productivity.

Despite the fact that we are experiencing a global decline in species richness (Diamond 1989), the movement of species among regions is causing increased regional richness (Simberloff 1981, Sax and Gaines 2003). These regional richness increases are direct tests of whether local communities are saturated, and the results of these natural experiments depend on historical and environmental conditions (Sax et al. 2005). Islands, for example, generally have lower species richness compared to similar sized mainland sites due to dispersal limitation (MacArthur and Wilson 1967). For this reason, Islands readily show increases in local richness as islands become invaded (Lonsdale 1999, Sax et al. 2003), something first commented on by Charles Darwin (see review in Cadotte 2006c).

However, what do mainland studies reveal about community invasion resistance? Here, presumably, differences in species richness depend upon spatially varying historical and environmental conditions. Small scale plant community experiments that manipulate resident richness or functional group diversity, while controlling all extraneous environmental conditions, almost universally show that invasibility is negatively correlated with resident richness (Tilman 1997, Naeem et al. 2000, Symstad 2000, Dukes 2001). These results support local saturation, yet observational studies that examine invasive species density and richness at larger scales find that invasions are generally positively correlated with native diversity (Lonsdale 1999, Stohlgren et al. 1999, Sax 2002, Lu & Ma 2005, but see considerations by Fridley et al. 2004), apparently supporting the conclusion that communities are unsaturated.

The way to reconcile these results lies in viewing communities as the product of numerous processes. Regions can be defined by variables other than resident diversity and these variables can have direct effects on local community invasibility (Byers and

Noonburg 2003, Ohlemüller et al. 2006, Stevens 2006). Regions have differing nutrient dynamics, moisture gradients, or disturbance frequencies, for example. At small scales, under uniform environmental conditions, more diverse assemblages better resist invasion than less diverse ones. However at larger scales, both native and non-native richness vary with large scale factors that promote richness (Levine and D'Antonio 1999, Levine 2000, Byers and Noonburg 2003). Burke and Grime (1996) found that with the same resident community, invasions increased as a result of either nutrient enrichment or disturbance. Similarly, human-caused changes to the amount of land cover can directly influence local invasions (Ohlemüller et al. 2006). Lavine (2000) found a mechanism for these scale discrepancies. He examined riparian tussocks, and showed that more diverse ones tend to resist invasions better, but at a larger scale propagule supply was strongly correlated with both native and non-native richness.

If a conservation priority is to control the spread of non-native species then predicting when and where these species will invade would be a powerful tool. Though absolute prediction is likely unobtainable (see review of Cadotte et al. 2006b), ecologists and managers need to understand two fundamental aspects of the invasion process: who is likely to be an invader and which systems are likely to be invaded (e.g., Drake et al. 1989). By understanding how community saturation operates in nature, and the extent to which other extrinsic factors regulate local diversity, understanding which systems are likely to be invaded may be obtainable.

4. *Invasive species dynamics at multiple scales.*

Whether or not communities are open to invasions may be under the control of large-scale processes, but what about the invaders themselves? A recent special issue of *Biological Invasions*, titled "Biological Invasions across Scales" (Pauchard and McKinney 2006), explicitly explores invader dynamics, patterns and impacts at multiple scales. The guest editors' rationale for this special issue was that mechanistic studies operate at local, small scales, while observational studies of invasion patterns were at much larger scales and little work has been done to link work done at these two scales (Pauchard and McKinney 2006).

Only recently have studies considered the causes and consequences of invasions at multiple scales. Collingham et al. (2000), examined temporal patterns of invasions of *Fallopia japonica*, *Heracleum mantegazzianum* and *Impatiens glandulifera*, and found that these species seemed to attain maximal distributions at larger scales faster than local ones. Similarly, Hamilton et al. (2005), examining Australian plant invaders, found that these species spread faster at the continental scale compared to the landscape scale (see Fig. 7.5 as an illustration). They found that seed mass was the best predictor at both of these scales, meaning that propagule availability controlled landscape and continental abundance patterns (Hamilton et al. 2005). Further, in a study of exotic plant species of Mediterranean Islands, Lloret et al. (2004) found that wind-dispersed species had higher abundances at the large (across all islands) scale, while dispersal syndrome was a weak predictor at the within-island scale. Finally, in a spatially-explicit study of *Rhamnus cathartica* invasions in Minnesota, USA, Knight and Reich (2005) showed that invasions into local habitats was strongly limited by native diversity and cover, while at larger scale it was controlled by propagule availability from large seed-producing individuals.

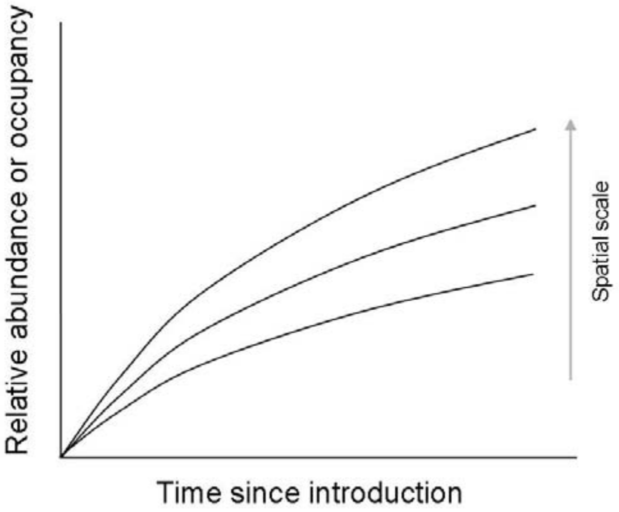

Figure 7.5: Hypothesized relationship of time since introduction on a relative measure of abundance or occupancy. Shown here is the relationship at three different scales, and increasing scale (e.g., local to regional to continental) results in increased slope of the relationship.

Studies examining plant invasions at large scales generally find that wind-dispersed species obtain higher abundances (Cadotte et al. 2006b), but why do species appear to spread faster at larger scales? Rates of exotic invader spread at local scales varies from 2 to 370 m/year, while rates at regional scales can be orders of magnitude faster, up to 167 km/year for *Wedelia trilobata* in Australia (see Pyšek and Hulme 2005)!

The reason for these seemingly counter-intuitive findings is that invasive exotics appear to undergo two spatially-dependent dispersal processes, such that local dispersal tends to be slower than large-scale dispersal (Pyšek and Hulme 2005, Havel and Medley 2006, Pauchard and Shea 2006). Local dispersal consists of species ability to spread throughout local habitats, which depends upon local environmental conditions and resident community composition (Havel and Medley 2006, Pauchard and Shea 2006). While at regional, landscape and global scales, dispersal is dependent upon human activities, such as trade, tourism, fishing, agriculture, etc. (Hulme 2003, Muirhead and MacIsaac 2005, Havel and Medley 2006, Pauchard and Shea 2006). Human-altered landscapes change invader dispersal dynamics as fragmentation and edge effects cause increased susceptibility of local patches (With 2002). Post fragmentation patches are not isolated islands, rather the surrounding inter-patch matrix includes numerous species that send propagules into intact patches (Murphy and Lovett-Doust 2004). Therefore increases in the matrix proportion of the landscape or edge habitat results in increased propagule pressure (see Lockwood et al. 2005 for a review of propagule pressure).

Given that human-caused, large-scale dispersal can be so rapid and pervasive, what are the potential impacts? For local communities, impacts likely include species exclusions, reduced abundances and altered trophic interactions (e.g., Pauchard and Shea

2006). However, there are serious potential large-scale impacts. Widespread invaders may alter natural disturbance or geochemical cycling regimes (Pauchard and Shea 2006). For example, invasive grasses and shrubs my increase fire hazard (Dibble and Rees 2005, Misty and Berardi 2005). Further, invaders may alter ecosystem function. For example, *Spartina* spp. invasions into coastal wetlands change nutrient cycling and tropic interactions, thus altering ecosystem function (Levin et al. 2006).

Beyond these process effects, there may be serious, large-scale diversity effects associated with invasions. Whether or not there are local extinctions associated with species invasions, the movement of species among regions results in those two regions being more similar (McKinney and Lockwood 1999, Lockwood and McKinney 2001). This biotic homogenization is a result of the fact that we see species declines at continental and global scales (Sax and Gaines 2003) and has numerous evolutionary, biogeographical and ecological consequences (Olden et al. 2004). Examining patterns of biotic homogenization can highlight the conservation concern associated with exotic species invasions. Lockwood (2006) examined diversity patterns of native and exotic passerines in Hawaii, where species diversity and endemism are threatened by species invasions, and she found that local, within-island, diversity remained unchanged or increased, as local extinctions were largely offset by introductions. However, she showed that among-island diversity, or beta diversity, was reduced, showing the true impacts of invasions on diversity and that local endemism was being eroded (Lockwood 2006).

What does the fact that invasion dynamics operate at multiple scales mean for conservation? Once invaders are established regionally, local removals will be for naught if invaders can simply re-colonize through human activities (Manchester and Bullock 2000). It means that our invasion removal efforts have to proceed on two fronts: local removals and eliminating or prevent human-mediated dispersal pathways at larger scales (Manchester and Bullock 2000, Pyšek and Hulme 2005, Pauchard and Shea 2006). Hence, conservationists can only act locally, but must pursue policies that have large-scale implications.

5. *Tradeoffs, neutral dynamics and spatial coexistence.*

When it comes to mechanisms explaining species coexistence, the competition-colonization tradeoff has long been considered one of the most important in spatially-structured environments (Levins and Culver 1971, Horn and MacArthur 1972). This tradeoff predicts that better competitors are inferior colonizers and vise versa, and is a key assumption in numerous models of spatial coexistence (e.g., Slatkin 1974, Connell 1978, Hastings 1980, Petraitis et al. 1989, Caswell and Cohen 1991, Dial and Roughgarden 1998, Pacala and Rees 1998, Amarasekare and Possingham 2001, Amarasekare 2003). Furthermore, several authors believe that competition-colonization tradeoffs are an important key for understanding patterns of coexistence at larger spatial scales (Amarasekare 2003, Kneitel and Chase 2004).

Why this tradeoff is so important is that many ecologists view patterns of coexistence and diversity as produced by non-equilibrium dynamics (Huston 1979, Petraitis et al. 1989). Mechanisms producing non-equilibrium conditions are largely abiotic, including resource and environmental fluctuations and disturbances. Local disturbances reset succession to an early stage, which allows colonists an opportunity to settle on competitor-free habitat. As time moves forward, better competitors/poorer colonizers gradually replace the early colonists (Connell and Slatyer 1977). Several models examining patch occupancy and localized disturbances have found that the occupancy of late-successional species (or dominant competitors) declines with increasing disturbance frequency, while the reverse is true for colonizing species (Hastings 1980, Caswell and Cohen 1991, Amarasekare and Possingham 2001). Further, in an examination of native versus exotic plant responses to disturbances, Allcock and Hik (2003) showed that exotics, which tend to be weedy, increased with disturbance frequency. They also showed that the natives tend to decline with disturbances (Allcock and Hik 2003). Their explanation is an evolutionary one. Successful exotics tend to be adapted to ruderal, ephemeral habitats and thus exhibit traits often associated with "r-selected" species, while the majority of native plants tend to be adapted to habitats with low disturbance regimes (at least in a pre-human settlement regime) and thus exhibit relatively "K-selected" traits (Allcock and Hik 2003).

However, trait based approaches, such as competition-colonization tradeoffs, have been questioned as simpler, neutral models have come to the fore. Neutral dynamics describe metacommunities in which trophically-similar species are functionally equivalent, thus mechanisms controlling species diversity do not depend upon species identity (such as determining who are good competitors or good colonizers) (Bell 2000, 2001, Hubbell 2001). The reason for the appearance of neutral models was that niche-based approaches often predict that fewer species should persist at any given time or place, than what we actually observe in nature. Hubbell's (2001) formulation of the neutral model stands as the milestone for the recent paradigm shift, and it is conceptually simple (see Chave 2005 for a review of other formulations). Local diversity depends upon species abundances in the metacommunity, the dispersal rate into local habitats, stochastic deaths and the creation of new species (speciation) into the metacommunity. Neutral dynamics have been an extremely active area of research over the past few years (Fig. 7.6). Yet, neutral theory has not fared well in many of these studies. Tests of neutral theory has revealed that neutral dynamics may be a good explanation at some scales, but not others (Condit et al. 2002), or that neutral dynamics potentially explain abundance patterns, but not composition and individual occupancy patterns (Chave 2005, Wooton 2005, Harpole and Tilman 2006). Karst et al. (2005) surmised that species responses to small and large scale environmental gradients effectively relegated patterns produced by neutral dynamics to obscurity. Attempts have been made to reconcile neutral and niche-based mechanisms into a single model (Gravel et al. 2006), However, a number of authors have claimed that modern niche theories, which incorporate complexities such as stochasticity, interaction complexities and nonequilibrium dynamics, discussed above, often predict coexistence, high diversity and species exclusions as a rather rare event (Chesson 2000, Tilman 2004, Chase 2005).

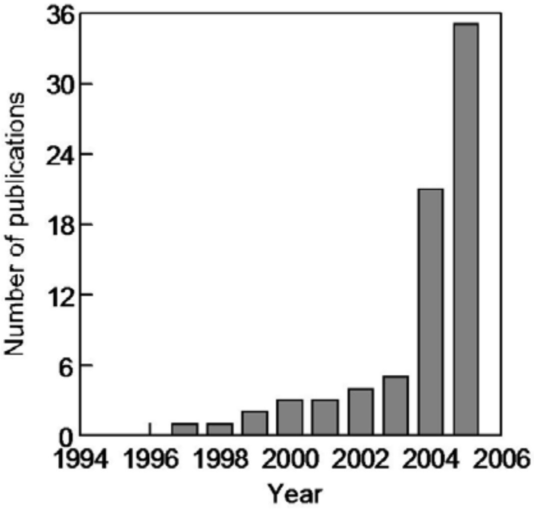

Figure 7.6: Number of ecology citations using the term “neutral theory”.

Figure 7.7 graphically summarizes the main differences between neutral and trait-based diversity mechanisms. In the neutral model (Fig. 7.7A), the metacommunity (J_m) is the accumulation of local abundances of individual species (*i*), and new species added via speciation (*v* –which is not shown in Fig. 7.7, as this comparison is over ecological time). Species richness, *S*, in habitat *j* is a function of the metacommunity, local birth-death rates (*r*) and an immigration rate of individuals (*m*):

$$S_j \approx f(m, r, J_m)\,. \qquad \text{Eq(4)}$$

Here, the neutral model does not include any successional dynamics, while the trait-based, nonequilibrium model assumes that local patches are periodically disturbed, initiating new successional trajectories (Fig. 7.7B). A newly opened patch will first be colonized by superior colonists, and eventually replaced by better and better competitors (which themselves are relatively poor colonizers). Therefore, dispersal rate in this model (*m’*) is a function of species identity (*i*), such that increasing identity results in a decreased probability of colonization in time step (*t*);

$$S_j \approx f(m', t, r, J_m)\,. \qquad \text{Eq(5)}$$

Also, time is a surrogate measure for successional change via competition. As species accumulated over time, the early colonists increasingly are likely to go locally extinct. This trait-based nonequilibrium model also promotes metacommunity coexistence since heterogeneity is promoted by local disturbances creating local habitats at differing successional stages. Thus, coexistence in these systems is regional rather than local, so that even though species exclusion is observed locally, regionally, there are patches at

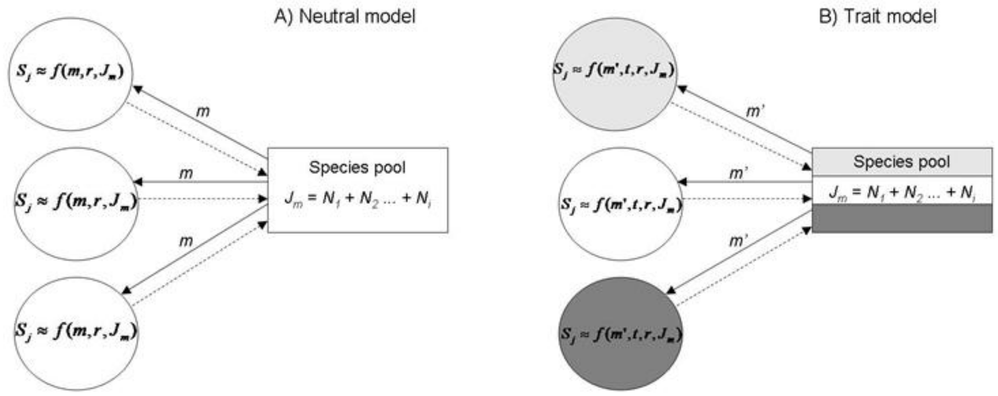

Figure 7.7: Graphical representations of relationship between species pool (metacommunity membership) and local diversity. In the A) neutral model individual habitat (*j*) identity is unimportant. Local richness (*S*) is a function of immigration rates (*m*, solid arrows), intra-patch birth-death processes (*r*) and metacommuity abudance (J_m) which is a product of individual summed abundances (*N*). In the B) trait model, patch identity does matter, and here the different shading refers to different time since disturbance (successional stage). Richness controls are similar to the neutral model except that time since disturbance (*t*) matters for successional (competitive) stage and immigration is not equivalent, but an inverse function of competitive ability (*m'*).

different successional stages (Denslow 1980, Caswell and Cohen 1991, Ellner and Fussman 2003).

Which model should conservation biologists and managers use as a roadmap for projects? Although some systems seem to display neutral dynamics (e.g., tropical forests, Chave 2005), the neutral model, in my opinion, would be a dangerous paradigm for conservation (see too Chase 2005). Neutral dynamics would lead us to undervalue individual species differences, the role of habitat heterogeneity and severe species interactions (e.g., invasive plants that dominate local habitats). Some neutral dynamics should be examined in lieu of conservation issues though. For example, since extinctions are essentially random walk processes, they should take a long time to happen. Further, adding a species to the metacommunity (analogous to speciation) should result in either increased average richness in local communities, but also increased extinction risk for all other species since neutral models assume a fixed community carry capacity (Hubbell 2001).

Trait-based approaches reveal that management at larger scales ought to promote successional heterogeneity. Of course this necessitates that species can disperse among patches, especially early successional species. Since managers can not directly manipulate species traits in order to promote coexistence, especially at larger scales, the only tool we have is to manipulate local patches to favor certain traits.

Conclusions and conservation implications.

My purpose at the outset was to show how conservation and management thinking can and should be influenced by ecological processes operating at or across spatial scales. The purpose was not to solve any particular conservation problems *per se*, but that most of our direct management and conservation tactics are local in nature and we can plan for effects are larger spatial scales. Of course, there are more conservation options than just manipulating local conditions (Fig. 7.8). At local scales, there is a suite of specific interventions available, but as we move up in scale, what can be done becomes more general and less “hands-on”, including policies and legislation (Fig. 7.8, Hobb 1998). However, in undertaking local conservation and management activities, we can be affecting large scale processes or these large processes can have implications for our local activities.

However, defining processes at different scales, and even just defining those scales, is not a nominal task. Different groups of organisms use and perceive of space differently (Kotliar and Wiens 1990, Kolasa and Waltho 1998). For example, avian predators may not “perceive” habitat differences between old-fields, tall grass prairies or oak savannas, while different suites of plants and ground-dwelling mammals occupy these habitats differentially and hence “perceive” heterogeneity at this scale. Therefore how we define scale should vary with the taxonomic groups that are of specific management concern.

Much of this review has focused on the metacommunity, which can be both a scale and a set of processes. Delineating the metacommunity can be a difficult and data-intensive process. Again, the metacommunity can vary for different taxonomic groups, from extremely small spatial scales, such as the aquatic arthropods living in the fluid

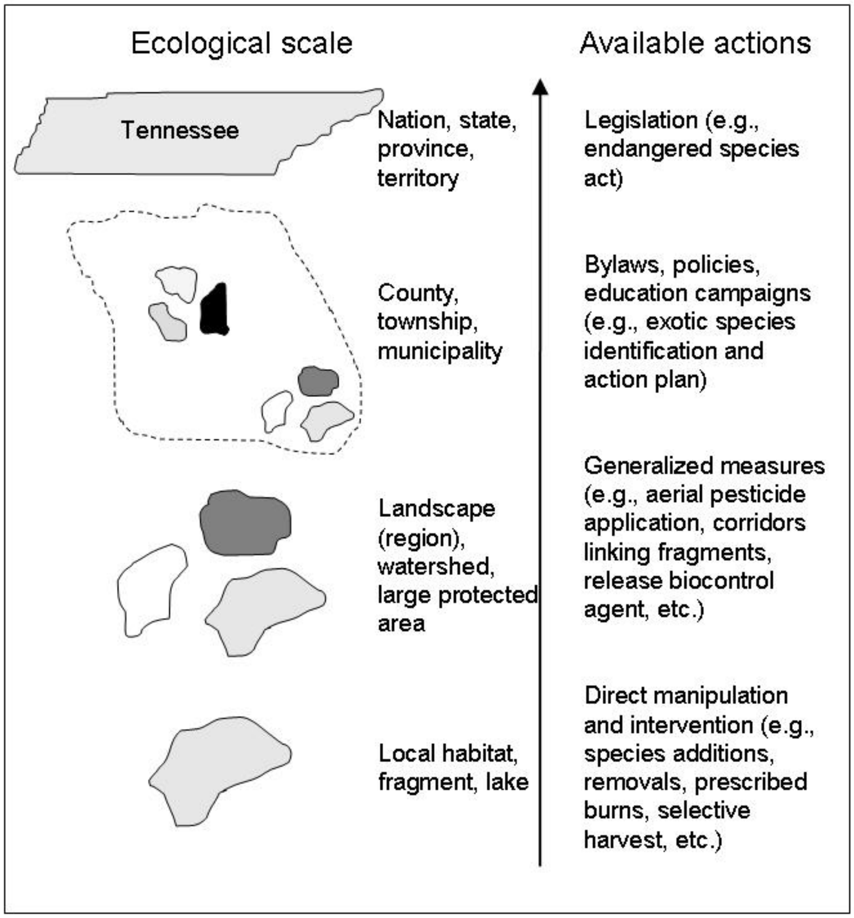

Figure 7.8: The relationship between ecological scale and the actions available to the conservation and management of ecological resources. These actions are top-down in that everything above any scale is available to activities at that scale, but activities at lower scales is likely not feasible to the scales above.

within bromeliad and pitcher plant leaves (e.g., Srivastava et al. 2004), or extremely large, for example, because of their pervasive dispersal, the protozoan metacommunity appears to be global in size (Finlay and Fenchel 2004)! Most metacommunity thinking is about what happens over multiple generations, and conservation managers do not have the luxury of long time series data. Yet, metacommunity theory likely has general precepts that maybe useful, as presented in this review.

Generally, when we implement management policies on local habitats, we should be cognizant of the reality that local patterns are already a partial product of large scale processes. By understanding processes potentially operating at different scales of organization, perhaps we can get a better gauge the potential success or failure of any action. While we act locally, we should be thinking regionally.

LITURATURE CITED

Addicott J.F. 1974. Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology 55: 475–492

Allcock, K. G. and D. S. Hik. 2003. What determines disturbance-producitvity-diversity relationships? The effect of scale, species and environment on richness patterns in an Australian woodland. Oikos 102: 173-185.

Allen, T.F.H. 1998. The landscape "level" is dead: persuading the family to take it off the respirator. Pp. 35-54 in D.L. Peterson and V.T. Parker (eds.), Ecological scale: theory and applications. Columbia University Press, New York, NY.

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, IL.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6: 1109-1122.

Amarasekare, P., M. F. Hoopes, N. Mouquet, and M. Holyoak. 2004. Mechanisms of coexistence in competitive metacommunities. American Naturalist 164: 310-326.

Amarasekare P. and R.M. Nisbet. 2001 Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158: 572-584

Amarasekare, P. and H. Possingham. 2001. Patch dynamics and metapopulation theory: the case of successional species. Journal of Theoretical Biology 209: 333-344.

Barradas, I., H. Caswell and J. E. Cohen. 1996. Competition during colonization vs competition after colonization in disturbed environments: a metapopulation approach. Bulletin of Mathematical Biology 58: 1187-1207.

Bell, G. 2000. The distribution of abundance in neutral communities. American Naturalist 155: 606-617.

Bell, G. 2001. Neutral macroecology. Science 293: 2413-2418Bengtsson, J. 1991. Interspecific competition in metapopulations. Biological Journal of the Linnean Society 42: 219-237.

Bohannan, B.J. and R.E. Lenski. 1997. Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. Ecology 78: 2303-2315

Bohannan, B.J. and R.E. Lenski. 1999. Effect of prey heterogeneity on the response of a model food chain to resource enrichment. American Naturalist 153: 73-82

Brotons, L., P. Pons, and S. Herrando. 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? Journal of Biogeography 32: 789-798.

Brown, R. L., and J. D. Fridley. 2003. Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density. Oikos 102: 15-24.

Brown J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Buckling, A., R. Hassen, G. Bell and P.B. Rainey. 2000. Disturbance and diversity in experimental microcosms. Nature 408: 961-964.

Burke, M.J.W. and J.P. Grime. 1996. Experimental study of plant community invasibility. Ecology 77: 776-790.

Burkey, T.V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria and protozoa communities as model ecosystems. American Naturalist 150: 569-

591.
Byers, J.E., and E.G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. Ecology 84: 1428-1433.
Cadotte, M.W. 2006a. Dispersal and species diversity: a meta-analysis. The American Naturalist 168 (in press).
Cadotte, M.W. 2006b. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. Ecology 87: 1008-1016.
Cadotte, M.W. 2006c. Darwin to Elton: Early ecology and the problem of invasive species. Pp. 15-33, In: M.W. Cadotte, S. M. McMahon and T Fukami (eds) Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer, Dordrecht, The Netherlands.
Cadotte, M.W., J.A. Drake, and T. Fukami. 2005. Constructing nature: laboratory models as necessary tools for investigating complex ecological communities. Advances in Ecological Research 37: 333-353.
Cadotte, M.W., A. Fortner, and T. Fukami. 2006a. The effects of enrichment, dispersal, predation and spatial scale on community structure. Oecologia, in press.
Cadotte M.W. and T. Fukami. 2005. Dispersal, spatial scale and species diversity in a hierarchically structured experimental landscape. Ecology Letters 8: 548-557.
Cadotte, M.W., D.V. Mai, S. Jantz, M. Keele and J.A. Drake. In review. On testing the competition-colonization tradeoff in a multispecies assemblage.
Cadotte, M.W., B. Murray and J. Lovett-Doust. 2006b. Using database analyses to test widespread ecological generalities in invasions biology. Biological Invasions (In Press).
Caley, M.J. and D. Schluter. 1997. The relationship between local and regional diversity. Ecology 78: 70-80.
Cardinale, B.J., H. Hillebrand, and D.F. Charles. 2006. Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. Journal of Ecology, in press.
Carpenter S.R. 1996 Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77: 677-680
Casagrandi, R. and M. Gatto. 2002. Habitat destruction, environmental catastrophes and metapopulation extinction. Theoretical Population Biology 61: 127-140.
Caswell, H. and J. E. Cohen. 1991. Disturbance, interspecific interaction and diversity in metapopulations. Biological Journal of the Linnean Society 42: 193-218.
Chalcraft D.R. and W.J. Resetarits. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? Ecology 84: 2407-2418.
Chase, J.M. 2003. Community assembly: when should history matter? Oecologia 136: 489-498.
Chase, J.M. 2005. Towards a really unified theory for metacommunities. Functional Ecology 19: 182-186.
Chase, J.M. and M.A. Leibold. 2002. Spatial-scale dictates the productivity-biodiversity relationship. Nature 416: 427-430.
Chase, J.M, and M.A. Leibold. 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago, IL.

Chase, J.M., and W.A. Ryberg. 2004. Connectivity, scale-dependence, and the productivity-diversity relationship. Ecology Letters 7:676-683.

Chave, J. 2004. Neutral theory and community ecology. Ecology Letters 7: 241-253.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343-366.

Chesson, P. and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. The American Naturalist 150: 519-553.

Cohen, G.M., and J.B. Shurin. 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103: 603-617.

Collingham, Y.C., R.A. Wadsworth, B. Huntly and P.E. Hulme. 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scales and extent. Journal of Applied Ecology 37: S13-S27.

Collins, S.L., S.M. Glenn and D.J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76: 486-492.

Condit, R., Pitman, N., Leigh, E. G. Jr., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Agular, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbel, S.P. 2002. Beta-diversity in tropical forest trees. Science 295: 666-669.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.

Cornell, H.V. 1985. Species assemblages of cynipid gall wasps are not saturated. American Naturalist 126: 565-569.

Cornell, H.V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. Pages 243-252 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois.

Cornell, H.V., and R.H. Karlson. 1997. Local and regional processes as controls of species richness. Pages 250-268 *in* D. Tilman and P. Kareiva, eds. Spatial ecology: The role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, New Jersey.

Cornell, H.V., and J H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61: 1−12.

Cottenie, K., and L. De Meester. 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85: 114-119.

Cottenie, K., N. Nuytten, E. Michels, and L. De Meester. 2003. Zooplankton metacommunity structure: regional versus local biotic and abiotic processes in a set of interconnected ponds. Ecology 84: 991-1000.

Darwin, C. 1859. The Origin of the Species. J. Murray, London.

Davis, H. G. 2005. r-Selected traits in an invasive population. Evolutionary Ecology 19: 255-274.

Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes: Oecologia. 46 18–21.

Dial, R. and J. Roughgarden. 1998. Theory of marine communities: the intermediate disturbance hypothesis. Ecology 79: 1412-1424.

Diamond, J.M. 1989. The present, past and future of human-caused extinctions. Philosophical Transactions of the Royal Society of London, Series B 325: 469-477.

Dibble, A.C. and C.A. Rees. 2005. Does the lack of reference ecosystems limit our science? A case study in nonnative invasive plants as forest fuels. Journal of Forestry 103: 329-338.

Drake, J.A. 1991. Community assembly mechanics and the structure of an experimental species ensemble. American Naturalist **137**: 1-26.

Drake, J.A., T.E. Flum, G.J. Witteman, T. Voskuil, A.M. Hoylman, C. Creson, D.A. Kenny, G.R. Huxel, C.S. Larue, and J.R. Duncan. 1993. The construction and assembly of an ecological landscape. Journal of Animal Ecology 62: 117-130.

Drake J.A., G.R. Huxel and C. Hewitt. 1996. Microcosms as models for generating and testing community theory. Ecology 77: 670-677.

Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, editors. 1989. Biological invasions: a global perspective. John Wiley & Sons, New York.

Ellner, S.P. and G. Fussman. 2003. Effects of successional dynamics on metapopulation persistence. Ecology 84: 882-889.

Elton, C.S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8: 50-59.

Finlay, B.J. and T. Fenchel. 2004. Cosmopolitan metapopulations of free-living microbial Eukaryotes. Protist 155: 237-244.

Flinn, K.M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3: 243-250.

Forbes, A.E., and J.M. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96: 433-440.

Foster, B.L. 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4:530-535.

Foster, B.L., and D. Tilman. 2003. Seed limitation and the regulation of community structure in Oak Savanna grassland. Journal of Ecology. 91:999-1007.

Foster, B.L., T.L. Dickson, C.A. Murphy, I.S. Karel, and V.H. Smith. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. Journal of Ecology 92: 435-449.

Fox, J.W. 2002. Testing a simple rule for dominance in resource competition. American Naturalist 159: 305-319.

Fridley, J.D., Brown, R.L., and Bruno, J.F. 2004. Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. Ecology 85: 3215-3222.

Fukami, T. 2001. Sequence effects of disturbance on community structure. Oikos 92: 215-224.

Fukami, T. 2004: Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. Population Ecology 46: 137-147.

Fukami, T. and P.J. Morin. 2003. Productivity-biodiversity relationships depend on the history of community assembly. Nature 424: 423-426.

Gause, G.F. 1934. The Struggle for Existence. Hafner Publishing Company, New York, NY.

Gause, G.F. 1935. Experimental demonstration of Volterra's periodic oscillation in the numbers of animals. Journal of Experimental Biology 12: 44-48.

Gehring , C.A. , J.E. Wolf, and T.C. Theimer. 2002. Terrestrial vertebrates promote arbuscular mycorrhizal fungal diversity and inoculum potential in a rain forest soil. Ecology Letters 5: 540-548.

Gering, J.C., and T.O. Crist. 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. Ecology Letters 5: 433-444.

Gibson, D.J., B.A. Middleton, K. Foster, Y.A.K. Honu, E.W. Hoyer and M. Mathis. 2005. Species frequency dynamics in an old-field succession: effects of disturbance, fertilization and scale. Journal of Vegetation Science 16: 415-422.

Gilbert F., A. Gonzalez, and I. Evans-Freke. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. Proceedings of the Royal Society of London B 265, 577-582.

Gleason, H.A. 1917. The structure and development of the plant association. Bulletin of the Torrey Botanical Club 44: 463-481.

Gonzalez, A. and E.J. Chaneton. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented landscape. Journal of Animal Ecology 71: 594-602.

Gotelli, N.J. 1991. Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. American Naturalist 138: 768-776.

Gravel, D., Canham, C.D., Beaudet, M., Messier, C. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9: 399-409.

Grinnell, J. 1917. The niche relationships of the California thrasher. Auk 34: 427-433.

Grinnell, J. 1925. Risks incurred to the introduction of alien game birds. Science 61: 621-623.

Gross. K.L., G.G. Mittelbach, and H.L. Reynolds. 2005. Grassland invisibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 86: 476-486.

Gurevitch, J., P. Curtis, and M.H. Jones. 2001. Meta-analysis in ecology. Advances in Ecological Research 32:199-247.

Gurevitch, J., and L.V. Hedges. 2001. Meta-analyses: Combining the results of independent experiments. Pages 347-369 *in* S.M. Scheiner and J. Gurevitch, eds. Analysis of Ecological Experiments. Oxford University Press, New York, NY.

Gurevitch, J., J.A. Morrison, and L.V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. American Naturalist 155: 435-453.

Hamer, K.C. and J.K. Hill. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. Conservation Biology 14: 1435-1440.

Hamilton, M.A., B.R. Murray., M.W. Cadotte, G.C. Hose, A.C. Baker, C. J. Harris, and D. Licari. 2005. Life-history correlates of plant invasiveness at regional and continental scales. Ecology Letters 8: 1066-1074.

Hanski, I. 1981. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42: 17-38.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210-221.

Hanski, I. and D. Simberloff. 1997. The metapopulation appraoch, its history, conceptual domain, and application to conservation. Pages 5-26, in I. Hanski and M. E. Gilpin (eds): Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, New York, NY.

Harpole, W.S., Tilman, D. 2006. Non-neutral patterns of species abundance in grassland communities. Ecology Letters 9: 15-23.

Harrison, S. 1994. Metapopulations and conservation. Pp. 111-128, in P. J. Edwards, N. R. Webb and R. M. May (eds): Large-scale ecology and conservation. Blackwell, Oxford, UK.

Harrison, S. and A.D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pp. 27-42, in I. Hanski and M. E. Gilpin (eds): Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, New York, NY.

Harrison, S., C.D. Thomas, and T.M. Lewinsohn. 1995. Testing a metapopulation model of coexistence in the insect community on ragwort (*Senecio jacobaea*). American Naturalist 145: 546–562.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18: 363-373.

Hastings, A. 2003. Metapopulation persistence with age-dependent disturbance or succession. Science 301: 1525-1526.

Hastings, A. 2004. Transients: the key to long-term ecological understanding? Trends in Ecology and Evolution 19: 39-45.

Havel, J.E. and K.A. Medley. 2006. Biological invasions across spatial scales: intercontinental, regional, and local dispersal of cladoceran zooplankton. Biological Invasions 8: 459-473.

Hobb, R.J. 1998. Managing ecological systems and processes. Pp. 459-484 in D.L. Peterson and V.T. Parker (eds.), Ecological scale: theory and applications. Columbia University Press, New York, NY.

Holmes, E.E., H.B. Wilson. 1998. Running from trouble: long distance dispersal and the competitive coexistence of inferior species. American Naturalist 151: 578-586.

Holt, A.R, P.H. Warren, and K.J. Gaston. 2004. The importance of habitat heterogeneity, biotic interactions and dispersal in abundance–occupancy relationships. Journal of Animal Ecology 73: 841-851.

Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population biology 12: 197-229.

Holt, R.D. 1993. Ecology at the mesoscale: The influence of regional processes on local communities. Pages 77-88 *in* R. Ricklefs and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago, IL.

Holt, R.D. 1997. From metacommunity dynamics to community structure: some consequences of spatial heterogeneity. Pp. 149-164, in I. Hanski and M. E. Gilpin (eds): Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, New York, NY.

Holt, R.D. and J.H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25: 495-520.

Holt, R.D., J.H. Lawton, K.J. Gaston and T.M. Blackburn. 1997. On the relationship between range size and local abundance: back to basics. Oikos 78: 183-190.

Holyoak, M. 2000. Habitat subdivision causes changes in food web structure. Ecology Letters 3: 509-515.

Holyoak, M., and S.P. Lawler. 1996. Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. Ecology 77: 1867-1879.

Holyoak M. and S.P. Lawler. 1996b. The role of dispersal in predator-prey metapopulation dynamics. Journal of Animal Ecology 65: 640-652.

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

Hoopes, M.F., R.D. Holt and M. Holyoak. 2005. The effects of spatial processes on two species interactions. Pp. 35-67, in M. Holyoak, M. A. Leibold and R. D. Holt (eds): Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, IL.

Horn, H.S. and R.H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53: 749-752.

Hubbell, S.P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27: 343-383.

Hulme, P.E. 2003. Biological invasions: winning the science battles but losing the conservation war? Oryx 37: 178-193.

Huston, M.A. 1979. A general hypothesis of species diversity. American Naturalist 113: 81-101.

Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393-401.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22, 415-427.

Jacquemyn, H., J. Butaye and M. Hermy. 2001. Forest plant species richness in small fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. Journal of Biogeography 28: 801-812.

Jakobsson, A. and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plots. Oikos 88: 494-502.

Jakobsson, A. and O. Eriksson. 2003. Tradeoffs between dispersal and competitive ability: a comparative study of wind-dispersed Asteraceae forbs. Evolutionary Ecology 14: 233-246.

James, C.D., and R. Shine. 2000. Why are there so many coexisting species of lizards in

Australian deserts? Oecologia 125:127-141.

Kadmon, R. and Y. Benjamini. 2006. Effects of productivity and disturbance on species richness: a neutral model. American Naturalist (in press).

Kaunzinger C.M.K. and P.J. Morin. 1998. Productivity controls food-chain properties in microbial communities. Nature 395: 495-497

Kellogg, C. H. and S. D. Bridgham. 2004. Disturbance, herbivory and propagule dispersal control dominance of an invasive grass. Biological Invasions 6:319-329.

Kneitel, J.M., and J.M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters 7: 69-80.

Kneitel, J.M., and T.E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. American Naturalist 162: 165-171.

Knight, K.S. and P.B. Reich. 2005. Opposite relationships between invasibility and native species richness at patch versus landscape scales. Oikos 109: 81-88.

Kolasa, J. 1989. Ecological systems in a hierarchical perspective: breaks in community structure and other consequences. Ecology 70: 36-47.

Kolasa, J., J.A. Drake, G.R. Huxel and C.L. Hewitt. 1996. Hierarchy underlies patterns of variability in species inhabiting natural microcosms. Oikos, 77, 259-266.

Kolasa, J. and N. Waltho. 1998. A hierarchical view of habitat and its relationship to species abundance. In: Peterson DL, Parker VT (eds) Ecological Scale: Theory and Applications. Columbia University Press, New York, NY, pp. 55-76.

Kondoh, M. 2001. Unifying the relationship of species richness to productivity and disturbance. Proceedings of the Royal Society, Series B 268: 269-271.

Kotliar, N.B. and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Kunin, W.E. 1998. Biodiversity at the Edge: a Test of the Importance of Spatial 'Mass Effects' in the Rothamsted Park Grass Experiments. Proceedings of the National Academy of Sciences 95: 207-212.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5-13.

Law, R., and R.D. Morton. 1993. Alternative permanent states of ecological communities. Ecology 74:1347–1361.

Lawton, J.H. 1999. Are there any general laws in ecology? Oikos 84: 177 -192.

Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147: 784-812.

Leibold M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. B. 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.

Levey, D.J., B.M. Bolker, J.J. Tewksbury, S. Sargent, and N.M. Haddad. 2005. Effects of landscape corridors on seed dispersal by birds. Science 309:146-148.

Levin, L.A., C. Neira and E.D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87: 419-432.

Levin, S.A. and R.T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Science, USA 71: 2744-2747.

Levine, J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288: 852-854.

Levine, J.M. and C.M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15-26.

Levine, J.M., and M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. American Naturalist 160: 452-467.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237-240.

Levins, R. and D. Culver. 1971. Regional coexistence of species and competition between rare species. Proceedings of the National Academy of Sciences 68: 1246-1248.

Levins, R. and Lewontin, R. 1985. The Dialectical Biologist. Harvard University Press, Cambridge, MA.

Lloret, F., F. Médail, G. Brundu and P.E. Hulme. 2004. Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? Global Ecology and Biogeography 13: 37-45.

Lockwood, J.L. 2006. Life in a double-hotspot: the transformation of Hawaiian passerine bird diversity following invasion and extinction. Biological Invasions 8: 449-457.

Lockwood, J.L., P. Cassey and T. Blackburn. 2005. The role of progagule pressure in explaining species invasions. Trends in Ecology and Evolution 20: 223-228.

Lockwood, J.L. and M.L. McKinney (eds.). 2001. Biotic Homogenization. Kluwer Academic, Dordrecht, The Netherlands.

Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. American Naturalist 156: 14-33.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. Ecology Letters 3: 73-76.

Loreau, M. and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. American Naturalist 154: 427-440.

Loreau, M., N. Mouquet and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences 100: 12765-12770.

Lu, Z. and K. Ma. 2005. Scale dependent relationships between native plant diversity and the invasion of croftonweed (*Eupatorium adenophorum*) in southwest China. Weed Science 53: 600-604.

Luckinbill, L.S. 1974. The effects of space and enrichment on a predator-prey system. *Ecology* 55: 1142-1147.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

MacArthur, R.H. 1972. *Geographical ecology*. Princeton University Press, Princeton, NJ.

MacArthur, R.H. and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101: 377-385

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Mackey, R.L., and D.J.Currie. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82: 3479-3492.

Manchester, S.J. and J.M. Bullock. 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. Journal of Applied Ecology 37: 845-864.

Matthiessen, B. and H. Hillebrand. 2006. Dispersal frequency affects local biomass production by controlling local diversity. Ecology Letters (in press).

McCabe, D.J., and N.J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroivertebrates. Oecologia 124: 270-279.

McCarthy, M.A. and D.B. Lindermayer. 1999. Incorporating metapopulation dynamics of greater gliders in reserve design in disturbed landscapes. Ecology 80: 651-667.

McKinney, M.L. and J.L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14: 450-453.

McPeek, M.A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. Ecological Monographs 68: 1-23

Misty, J. and A. Berardi. 2005. Assessing fire potential in a Brazilian savanna nature reserve. Biotropica 37: 439-451.

Mitchell-Olds, T. and R.E. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. Evolution 41: 1149-1161.

Mouquet, N., P. Leadley, J. Meriget, and M. Loreau. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. Oikos 104: 77-90.

Mouquet, N. and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. American Naturalist 159: 420-426

Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. American Naturalist 162: 544-557.

Mouquet, N., T.E. Miller, T. Daufresne and J.M. Kneitel. 2006. Consequences of varying regional heterogeneity in source-sink metacommunities. Oikos, in press.

Mouquet, N., P. Munguia, J.M. Kneitel, and T.E. Miller. 2003. Community assembly time and the relationship between local and regional species richness. Oikos 103: 618-626.

Muirhead, J.R. and H.J. MacIsaac. 2005. Evolution of lakes as hubs in an invasion network. Journal of Applied Ecology 42: 80-90.

Murphy, H.T. and J. Lovett-Doust. 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105: 3-14.

Murtaugh, P.A. 2002. Journal quality, effect size, and publication bias in meta-analyses. Ecology 83: 1162-1166.

Naeem, S., J.M.H. Knops, D. Tilman, K.M. Howe, T. Kennedy and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91: 97-108.

Nee, S. and R.M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. The Journal of Animal Ecology 61: 37-40.

Nee, S., R.M. May and M.P. Hassell. 1997. Two-species metapopulation models. Pp. 123-147, in I. Hanski and M.E. Gilpin (eds): Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, New York, NY.

Nicholson, A.J. and V.A. Bailey. 1935. The balance of animal populations. Proceedings of the Zoological Society of London 3: 551-598.

Noss, R.F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1: 159-164.

Ohlemüller, R., Walker, S. and Wilson, J.B. 2006. Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. Oikos 112: 493-501.

Oksanen, L., S.D. Fretwell, J. Arruda and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118: 240-261

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19: 18-24.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ.

Osenberg, C.W., O. Sarnelle, S.D. Cooper, and R.D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics and models. Ecology 80:1105-1117.

Ostman, O., J.M. Kneitel and J.M. Chase. 2006. Disturbance alters habitat isolation's effect o biodiversity in aquatic microcosms. Oikos (in press).

Pacala, S. W. and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. American Naturalist 152: 729-737.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100: 65-75.

Pärtel, M., R. Kalamees, M. Zobel, and E. Rosén. 1998. Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. Ecological Engineering 10: 275-286.

Pauchard, A. and M.L. McKinney. 2006. Introduction: biological invasions across scales. Biological Invasions 8: 397-398.

Pauchard, A. and K. Shea. 2006. Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399-413.

Peterson, D.L., Parker, V.T. 1998. Ecological scale: theory and applications. Columbia University Press, New York, NY.

Peterson, D.J. 1992. Free-living Freshwater Protozoa. CRC Press, Inc, Boca Raton, FL.

Petraitis, P.S., R.E. Latham, and R.A. Niesenbaum. 1989. The maintenance of species-diversity by disturbance. The Quarterly Review of Biology 64: 393-418.

Pianka, E.R. 1966. Latitudinal gradients in species diversity: A review of concepts. American Naturalist 100: 33-46

Pianka, E.R. 1970. On r- and K- selection. The American Naturalist 104: 595-597.

Pickett, S.T.A. and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc. New York, NY.

Price, J.E., and P.J. Morin. 2004. Colonization history determines alternate community states in a food web of intraguild predators. Ecology 85:1017-1028.

Procheş, Ş., J.R.U. Wilson, R. Veldtman, J.M. Kalwij, D.M. Richardson and S.L. Chown. 2005. Landscape corridors: possible dangers? Science 310: 781-782.

Pyšek, P. and P.E. Hulme. 2005. Spatio-temporal dynamics of plant inavsions: linking pattern to process. Écoscience 12: 302-315.

Rantalainen, M.L., J. Haimi, and H. Setälä. 2004. Testing the usefulness of habitat corridors in mitigating the negative effects of fragmentation: the soil faunal community as a model system. Applied Soil Ecology 25: 267-274.

Rees, M. 1995. Community structure in sand dune annuals: Is seed weight a key quantity? Journal of Ecology 83: 857-863.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. Science, 235, 167−171.

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

Rogers, W. E. and D. C. Hartnett. 2001. Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. American Journal of Botany 88: 1634-1642.

Rosenzweig, M.L. 1973. Exploitation in three trophic levels. American Naturalist 107: 275-294.

Roxburgh, S.H., K. Shea, and J.B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85: 359-371.

Russel, R, Wood, S.A., Allison, G., Menge, B.A. 2006. Scale, environment and trophic status: the context-dependency of community saturation in rocky intertidal communities. American Naturalist (in press).

Sax, D.F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Diversity and Distributions 8: 193-210.

Sax, D.F. and S.D. Gaines. 2002. Species diversity: from global decreases to local increases. Trends in Ecology and Evolution 18: 561-566.

Sax, D.F., S.D. Gaines, and J.H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. American Naturalist 160: 766-783.

Scholes, L., P.H. Warren, and A.P. Beckerman. 2005. The combined effects of energy and disturbance on species richness in protist microcosms. Ecology Letters 8: 730-738.

Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17: 170-176.

Shea, K., S.H. Roxburgh, and E.S.J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7: 491-508.

Shmida, A., and M.V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography **12**:1-20.

Shurin, J.B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81: 3074-3086.

Shurin, J.B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology 82: 3404-3416.

Shurin, J.B. and E.G. Allen. 2001. Effects of competition, predation, and dispersal on species richness at local and regional levels. American Naturalist 158: 624-637.

Simberloff, D. 1981. Community effects of introduced species. Pages 53-81 *in* M. H. Nitecki, ed. Biotic crises in ecological and evolutionary time. Academic Press, New York.

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

Simberloff, D. 2004. Community ecology: is it time to move on? American Naturalist 163: 787-799.

Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1:63–71.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55: 128-134.

Smith, D.G. 2001. Pennak's Freshwater Invertebrates of the United States: Porifera to Crustacea. John Wiley and Sons, Inc, New York, NY.

Smith, S.A., and J.B. Shurin. 2006. Room for one more? Evidence for invasibility and saturation in ecological communities. Pages 425-450 *in* M.W. Cadotte, S.M. McMahon and T. Fukami, eds. Conceptual ecology and invasions biology: reciprocal approaches to nature. Springer, Dordrecht, The Netherlands.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequalibrium maintenance of species diversity. Ecology 60: 1225-1239.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.

Spalding, V.M. 1909. Distribution and Movement of Desert Plants. Carnegie Institute of Washington, Washington, DC.

Spencer, M, and P.H. Warren. 1996. The effects of energy input, immigration and habitat size on food web structure: a microcosm experiment. Oecologia 108: 764-770.

Srivastava, D.S. 1999. Using local-regional richness plots to test for species saturation: Pitfalls and potentials. Journal of Animal Ecology 68: 1-17.

Srivastava, D.S., J.Kolasa, J. Bengtsson, A. Gonzalez, S.P. Lawler, T.E. Miller, P. Munguia, T. Romanuk, D.C. Schneider and M.K. Trzcinski. 2004. Are natural microcosms useful model systems for ecology? Trends in Ecology and Evolution. 19:379-384.

Steiner, C.F. 2001. The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. Ecology 82: 2495-2506

Stevens, M.H.H. 2006. Placing local plant species richness in the context of environmental drivers of metacommunity richness. Journal of Ecology 94: 58-65.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Suding, K.N. and D. Golberg. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. Ecology 82: 2133-2149.

Symstad, A.J. 2000. A test of the effects of functional group richness and compostition on grassland invasibility. Ecology 81: 99-109.

Terborgh, J.W. and J. Faaborg. 1980. Saturation and bird communities in the West Indies. American Naturalist 116: 178-195.

Tewksbury, J.J., D.J. Levey, N.M. Haddad, S. Sargent, J.L. Orrock, A. Weldon, B.J. Danielson, J. Brinkerhoff, E.I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. Proceedings of the National Academy of Sciences 99:12923-12926.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81-92.

Turnbull, L.A., M. Rees, and M.J. Crawley. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. Journal of Ecology 87: 899-912.

Veech, J.A., K.S. Summerville, T.O. Crist, and J.C. Gehring. 2002. The additive partitioning of species diversity: recent review of an old idea. Oikos 99: 3-9.

Waide, R.B., M.R. Willig, C.F. Steiner, G. Mittelbach, L. Gough, S.I. Dodson, G.P. Juday and R. Parmenter. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300

Warming, E. 1909. Oecology of Plants: An Introduction to the Study of Plant Communities. Clarendon Press, Oxford, UK.

Warren, P.H. 1996. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scale. Oecologia 105: 132-140.

Warren, P.H., R. Law, and A.J. Weatherby. 2006 Invasion biology as a community process: messages from microbial microcosms. Pages 343-367 *in* M. W. Cadotte, S. M. McMahon and T. Fukami, eds. Conceptual Ecology and Invasions biology: Reciprocal Approaches to Nature. Springer, Netherlands.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Whittaker, R.J., K.J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography **28**: 453-470

Wilson, D.S. 1992. The effect of complex interactions on variation between units of a metacommunity, with implications for biodiversity and higher levels of selection. Ecology **73**: 1984-2000.

Wilson, J.B., J.B. Steel, M.E. Dodd, B.J. Anderson, I. Ullmann, and P. Bannister. 2000. A test of community assembly using the exotic communities of New Zealand roadsides in comparison to British roadsides. Journal of Ecology **88**: 757-764.

With, K.A. 2002. The landscape ecology of invasive spread. Conservation Biology 16: 1192-1203.

Wootton, J.T. 2005. Field parameterization and experimental test of the neutral theory of biodiversity. Nature 433: 309-312.

Wootton JT, Power ME (1993) Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences* 90: 1384-1387

Xiong, S., M.E. Johansson, F.M.R. Hughes, A. Hayes, K.S. Richards, and C. Nilsson. 2003. Interactive effects of soil moisture, vegetation canopy, plant litter and seed addition on plant diversity in a wetland community. Journal of Ecology 91: 976-986.

Young, T.P., J.M. Chase, and R.T. Huddleson. 2001. Community succession and assembly. Ecological Restoration 19:5-18.

Yu, D.W., and H.B. Wilson. 2001. The competition-colonization trade-off is dead; long live the competition-colonization trade-off. American Naturalist 158: 49-63.

Zobel, M. 1997. The relative role of species pools in determining plant species richness - an alternative explanation for species coexistence? Trends in Ecology and Evolution 12: 266-269.

Zobel, M., and R. Kalamees. 2005. Diversity and dispersal ? can the link be approached experimentally? Folia Geobotanica 40: 3-12.

Zobel, M., M. Otsus, J. Liira, M. Moora, and T. Möls. 2000. Is small-scale species richness limited by seed availability or microsite availability? Ecology 81: 3274-3282.

APPENDICES

APPENDIX 1

Supplemental material for Chapter 2

Meta-analysis methodology and statistical tests

Much of what follows in this appendix is adapted from Gurevitch and Hedges (2001). For the i^{th} study I computed an unbiased standardized mean difference (referred to as Hedges' *d*):

$$d_i = \frac{\bar{x}_i^e - \bar{x}_i^c}{s_i} J ,$$

where $\bar{x}$ is the mean diversity value of the experimental treatment (*e*) and the control (*c*), respectively, and s_i is the pooled standard deviation and *J* the correction term for small sample bias. The pooled standard deviation is calculated as:

$$s_i = \sqrt{\frac{(N_i^e - 1)(s_i^e)^2 + (N_i^c - 1)(s_i^c)^2}{N_i^e + N_i^c - 2}} ,$$

where *N* is the sample size of the treatment (*e*) and control (*c*) for the i^{th} study. The correction, *J*, is calculated as:

$$J = 1 - \frac{3}{4(N_i^e + N_i^c - 2) - 1} ,$$

and as $N \to \infty$, $J \to 1$.

I also calculated a sampling variance for the i^{th} study:

$$v_i = \frac{N_i^e + N_i^c}{N_i^e N_i^c} + \frac{d^2}{2(N_i^e + N_i^c)} ,$$

which in turn allows for the calculation of the study confidence interval, CI:

$$CI_i = d_i \pm t_{\alpha/2, N-1} \sqrt{v_i} \Big/ \sqrt{N_i^e + N_i^c} ,$$

so that individual studies with having significant treatment effects will have a mean effect (*d*) and CI that does not overlap with 0.

Fixed effects model. A standardized measure from *k* studies is combined into a grand mean effect:

$$\bar{\bar{E}} = \frac{\sum_{i=1}^{k} w_i d_i}{\sum_{i=1}^{k} w_i} ,$$

where $w_i = 1/v_i$. The variance of this grand mean:

$$\bar{\bar{v}}_E = \frac{1}{\sum_{i=1}^{k} w_i} ,$$

allows the calculation the grand mean confidence interval.

An important assumption is that the studies used in the meta-analyses have homogeneous responses to the treatments. I used Cochran's Q test:

$$Q = \sum w_i \left(d_i - \overline{\overline{E}}\right)^2,$$

which is analogous to the within-class variation in an ANOVA test. This Q statistic has a χ^2_{k-1} distribution. If I fail to detect significance then I used the fixed effects model, else I used a mixed effects model for describing the grand mean effects.

<u>*Mixed effects model.*</u> A general calculations for the mixed effects model are basically the same, except the variances are adjusted. For the grand mean effect:

$$\overline{\overline{E}}^* = \frac{\sum_{i=1}^{k} w_i^* d_i}{\sum_{i=1}^{k} w_i^*},$$

where $w_i^* = 1/v_i^*$. The variance of this grand mean:

$$\overline{\overline{v}}_E^* = \frac{1}{\sum_{i=1}^{k} w_i^*},$$

allows the calculation the grand mean confidence interval. The difference here is that v_i^* is calculated differently. Here

$$v_i^* = v_i + \hat{\sigma}^2_{pooled},$$

where

$$\hat{\sigma}^2_{pooled} = \frac{Q - (k-1))}{c_i},$$

and the constant, *c*, is:

$$c_i = \sum_{i=1}^{k} w_i - \frac{\sum_{i=1}^{k} w_i^2}{\sum_{i=1}^{k} w_i}.$$

For either the fixed or mixed models, beyond examining the CI, I used a non-directional test, analogous to a Chi-square test:

$$\chi^2_k = \sum_{i=1}^{k} w_i d_i^2,$$

which gives a significance value to the grand mean departure from zero.

APPENDIX 2:

Supplemental material for Chapter 3

Appendix 2.A: The biological community.

Table 2.A.1: Species used, their taxonomic affiliations, maximum size, relative size class, and dietary needs: B = bacterivore, O = omnivory on small flagellates and/or ciliates, S = scavenger of decaying organisms, P = photosynthetic, and R = direct resource utilization. (Data from personal observations, Patterson [1992] for protozoans and Smith [2001] for rotifers.)

Species	Type	Maximum size (μm)	Size class	Diet
Blepharisma americanum	Ciliate	300	L	B/O
Chilomonas sp.	Flagellate	40	S	B
Coleps sp.	Ciliate	50	S	B/S
Colpidium striatum	Ciliate	100	M	B
Euplotes sp.	Ciliate	150	M	B/O
Lepadella sp.	Rotifer	150	M	B/O
Microflagellates	Flagellate	<10	S	B
Paramecium Aurelia	Ciliate	150	M	B
Paramecium bursaria	Ciliate	200	M	B/P
Paramecium caudatum	Ciliate	250	L	B
Philodina sp.	Rotifer	400	L	B/O
Spirostomum sp.	Ciliate	1000	L	B
Tetrahymena thermophila	Ciliate	50	S	B/R
Uronema sp.	Flagellate	25	S	B

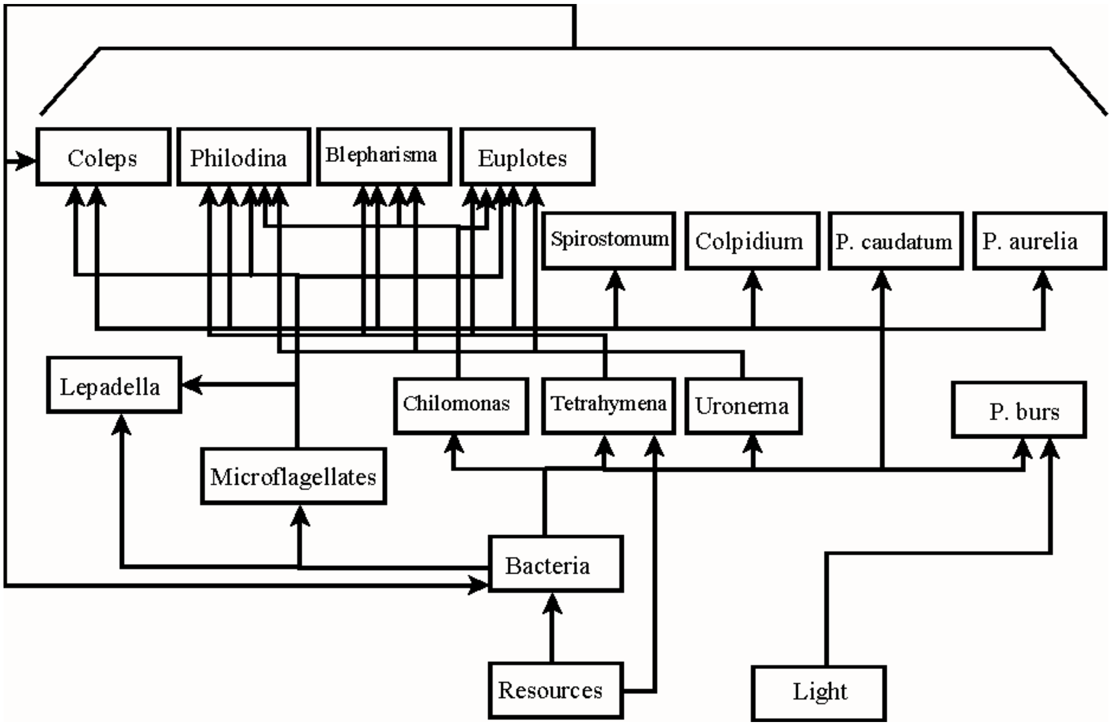

Fig. 2.A.1: The potential complete food web for the organisms used in this experiment.

Appendix 2.B: Treatment effects over time.

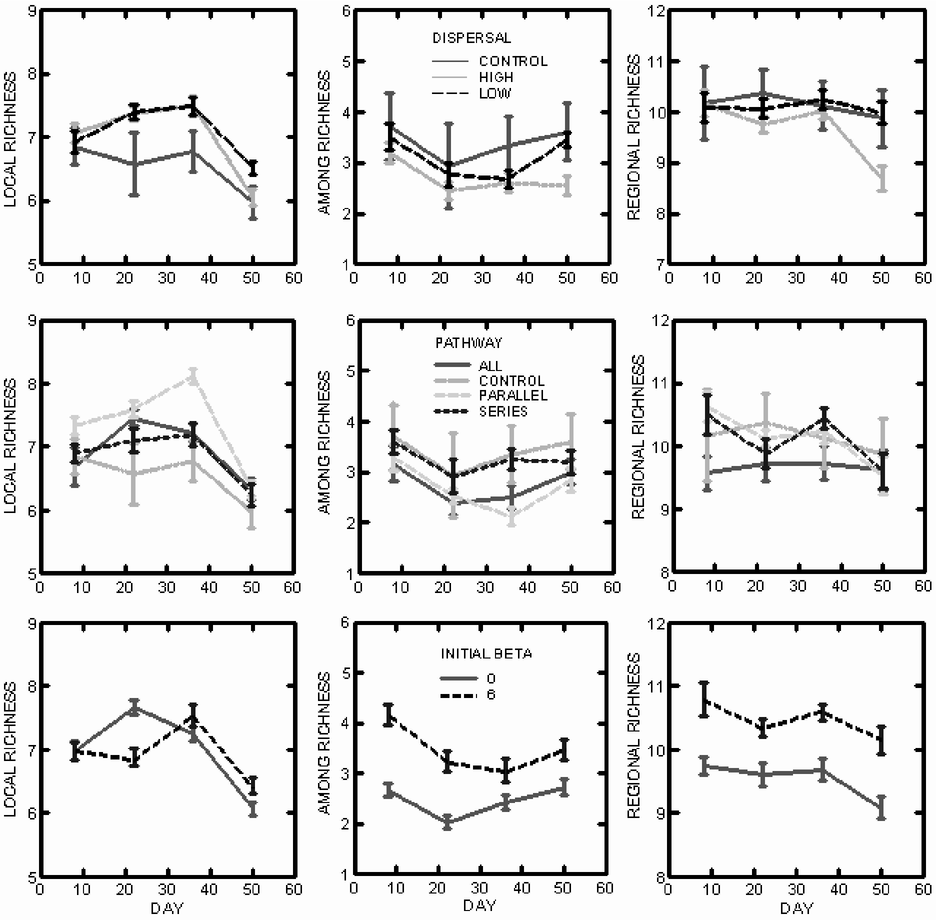

Fig. 2.B.1: The temporal richness trajectories for dispersal rate, dispersal pathway and initial beta at the three spatial scales.

Appendix 2.C: Graphical representation of single species responses to experimental treatments.

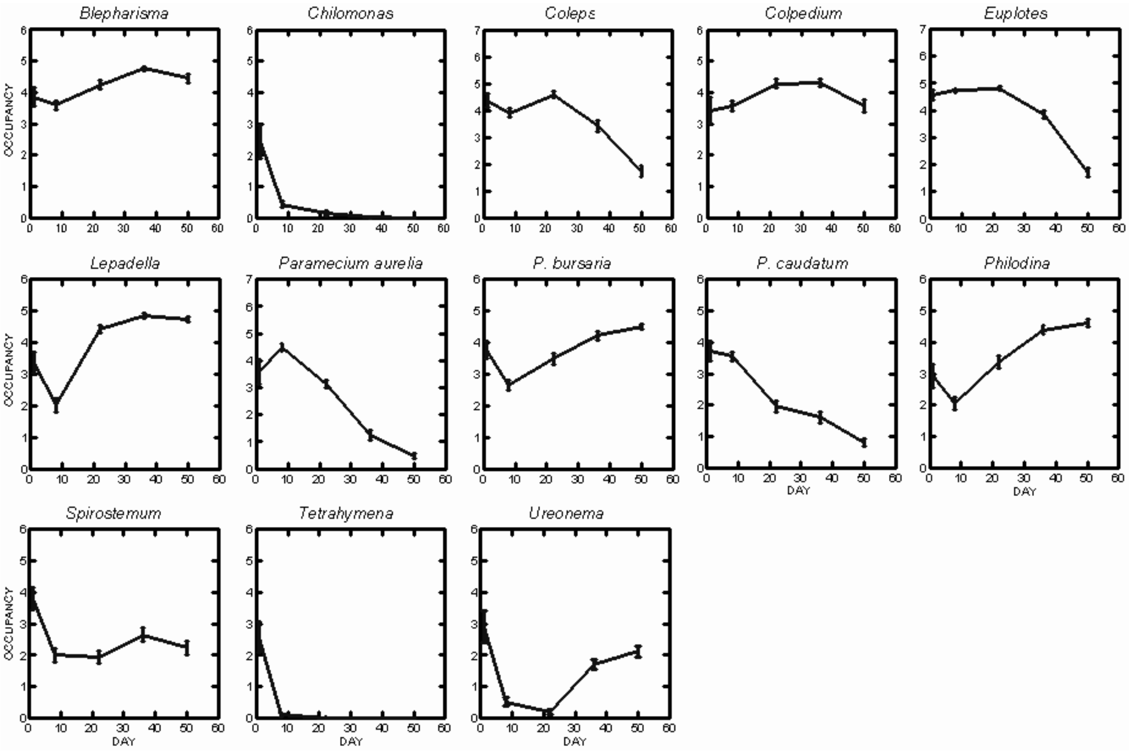

Fig. 2.C.1: Occupancy patterns for each species over time.

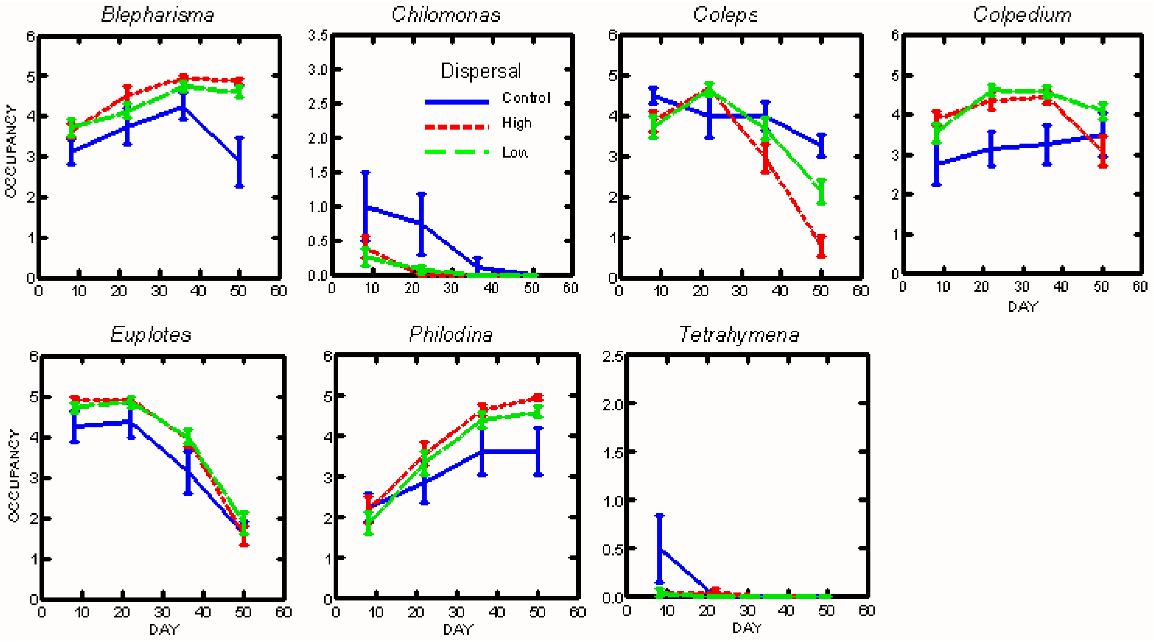

Fig. 2.C.2: Species occupancy patterns for the three dispersal treatments. Shown are species significantly affected by dispersal treatment (see Table 3.1).

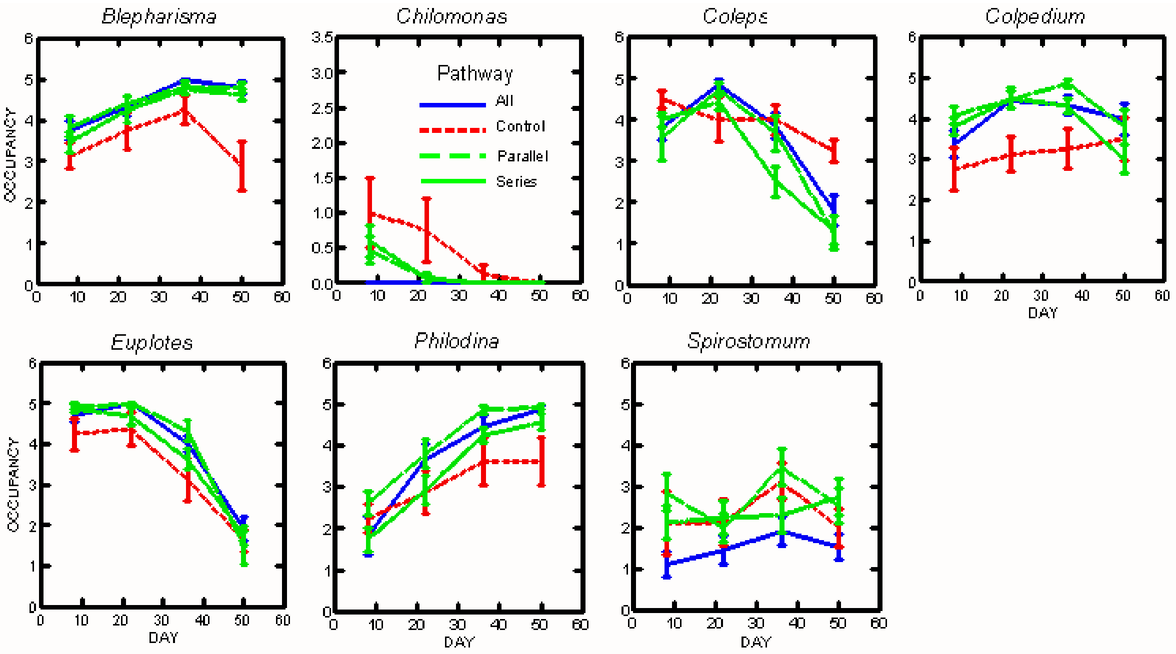

Fig. 2.C.3: Species occupancy patterns for the four dispersal pathway treatments. Shown are species significantly affected by pathway treatment (see Table 3.1).

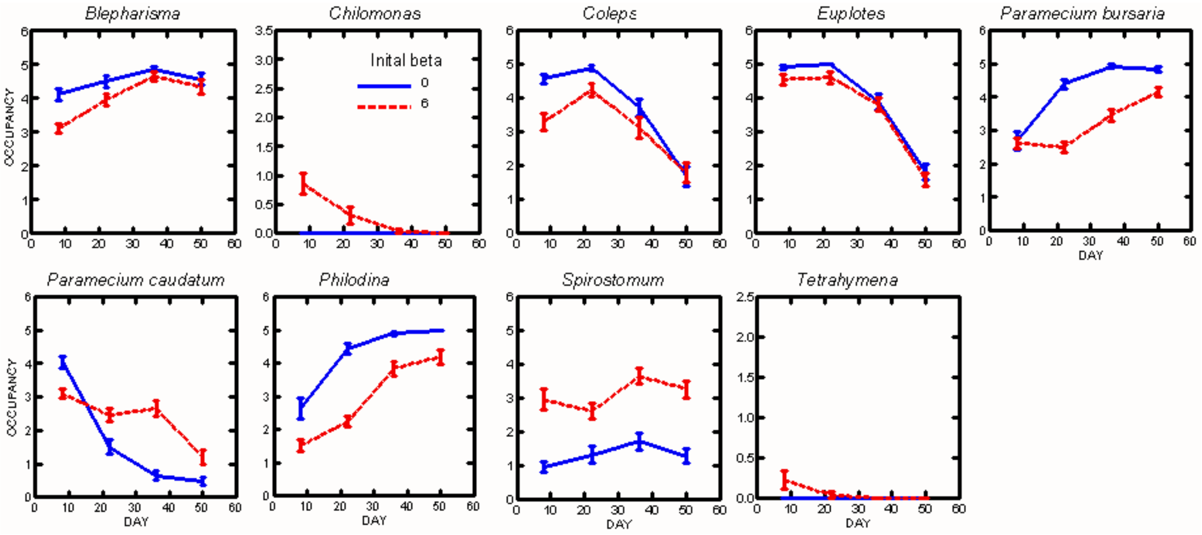

Fig. 2.C.4: Species occupancy patterns for the two initial beta treatments. Shown are species significantly affected by initial beta treatment (see Table 3.1).

VITA

Marc William Cadotte was born July 7th, 1975 in Windsor, Ontario, Canada. He attended elementary schools in Hearst, Ontario and Chatham, Ontario. He graduated secondary school OAS programme from Chatham-Kent Secondary School in 1994. Serendipity then led him back to Windsor for further educating at the University of Windsor. There he graduated with an Honors Bachelor of Science, majoring in biology, in 1999. He then continued on there, graduating with a Masters of Science, majoring in biology, in 2001. His Masters research was carried out in southeastern Madagascar, studying the effects of forest fragmentation on tree and shrub communities. He started his PhD at the University of Tennessee at Knoxville, working James Drake, in January, 2002 and defended May 2006. He will join the Department of Ecology, Evolution and Marine Biology at the University of California, Santa Barbara as postdoctoral fellow. He hopes to eventually procure a university professorship one day, hopefully in Canada.