

**THE INFLUENCE OF LANDSCAPE-SCALE SPATIAL-
ENVIRONMENTAL STRUCTURE ON THE
PREDICTABILITY OF LOCAL COMMUNITY
COMPOSITION**

by

Laura Elizabeth Super

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ABSTRACT

A primary goal in ecology is to understand why localities with similar abiotic environmental conditions often exhibit differences in species composition. Previous work points to the potential importance of historical or regional processes, such as priority effects and dispersal limitation, but the ways in which landscape structure moderates the impacts of such processes remain unclear. Using spatially explicit simulations of competitive metacommunities, I investigated if spatial autocorrelation of the environment (SAE), the degree of clustering of similar environments, in the broader landscape interacted with dispersal capacity to affect the predictability of local community composition. My study employed a fully crossed factorial design of SAE (random configuration to high positive SAE), dispersal capacity (local versus global [control]), and fundamental niche scenario (niche-differentiated versus neutral [control]). I quantified community composition predictability by measuring Bray-Curtis similarity among the same localities of replicate metacommunities. The results showed that in the absence of either niche differentiation or spatially restricted dispersal, variation in SAE had no impact on the predictability of local community composition. In contrast, in the presence of both niche differentiation and spatially restricted dispersal (characteristics of many metacommunities in nature), increasingly positive SAE increased community composition predictability. This was attributed to the enhancement of landscape connectivity facilitating deterministic species-environmental sorting of differentially adapted species, which reduced the influence of stochastic community assembly processes. Thus, the results suggest that the variation in local species composition often

observed among sites with similar environmental conditions could be attributed in part to differences in the spatial configuration of environmental conditions within the broader landscape. My work has potentially profound implications for basic and applied ecology. For example, the results suggest that practitioners should expect the reliability of composition-environment correlations to vary depending upon the spatial attributes of the ecosystem in question; they should be most useful as predictive tools within ecosystems characterized by strongly positive SAE. The results also yield an apparently novel and testable prediction: ecosystems characterized by high positive SAE will exhibit more repeatable community composition-environment relationships than ecosystems characterized by less clustering of similar environmental conditions in the landscape.

PREFACE

Unless otherwise noted, the below information refers to work in Chapter 2 of this thesis. The research question and study design were developed by Laura Super under the supervision of Dr. Jason Pither. The thesis writing (entire thesis), metacommunity simulation experiments, and analyses were completed by Laura Super, with revision and guidance from Dr. Pither. Computer code associated with the thesis research was written by Dr. Pither and Laura Super. Sensitivity analysis simulations were conducted by Laura Super via the use of high performance computing on the clusters of the Western Canada Research Grid (WestGrid), and on the UBCO SARAHS cluster, with advisement from UBCO IT staff.

TABLE OF CONTENTS

ABSTRACT.....	ii
PREFACE.....	iv
TABLE OF CONTENTS	v
LIST OF TABLES	vii
LIST OF FIGURES.....	viii
LIST OF ABBREVIATIONS	ix
GLOSSARY	x
ACKNOWLEDGEMENTS.....	xiv
DEDICATION	xvi
1. GENERAL INTRODUCTION	1
1.1. Introduction.....	1
1.2. Assembly Theories: Explaining Composition-Environment Relationships	2
1.2.1. Niche Theory	3
1.2.2. Neutral Theory	5
1.2.3. Historical-Regional Theory	7
1.3. Influence of Landscape Structure on the Predictability of Community Composition	8
1.3.1. Definitions of Key Landscape Structure Terms	8
1.3.2. Landscape Connectivity and Species-Environmental Sorting.....	9
1.4. Thesis Research.....	10
1.4.1. Explanatory Variable: Spatial Autocorrelation of the Environment.....	10
1.4.2. Research Question, Hypotheses, and Predictions	11
1.4.3. Overview of Chapters.....	12
2. DISPERSAL AND SPATIAL-ENVIRONMENTAL STRUCTURE INTERACT TO INFLUENCE LOCAL ENVIRONMENTAL DETERMINISM OF COMMUNITY COMPOSITION.....	14
2.1. Introduction.....	14
2.2. Methods	20
2.2.1. Simulation Model.....	20
2.2.2. Experimental Design.....	24
2.2.2.1. Degree of Positive Spatial Autocorrelation of the Environment	24
2.2.2.2. Fundamental Niche Scenario	25
2.2.2.3. Propagule Dispersal Capacity.....	26
2.2.3. Sampling the Metacommunity	27
2.2.4. Community Composition Predictability.....	28
2.2.5. Parameter Values and Analyses for Main Results and Supplementary Material	29
2.3. Results.....	31
2.4. Discussion	34
2.4.1. Take Home Message	34
2.4.2. Processes that Drive Community Composition Predictability	34
2.4.3. Composition-Environment Relationships Across Ecosystems.....	37

2.4.4.	The Deterministic-Stochastic Community Assembly Continuum.....	38
2.4.5.	Conclusion.....	39
2.5.	Supplementary Material.....	40
2.5.1.	Supplementary Material A: Environment Evenness.....	40
2.5.1.1.	Results.....	42
2.5.1.2.	Discussion.....	45
2.5.2.	Supplementary Material B: Beta Diversity Measures and Time-Steps.....	47
2.5.2.1.	Results.....	47
2.5.2.2.	Discussion.....	50
2.5.3.	Supplementary Material C: Demographic Parameter Sensitivity Analyses.....	51
2.5.3.1.	Results.....	51
2.5.3.2.	Discussion.....	51
3.	CONCLUSION.....	52
3.1.	Goal of Thesis.....	52
3.2.	Thesis Work in Light of Recent Research.....	52
3.2.1.	Landscape Connectivity and Plant Community Patterns.....	52
3.2.2.	Caution Regarding Variation Partitioning Analyses.....	53
3.3.	Potential Significance.....	54
3.3.1.	Basic Ecology.....	54
3.3.2.	Applied Ecology.....	56
3.3.3.	Research Strengths.....	56
3.3.4.	Research Limitations.....	58
3.3.5.	Future Directions.....	59
3.3.6.	Overall Conclusion.....	61
	REFERENCES.....	63

LIST OF TABLES

Table 2.1 Summary of the metacommunity simulation routine and parameters.	23
Table 2.2 Overview of model parameters for the main experiment and sensitivity analyses.....	30
Table 2.3 Summary of the results from varying the beta diversity resemblance measure and number of time-steps.....	48
Table 2.4 Summary of the results from varying demographic parameters.	51

LIST OF FIGURES

Figure 2.1 Schematic of the experimental approach.	19
Figure 2.2 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment.	32
Figure 2.3 Among-replicate similarity (community composition predictability) at the same interval of environmental conditions.	33
Figure 2.4 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment and low environment evenness.	42
Figure 2.5 A comparison of the results given high and low environment evenness.	43
Figure 2.6 Among-replicate similarity (community composition predictability) at the same interval of environmental conditions given high and low environment evenness.	44
Figure 2.7 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment for higher local richness.	45
Figure 2.8 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment at multiple time-steps.	50

LIST OF ABBREVIATIONS

SAE — Spatial autocorrelation of the environment

WestGrid — Western Canada Research Grid

GLOSSARY

Community: A group of species in a specified location.

Deterministic-stochastic community assembly continuum: A hypothesis that proposes that the relative importance of stochastic and deterministic community assembly varies among communities.

Environment amount: The frequency distribution of the amount of optimal abiotic environmental conditions per species.

Environment evenness: The relative abundance of optimal abiotic environmental conditions per species. The higher the environment evenness, the more the frequency distribution of the amount of optimal environmental conditions per species (environment amount) resembles a uniform distribution. In this thesis, high environment evenness refers to a uniform distribution of environment amount, and low environment evenness refers to a Gaussian distribution.

Environmental conditions: Refers to abiotic environmental conditions. The thesis research used a continuous gradient of environmental conditions. Because discrete habitats were not used, the term habitat is not used when referring to the thesis research. However, when referring to other studies (which often use "habitat" in different ways), the term habitat is used to mean the strict definition of habitat and also to refer to environmental conditions.

Environmental determinism: Refers to the abiotic environmental conditions deterministically driving community assembly. Strong environmental determinism means there will be high predictability of community composition in localities with particular environmental conditions.

Fundamental niche: The evolved physiological tolerance of species to underlying abiotic conditions, which dictates which environments are suitable and unsuitable.

Importance of deterministic relative to stochastic community assembly: The degree to which a local community is assembled due to stochastic processes (e.g., local stochastic extinction) versus deterministic processes (e.g., deterministic species-environmental sorting). In this thesis, the deterministic process of interest in species-

environmental sorting; when this process is of high importance, one observes highly repeatable (predictable) species composition in local communities that share identical environmental conditions.

Landscape composition: Generally defined in landscape ecology as the type and relative abundance of landscape elements, i.e., often habitat types, but the thesis research uses the term landscape composition to encompass continuous environmental conditions. The thesis research holds landscape composition constant (either high or low environment evenness) and varies landscape configuration.

Landscape configuration: The spatial arrangement of landscape elements, i.e., often habitats, but the thesis research uses the term landscape configuration with respect to the arrangement of continuous environmental conditions. The thesis research varies landscape configuration: the degree of positive spatial autocorrelation of the environment. In this thesis, landscape configuration is used interchangeably with spatial-environmental structure.

Landscape connectivity: The degree to which the environmental landscape facilitates (or impedes) the movement of organisms. The higher the landscape connectivity, the more species are able to move through the landscape.

Local stochastic extinction: Stochastic extinction of species in local communities that commonly occurs when population sizes are small.

Mass-effect: Involves the dispersal of species into suboptimal environmental conditions from an optimal environment. If mass-effect has a large role in structuring local community composition, then community composition will be less predictable than if species-environmental sorting was the dominate process driving community assembly.

Metacommunity: A set of communities connected by dispersal.

Metaecosystem: A set of ecosystems that are connected via flows of materials, energy, and organisms.

Neutral theory: In community ecology, there are various neutral theories that are commonly used as null models. A popular neutral theory in community ecology assumes that the individuals of all species have the same per capita rates of birth, death, migration, and speciation, and community assembly is solely due to stochastic processes.

Niche differentiation: In this thesis, metacommunities with niche differentiation have species with different fundamental niches. These different fundamental niches dictated the differential survival probabilities of the species depending on the environmental conditions.

Oligarchic dominance: In this thesis, oligarchic dominance refers to the effect of the species with the highest amount of optimal environment (oligarchs) deterministically out-competing other species.

Predictability of community composition: The degree of repeatability of community composition. If species-environmental sorting has a strong influence on community assembly, then one would observe highly repeatable (predictable) species composition in local communities in localities with very similar, or identical, environmental conditions. In this thesis, this refers to the ability to predict local species composition given environmental conditions. More specifically, it refers to among replicate metacommunity comparisons, i.e., local community composition in a metacommunity compared to local community composition in another metacommunity.

Priority effects: Arise due to initial colonization events, and increase stochastic community assembly. The initial seeding of the local communities in the thesis simulations made it so priority effects did not occur.

Propagule dispersal capacity: The distance that propagules disperse from the parent organism. Organisms with spatially limited (local) dispersal tend to have propagules fall nearby the parent. Organisms with spatially unlimited (global) dispersal have propagules disperse from the parent to potentially anywhere in the landscape.

Spatial autocorrelation of the environment: The spatial clustering of environmental conditions in the landscape. Positive spatial autocorrelation means that similar conditions tend to be clustered together, and negative spatial autocorrelation means similar environments tend to be far apart. When there is no spatial autocorrelation of the environment, this means that the clustering is no different than a random configuration.

Spatial-environmental structure: The spatial configuration of abiotic environmental conditions in the landscape. In this thesis, this term is used synonymously with landscape configuration.

Species-environmental sorting: Arises when differentially adapted species obtain optimal abundances at different gradient values that correspond to their species-specific adaptations, e.g., tolerance and competitive ability.

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To the diversity of life

1. GENERAL INTRODUCTION

1.1. Introduction

A fundamental task in ecology is to understand why different species compositions arise in locations with extremely similar, or identical, abiotic environmental conditions (Ricklefs 1987, Ricklefs and Schluter 1993, Chase 2003, Fukami et al. 2005). Obtaining accurate predictions of species composition as a function of local environmental conditions has a long history in ecology (Whittaker 1956, Gauch and Whittaker 1972, Whittaker 1975). This task is fundamental, for example, for developing strategies for environmental monitoring and assessment (Legendre et al. 2005). The difficulty is that numerous processes acting across scales of space and time can blur the otherwise predictable association between species composition and the environment (see Chase 2003, Trowbridge 2007, Matthews et al. 2009, Foster et al. 2011). Understanding the nature and specific impacts of these processes is a common goal among ecologists. For example, dispersal limitation is known to detract from composition-environment associations, because it impedes access to optimal environments by species (see Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Karst et al. 2005, Girdler and Barrie 2008, Legendre et al. 2009). However, acquiring direct evidence of dispersal limitation, and other potential sources of noise obscuring composition-environment relationships, is challenging in practice.

A useful approach is to seek out more general conditions promoting the predictability of composition-environment relationships. This can be achieved with

simulation modeling. This is the strategy I adopt in my thesis research. Specifically, I use simulation models to explore the idea that the spatial configuration of environmental conditions in the landscape might influence the predictability of community composition in localities with particular environmental conditions. Specifically, the goal of my thesis research is to address the following research question: does increasing the degree of positive spatial autocorrelation of the environment in the broader landscape increase the predictability of local community composition?

In the sections below, I provide background information on key topics that are directly related to the research question. First, community assembly theories, which have shaped perspectives on the predictability of community composition, are described: niche theory, neutral theory, and historical-regional theory. Next, key landscape structure terminology is defined, and a description is provided on how landscape connectivity can influence the importance of local environmental determinism (repeatable composition in relation to the environmental conditions). Then, in the thesis research section, additional background information is given, and the hypotheses and predictions related to the research question are discussed. Also, there is a thesis overview, which mentions additional simulations and analyses that supplement the main research question.

1.2. Assembly Theories: Explaining Composition- Environment Relationships

Community assembly theories provide a conceptual framework for understanding which factors determine species diversity (including composition and richness) in localities with particular environmental conditions (Chase and Leibold 2003). First, I

present background on deterministic assembly theory, i.e., niche theory, and the key concept of species-environmental sorting. Then, neutral theory — niche theory's antithesis — is briefly covered to point out the use of neutral models as null models, and to introduce the notion that contemporary ecologists view local community composition as arising due to the importance of deterministic relative to stochastic community assembly. Lastly, a brief description is given about theory that highlights how local community composition is influenced by broader scale temporal (historical) and spatial (regional) factors.

1.2.1. Niche Theory

Hutchinson (1957) played a major role in the quantification and definition of the niche concept (Chase and Leibold 2003). He defined a niche as an n -dimensional hypervolume that described the quantity of each limiting factor (n in number) an organism needed to survive. In particular, a species' fundamental niche was defined as the environmental conditions under which a species could exist in the absence of other species, i.e., the hypervolume of conditions to which a species has evolved physiological tolerance. The part of the fundamental niche in which a species actually resides, a restricted region due to interspecific interactions, was called the realized niche.

Inspired by Hutchinson's work, ecologists in the 1960s and 1970s developed what is now called niche theory: a collection of theoretical models that explore which and how many species reside in a given community (Chase and Leibold 2003). At this time, researchers were convinced that deterministic inter-specific competition for resources was a key underlying mechanism driving the assembly of communities (e.g.,

MacArthur and Levins 1967, Diamond 1975). While there was exploration of other factors, such as predation and environmental variability, there was intense focus on resource competition and the niche; this resulted in niche and resource competition being commonly associated in the ecological literature for decades (Chase and Leibold 2003).

After the initial surge of support, niche theory was highly criticized. For example, during the 1970s, proponents of null models (e.g., Simberloff 1978, Strong et al. 1979) indicated that niche-related studies were often conducted without adequate null hypotheses. The lack of appropriate null hypotheses called into question the validity of many studies inferring competition and using niche theory. Also, niche theory was criticized for not properly taking into account processes occurring at multiple spatial scales (Chase and Leibold 2003, Ricklefs 2004). In addition, critics highlighted that confusion arose when niche concepts were used in vague ways (Chase and Leibold 2003). However, many contemporary ecologists are embracing and revamping niche theory (Chase and Leibold 2003, Silvertown 2004, Tilman 2004, Schoener 2009). Such ecologists are mindful of using appropriate null models, making niche theory more relevant at multiple spatial scales, and clearly delineating the particular use of niche concepts (Chase and Leibold 2003).

An element of niche theory that is prevalent, implicitly or explicitly, in plant community ecology is the notion of niche-assembly along environmental gradient (see Whittaker 1956, Gauch and Whittaker 1972, Whittaker 1975, Austin 1985, Austin and Smith 1989, Chase and Leibold 2003, Leibold et al. 2004, Austin 2005, Karst et al. 2005), which has been termed species-environment sorting (Foster et al. 2011). Species-environmental sorting arises when differentially adapted species obtain optimal

abundances at different environmental gradient values that correspond to their species-specific adaptations, e.g., tolerance and competitive ability. In the 1950s to 1990s, the occurrence of variation in plant species composition along environmental gradients was often viewed as the result of species-environmental sorting (Whittaker 1956, Gauch and Whittaker 1972, Whittaker 1975, Austin 1985, Austin and Smith 1989). This view assumed species-environmental sorting would cause a close correspondence between a particular community composition and particular abiotic environmental conditions.

1.2.2. Neutral Theory

In contrast to deterministic species-environmental sorting, neutral theory assumes functional equivalence, which operationally means species have equal fitness in a given set of abiotic environmental conditions (see Bell 2001, Hubbell 2001). Under the assumption of functional equivalence, community composition arises due to stochastic processes, such as local stochastic extinction and stochastic dispersal. While functionally equivalent species assemble stochastically with respect to the underlying environmental conditions, spatial patterns irrespective of the environment can form in the landscape, owing to spatially limited dispersal. Thus, despite a lack of niche differentiation, neutral communities nonetheless can exhibit distance-decay in the similarity of local species composition (Hubbell 2001, Tuomisto et al. 2003, Legendre et al. 2005).

Neutral simulation models have also produced other community patterns, often strikingly similar to those observed in the field (e.g., Bell 2001, Hubbell 2001, Bell 2005). For example, Hubbell's (2001) model produced species relative abundance and species-area patterns similar to the patterns in surveys of tropical tree communities. In

another modeling study, Bell (2005) produced species co-occurrence patterns similar to those of systematic plant surveys in an old growth forest and in a highly humanized landscape.

The results from neutral models (especially Bell 2001, Hubbell 2001) ignited intense debate about whether community patterns were predominately shaped by stochastic or deterministic processes (see Whitfield 2002). After less than a decade of intense “neutral versus niche” debate, heated discussion has been replaced by discourse on niche-neutral reconciliation (e.g., Gravel et al. 2006, Hérault 2007). Current consensus is that communities lie along a deterministic-stochastic community assembly continuum, with neutral and classical niche theory representing the ends of the continuum (Gravel et al. 2006, Leibold and McPeck 2006, Cadotte 2007, Adler et al. 2007, Mutshinda et al. 2011).

An increasingly common use of neutral models is as null models to test hypotheses about the drivers of community patterns (see Gotelli and McGill 2006, Etienne and Rosindell 2011). Because neutral models have functionally equivalent species, the patterns arising from these models can be compared to the output of theoretical models, and to data from empirical research, where species have trait differences (e.g., Ulrich 2004, Bell 2005). The use of neutral models in this way allows researchers to assess whether community patterns arising in the field, and in simulation models, can occur due to stochastic community assembly processes alone. Null models of this sort are key for increasing our understanding of what factors can give rise to local community patterns (Bell 2001, Hubbell 2001, Ulrich 2004, Bell 2005, Gotelli and McGill 2006, Etienne and Rosindell 2011).

1.2.3. Historical-Regional Theory

In the late twentieth century, ecologists expressed the need to examine how local community patterns were influenced by both local factors and factors occurring at broader temporal (historical) and spatial (regional) scales (Ricklefs 1987, Ricklefs and Schluter 1993, Brown 1995). Many historical and regional factors are thought to obscure community composition-environment relationships. For example, the historical arrival of species into a locality may result in species being in higher abundance in suboptimal conditions than expected, a stochastic priority effect (Chase 2003, Trowbridge 2007). Also the number of species in the broader landscape (regional species pool size) can influence the predictability of local community composition: larger regional species pools are thought to create more stochastic community compositions given fixed local carrying capacity (Ricklefs and Schluter 1993, Hubbell 2001).

Metacommunity ecology brings to the fore the notion that dispersal is a regional scale process that influences local community composition in heterogeneous landscapes (Holyoak et al. 2005). Metacommunities are a set of communities connected by dispersal (Leibold et al. 2004, Holyoak et al. 2005). Dispersal plays a large role in whether community composition in metacommunities arises predominately due to deterministic species-environmental sorting or due to less predictable assembly via mass-effect. Mass-effect involves the dispersal of species into suboptimal environmental conditions from optimal environment (Mouquet and Loreau 2003). Intermediate rates of dispersal can result in strong mass-effect, and low (or very high) rates of dispersal can result in a high

strength of deterministic species-environmental sorting (Mouquet and Loreau 2003, Holyoak et al. 2005, Gravel et al. 2006, Ruokolainen et al. 2009). Also, the inability of species to reach optimal habitat in space, termed dispersal-limitation, can give rise to stochastic community composition patterns (Hubbell 2001, Tuomisto et al. 2003, Ozinga et al. 2004, Bell 2005, Ozinga et al. 2005). Furthermore, metacommunity modeling studies (e.g., Economo and Keitt 2008, Büchi et al. 2009, Economo and Keitt 2010) and field studies (e.g., Freestone and Inouye 2006, Minor et al. 2009) suggest that dispersal can interact with landscape structure to influence local community composition.

1.3. Influence of Landscape Structure on the Predictability of Community Composition

1.3.1. Definitions of Key Landscape Structure Terms

Generally, landscape ecologists describe landscape structure as having two components: landscape composition and landscape configuration (Fahrig and Nuttle 2003). Landscape composition refers to the type and relative abundance of habitat in the landscape, and landscape configuration refers to the spatial arrangement of habitats. Disentangling the influence of these two elements of landscape structure is difficult because the two are generally correlated (Guerry and Hunter 2002). For example, loss of habitat, which influences landscape composition, often results in changes of habitat isolation (a configuration feature). Commonly, landscape configuration is discussed in terms of discrete habitat patches (Fahrig and Nuttle 2003), but the same logic applies to

spatially arranging continuous environmental conditions (Palmer 1992, Büchi et al. 2009, Holland et al. 2009).

A key element of landscape structure is landscape connectivity, and is defined as the degree to which the landscape elements facilitate or impede the movement of organisms through the landscape (Taylor et al. 1993). Landscape connectivity is influenced by both the composition and the configuration of the landscape elements. If suitable habitat patches are in high abundance (landscape composition) and in close proximity to one another (landscape configuration), then landscape connectivity will be high; species will have accessible “stepping-stones” of suitable habitat across the landscape.

1.3.2. Landscape Connectivity and Species- Environmental Sorting

Species-environmental sorting, which leads to predictable community composition in localities, is thought to be influenced by landscape connectivity (Driscoll and Lindenmayer 2009, Flinn et al. 2010, Foster et al. 2011). In essence, this work suggests that with increasing landscape connectivity, there is increased species-environmental sorting relative to stochastic community assembly processes. It appears, however, that previous work leaves unanswered the question of how for species with spatially limited dispersal, landscape configuration and dispersal interact to influence the importance of stochastic relative to deterministic community assembly. The objective of my thesis is to use metacommunity simulations to ascertain how dispersal interacts with

landscape configuration to influence the strength of environmental determinism in driving local community composition.

1.4. Thesis Research

1.4.1. Explanatory Variable: Spatial Autocorrelation of the Environment

Spatial autocorrelation of the environment (SAE) refers to the phenomenon of spatial clustering of environmental conditions in the landscape, with positive SAE meaning that similar conditions tend to be clustered together, and negative SAE meaning similar conditions tend to be far apart (Holland et al. 2009). SAE is a key component of landscape configuration, and is commonplace in the terrestrial landscape (see Lechowicz and Bell 1991, Bell 1992, Bell et al. 1993, Legendre 1993, Schlesinger et al. 1996, Robertson et al. 1997, Richard et al. 2000, Stoyan et al. 2000, Karst et al. 2005, Bekele and Hudnall 2006, Bridges et al. 2007, Büchi et al. 2009). It also varies among ecosystems (c.f. Bell et al. 1993, Bridges et al. 2007), but a thorough comparative assessment of this variation appears to be lacking.

Despite its ubiquity, it seems that researchers have rarely investigated, or speculated, if SAE has an ecological role to play in influencing plant species patterns in nature (but see Karst et al. 2005, Dufour et al. 2006, Pinto and MacDougall 2010, McGlinn and Palmer 2011). Recently, Pinto and MacDougall (2010) studied the degree of habitat-matching of an endangered violet in locations that varied in SAE. This work

suggested that with increasingly positive SAE, it was more likely a species would be present in its optimal habitat.

Metacommunity simulation models have revealed that the degree of positive SAE can influence community patterns (Palmer 1992, Malanson 2002, Büchi et al. 2009). In one study, Büchi et al. (2009) showed that increasing positive SAE decreased the diversity within communities and increased the proportion of species investing in reproduction compared to species investing in dispersal or adult survival. In another study, Palmer (1992) showed that in comparison to landscapes with positive SAE, low and negative SAE promoted species coexistence, and increased species' habitat breadth. Also, previously there have been ideas that suggest an influence of SAE on the predictability of species assembly in metacommunities (see Holyoak et al. 2005). However, it appears no metacommunity research has tested if SAE alters the predictability of local community composition.

1.4.2. Research Question, Hypotheses, and Predictions

It has long been known that organisms with spatially limited dispersal are more likely to land in optimal environments if there is high positive SAE (Bell et al. 1993). However, as stated earlier, the influence of SAE on the predictability of community composition remains unclear. Recently, SAE was speculated as a potentially important factor governing the importance of stochastic relative to deterministic assembly within the context of plant communities (Karst et al. 2005, Pinto and MacDougall 2010). From this work, stems a prediction: with increasingly positive SAE, plants with spatially limited dispersal capacity will have propagules disperse from parent plants more often

into optimal environments, increasing the importance of deterministic species-environmental sorting relative to stochastic community assembly.

I hypothesized that for metacommunities composed of species with spatially restricted (local) dispersal and differential adaptation to the environmental conditions (niche-differentiated), increasing the degree of positive SAE would increase deterministic species-environmental sorting relative to stochastic community assembly processes. This, in turn, would result in a trend of increasing predictability of local community composition with increasing positive SAE. More specifically, a key driver of the positive trend was hypothesized to be increased landscape connectivity enabling species to assemble deterministically in environmental conditions. For the dispersal control, i.e., spatially unrestricted (global) dispersal, I expected no trend in community composition predictability with increasing positive SAE because propagules would disperse to all environmental conditions regardless of landscape configuration. Neutral metacommunities served as controls for the niche-differentiated metacommunities, and I expected the neutral metacommunities to have the lowest predictability of community composition due to purely stochastic assembly (see Bell 2001, 2005), and to exhibit no trend in community composition predictability with increasing positive SAE.

1.4.3. Overview of Chapters

The goal of my thesis research was to address the following research question: does increasing the degree of positive spatial autocorrelation of the environment in the broader landscape increase the predictability of local community composition?

Chapter 2 is presented in the form of a manuscript, and describes my metacommunity simulation study that was designed to assess the above research question. In addition, there is supplementary material for the manuscript, which includes supplementary simulations and analyses. This additional material examines how the results are influenced by environment evenness, beta diversity resemblance measures, the number of time-steps, and demographic parameter combinations.

Chapter 3 is the conclusion chapter of the thesis. It returns to the goal of the thesis research, puts the research in a broader context, indicates potential significance and applications of the research, discusses research strengths and limitations, gives future research directions, and ends with a statement of the potential contributions of the thesis.

2. DISPERSAL AND SPATIAL-ENVIRONMENTAL STRUCTURE INTERACT TO INFLUENCE LOCAL ENVIRONMENTAL DETERMINISM OF COMMUNITY COMPOSITION

2.1. Introduction

For decades ecologists have sought to understand the key question of why large differences in species composition arise in localities despite these locations having very similar abiotic environmental conditions (Ricklefs 1987, Ricklefs and Schluter 1993, and see Ricklefs 2004 for a historical review). Modeling studies increasingly show that community composition in localities depends on the relative importance of a variety of factors, including: local environmental determinism, stochastic processes, and processes occurring at broader temporal and spatial scales (Chase 2003, Tilman 2004, Gravel et al. 2006, Ruokolainen et al. 2009, Orrock and Watling 2010). Empirical research supports the idea that the higher the strength of local environmental determinism relative to other factors, the higher the predictability of local community composition, i.e., whether particular species compositions will repeatedly be found in localities with particular environmental conditions (e.g., Fukami et al. 2005, Karst et al. 2005, Chase 2007, Chase 2010, Flinn et al. 2010).

Dispersal is an important process influencing community composition because ecological communities are often part of a metacommunity, a set of local communities

connected by dispersal (Leibold et al. 2004, Holyoak et al. 2005). Recent work (e.g., Gravel et al. 2006, Ruokolainen et al. 2009) suggests that dispersal can influence the predictability of local community composition in metacommunities residing in landscapes with heterogeneous environmental conditions. Unpredictable species composition in localities can arise from high dispersal promoting mass-effect, i.e., inferior competitors persisting in suboptimal habitat because of dispersal from optimal habitat (cf. Mouquet and Loreau 2003). Low dispersal can also promote unpredictable local community composition due to dispersal-limitation, i.e., species do not reach optimal habitat (see Tuomisto et al. 2003, Ozinga et al. 2004, Legendre et al. 2005).

Neutral metacommunity models are increasing our understanding of how patterns of local community composition can arise purely due to stochastic dispersal and other stochastic processes (Bell 2001, Bell 2005, Economo and Keitt 2008, Economo and Keitt 2010). Recent work (Economo and Keitt 2008, 2010) indicates that the connectedness of landscape elements influences local community composition by these elements acting as stepping stones that facilitate the movement of species through the metacommunity. Economo and Keitt (2010), for example, show that the composition of local communities became more diverse as communities were more connected throughout the entire landscape. Neutral models have functionally equivalent species, so these models are most relevant to the limiting case where the underlying environmental conditions have no influence on species dynamics.

Species-environmental sorting refers to the predictable assembly of species in localities due to species being differentially adapted to the underlying environmental conditions (Whittaker 1956, Gauch and Whittaker 1972, Austin 1985, Leibold et al.

2004, Foster et al. 2011). Recent work (Driscoll and Lindenmayer 2009, Flinn et al. 2010, Foster et al. 2011) highlights the idea that increasing landscape connectivity, the degree to which the landscape facilitates the movement of organisms (*sensu* Taylor et al. 1993), reduces dispersal limitation, and enables more effective species-environmental sorting. Nevertheless, much remains to be learned about how the spatial configuration of environmental conditions in the broader landscape influences landscape connectivity and the predictability of local community composition.

Spatial autocorrelation of the environment (SAE) is the degree of clustering of similar environments in the broader landscape, with positive SAE meaning that similar environments are clustered (Karst et al. 2005, Holland et al. 2009). Recently, it has been speculated that for plant species with spatially restricted dispersal, landscapes exhibiting positive SAE will foster deterministic community assembly because propagules will disperse from their parent plant into similar optimal environmental conditions (see Karst et al. 2005, Pinto and MacDougall 2010). However, there is need for research that explicitly examines how the degree of positive SAE influences the predictability of community composition. Addressing this question is important for applied and basic ecology: given that ecosystems vary in landscape structure (see Bell et al. 1993, Bridges et al. 2007) it is important to understand whether this structure influences the degree of determinism of community assembly and community composition-environment correlations.

A previous metacommunity modeling study by Palmer (1992) suggested that species-habitat matching increased with increasing SAE. However, this work does not examine how local communities residing in particular localities are influenced by

metacommunity dynamics that are mediated by landscape structure. Economo and Keitt (2010) illustrate with neutral metacommunities the importance of community connectivity on community assembly. However, to my knowledge, no metacommunity studies have examined if changing the spatial configuration of environmental conditions in the landscape influences the importance of deterministic species-environmental sorting relative to stochastic community assembly.

I employed spatially explicit metacommunity simulations to assess the following research question: does increasing the degree of positive SAE in the broader landscape increase the predictability of local community composition? I hypothesized that increasing positive SAE would increase the importance of species-environmental sorting relative to stochastic community assembly processes in metacommunities composed of species with spatially restricted (local) dispersal and differential adaptation to the environmental conditions (niche-differentiated). I expected the shift in strength of species-environmental sorting to result in a positive trend between community composition predictability and the degree of positive SAE.

Because I sought to understand the interaction of local dispersal with spatial-environmental structure, a particular experimental approach was required (Fig. 2.1). First, a uniform distribution of environment amount (Fig. 2.1a) was used to reduce the influence of dominance that can arise with a Gaussian distribution of environmental amount (Gravel et al. 2006), whereby the species best adapted to the most common environmental conditions dominate regionally (Macía and Svenning 2005). Then, the same uniform distribution was spatially configured from a random configuration to high positive SAE (i.e., high clustering of similar environmental conditions), so that only

landscape configuration varied among landscapes; landscape composition remained fixed (Fig. 2.1b). In addition, there was a dispersal control (global dispersal) and a control for niche differentiation (functional equivalence) (Fig. 2.1c). Lastly, I quantified community composition predictability in the same localities (focal sites) of each replicate metacommunity (Fig. 2.1d) to understand how the same localities with the same environments would vary in their local community and environment associations depending on landscape configuration.

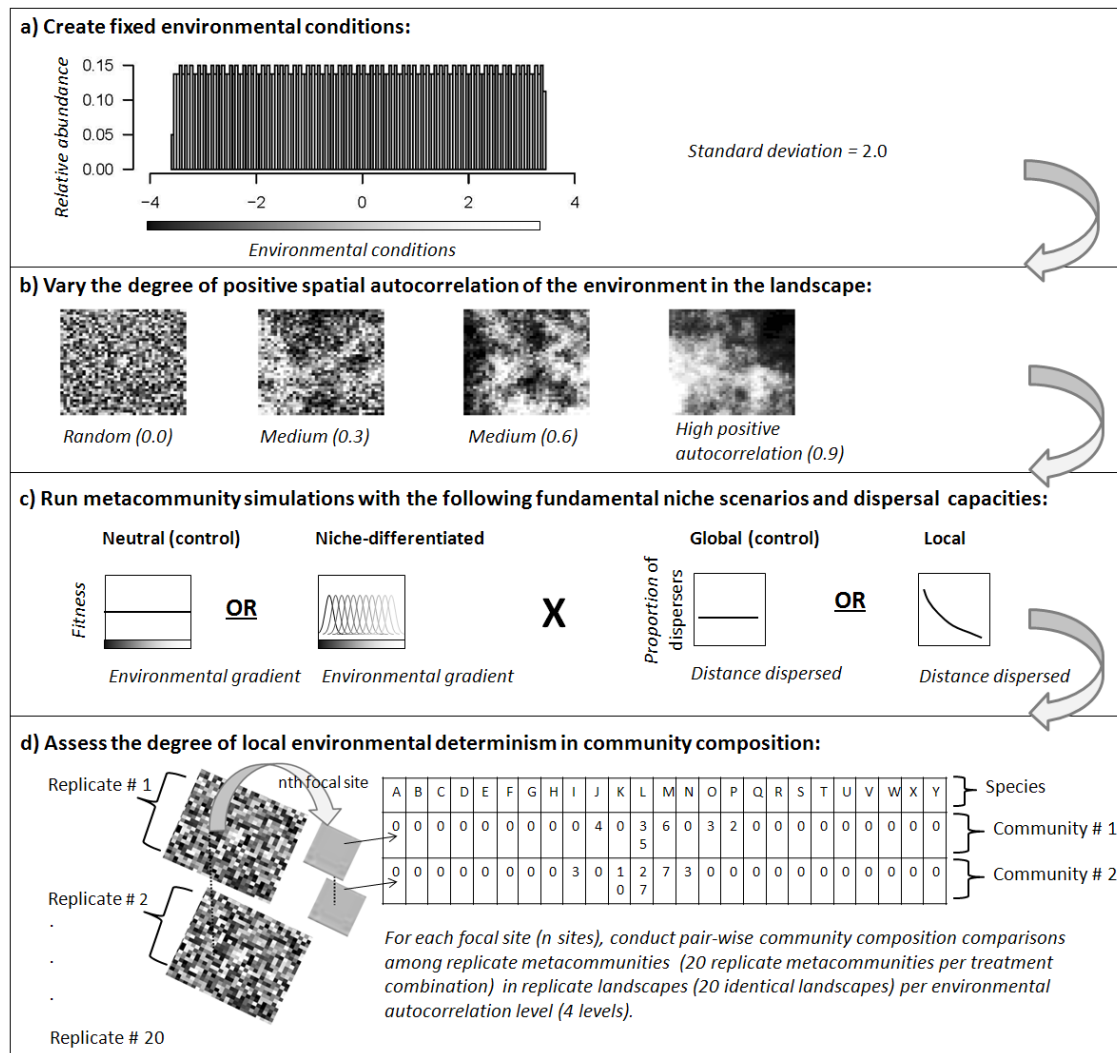


Figure 2.1 Schematic of the experimental approach. Environmental conditions were created (a), and spatially arranged in the landscape (b). Then, replicate metacommunity simulations with the four metacommunity treatments were run on replicate landscapes (c). Following this, community composition predictability was quantified by pair-wise Bray-Curtis similarity (1 - Bray-Curtis) comparisons of focal sites among replicate metacommunities; above, shows one focal site that has an environmental value close to 0 and community composition that varies depending on the replicate metacommunity (d).

2.2. Methods

2.2.1. Simulation Model

My study used a spatially explicit metacommunity simulation model, written in R (R Development Core Team). The bulk of the code was written by Jason Pither, but I made modifications, e.g., for the creation of landscapes, and decisions about parameter values, e.g., number of sampling times. Also, I designed code for using high performance computing on WestGrid's clusters; the cluster code saved at least two years worth of computer processing time. The model generally followed the approach of Bell (2001, 2005), which is appropriate for modeling sessile organisms, such as plants.

Bell's model had (i) all species immigrating at the same rate into the metacommunity, (ii) species only colonizing marginal communities in the metacommunity, and (iii) species undergoing a random walk. Our model modifies these three aspects of Bell's model. First, our model's rate of immigration into the metacommunity was directly proportional to dispersal rates among communities in the metacommunity, with the probability of immigration weighted depending on the metacommunity abundance of the species. Second, the destinations of immigrants depended upon the dispersal capacities of the individuals. We consider these two modifications to more realistically model immigration because our approach assumes the metacommunity is embedded in an area with similar metacommunities. Third, our local dispersal of propagules was governed by a modified Gaussian dispersal kernel (Clark et al. 1999) given by:

$$\text{Prob}(d) = 2pd/v[1+(d^2/v)]^{p+1} \quad (1)$$

where p and v control the shape of the kernel. Prob (d) dictates the distance that propagules disperse from parent organisms; with respect to immigration into the metacommunity, it is the probability that the individuals disperse d communities into the metacommunity. The modification of the dispersal kernel was used to add flexibility of dispersal behavior for future studies.

Below are the steps of the metacommunity simulation routine and the corresponding parameters (see Table 2.1 for a summary). Section numbers are provided for methods that are expanded upon in later sections.

Step 1: Initially, all communities were seeded with K (community carrying capacity) divided by S (number of species in the regional species pool) individuals of each species. When $S > K$, in the sensitivity analyses, communities were seeded with one individual per species. The initial even seeding of communities ensured dispersal limitation was not a factor governing succession at the outset of the simulation (Gravel et al. 2006). The number of communities in a replicate metacommunity was determined by the landscape lattice dimension, L , for a square lattice ($L \times L$); each lattice cell corresponded to an environmental value and a community.

Step 2: After initial seeding, emigration and immigration occurred. In time-step $t-1$, the number of emigrant propagules (propagules that dispersed out of the metacommunity) was enumerated. This number of individuals, but not necessarily the same species, immigrated in time-step t . The probability that an individual of a given species immigrated at time t was weighted by the given species' total abundance in the metacommunity at time-step $t-1$. In the event of spatially unlimited (global) dispersal, immigrants colonized the metacommunity cells at random. On the other hand, in the

presence of spatially limited (local) dispersal, immigrants colonized d lattice units (L) inwards from the edge of the metacommunity (Equation 1 and Section 2.2.2.3). Thus, most immigrants with local dispersal colonized communities near the edge of the landscapes, but some colonized further inwards.

Step 3: Following immigration, individuals in the metacommunity produced propagules at a probability of b (per capita birth rate).

Step 4: These propagules dispersed throughout the landscape with the probability u (per capita dispersal rate), which was the same for global and local dispersal (Section 2.2.2.3).

Step 5: Then, individuals died at a probability of z (per capita death rate).

Step 6: Next, in the culling stage, if K was exceeded, individuals were culled at random in the neutral scenario (Section 2.2.2.2) until the community size, K , was reached. On the other hand, for the niche-differentiated scenario, the culling step was the stage where niche differences came into play, according to an environmental (niche) response function (Equation 2 and Section 2.2.2.2).

Step 7: Finally, if a species had zero abundance in the metacommunity at time-step $t-1$, a single individual of that species immigrated in time-step t with a probability of q (rescue effect); this modeled the small probability that immigrants from populations elsewhere in the region could rescue locally extinct species in the metacommunity.

While **Step 1** only occurred once in a simulation run (initial seeding), **Steps 2 to 7** were repeated for each additional time-step. Depending on the situation, a maximum of 500 or 2000 time-steps after the initial seeding were run. This meant that simulations

ended at 501 and 2001 time-steps; this number of time-steps parallels the number used by other simulation studies (e.g., Gravel et al. 2006, Ruokolainen et al. 2009).

Table 2.1 Summary of the metacommunity simulation routine and parameters.

Step	Event	Parameters involved at event
1	Initial seeding of each community in a metacommunity	K (carrying capacity, the number of individuals in a community) S (regional species richness) L (landscape dimension for an $L \times L$ square lattice)
2	Immigration (emigration) occurs	u (per capita dispersal rate) d (dispersal distance; for local dispersal only) p, v (determine shape of the dispersal kernel; for local dispersal only) L
3	Individuals produce propagules	b (per capita birth rate)
4	Propagules disperse	u d p, v L
5	Individuals die	z (per capita death rate)
6	Culling stage (competition occurs)	K (carrying capacity; in communities where exceeded, culling occurs) λ (probability of surviving culling; function of E, μ, σ) E (species-specific environmental value; for the niche-differentiated scenario) μ (species-specific fundamental niche optimum; for the niche-differentiated scenario) σ (niche width; for the niche-differentiated scenario)
7	Rescue effect	q (rescue effect; may occur if a species goes extinct)

2.2.2. Experimental Design

The experimental design fully crossed the following treatments: (i) degree of positive SAE, (ii) fundamental niche scenario, and (iii) propagule dispersal capacity. There were 20 replicate metacommunities per treatment combination, resulting in 320 simulations for the main experiment. Additional simulations were performed to assess the sensitivity of the results to the following: the amount of optimal abiotic environmental conditions per species (henceforth, referred to as *environment amount*), beta diversity resemblance measures, time-steps, and demographic parameters (Supplementary material).

2.2.2.1. Degree of Positive Spatial Autocorrelation of the Environment

This research used continuous variation (Büchi et al. 2009) of environmental conditions along a single niche axis, a simplification used by other modeling studies (e.g., Palmer 1992, Tilman 2004, Bell 2005, Gravel et al. 2006, Vellend 2008, Ruokolainen et al. 2009). The arrangement of the environmental conditions was varied from a random configuration to high positive SAE (Fig. 2.1b), and was created with a Gaussian random field using a fractal model (“fractal B” model of the GaussRF function, Schlather 2009). The rationale for creating fractal-like landscapes is described at length by Palmer (1992). As a result of using GaussRF, the initial landscapes had environment amount following a Gaussian frequency distribution. In other words, the environmental conditions similar to the mean conditions were very abundant, and environmental

conditions farther away from the mean were in lower abundance. To avoid the influence of oligarchic dominance that would arise with a Gaussian distribution (Gravel et al. 2006), the spatially configured environmental conditions were replaced with environmental conditions from a uniform frequency distribution. To ensure that only landscape configuration was modified, the same uniform distribution (this kept landscape composition constant) was used for all SAE levels.

After replacing the environmental conditions, the SAE was quantified using a moving window function. Under the local dispersal scenario, each propagule generally dispersed from its natal site to one of the 8 surrounding neighbor sites. Thus, to calculate SAE, a 3 x 3 moving window function was used. This function cycled through each site in the landscape (landscape edges were not used; this resulted in 1521 sites) and calculated the variance in environmental conditions of all the neighbor sites compared to each central site. Larger moving windows (taking long distance dispersal into account) ranked the landscapes in the same order as the 3 x 3 window analysis. Then, the mean of all the neighbor variances was calculated to obtain the raw variance value. To standardize the variance measure, the raw variance value was divided by the maximum variance value (corresponding to the random landscape raw variance value), and this ratio was subtracted from one, i.e., $1 - (\text{raw variance}) / (\text{maximum raw variance})$.

2.2.2.2. Fundamental Niche Scenario

Metacommunities had species following either a niche-differentiated or neutral fundamental niche scenario. The probability (λ) that individuals in the niche-differentiated scenario survived culling (Step 6 in Table 2.1) in communities was

determined by a weighted lottery. The weighting factor was the product of the species-specific environmental condition value (E) and the relative abundance of the species for each community. The Gaussian environmental response (niche) function used to model niche-differentiated survival probabilities was:

$$\lambda(E) = \exp[-(E-\mu_i)^2 / 2\sigma^2] \quad (2)$$

The positions of species' fundamental environmental optima ($\mu_1, \mu_2, \dots \mu_S$) corresponded to the 1st to the S^{th} percentiles of the environmental conditions (Gravel et al. 2006), S being the number of species in the regional species pool (25 species at initial seeding, Step 1 in Table 2.1). Species' niche widths, governed by σ (Equation 2 above), were set to 0.75 times the standard deviation of the environmental conditions. Gaussian response functions are commonly used for the fundamental niches of niche-differentiated species in simulation studies (e.g., Palmer 1992, Gravel et al. 2006, Ruokolainen et al. 2009). These functions give the “middle species” more optimal environmental conditions if a Gaussian frequency distribution of environmental conditions is used (see Palmer 1992). In contrast to the niche-differentiated scenario, the neutral scenario had all the species' niche functions are assigned the value of 1. As a result, under the neutral scenario, the probability of surviving culling in a community was based only on the relative abundance of species in the community. In other words, for the neutral scenario, there were no species-specific differences corresponding to different environmental conditions.

2.2.2.3. Propagule Dispersal Capacity

The simulations had two propagule dispersal capacities: spatially limited (local) dispersal and spatially unlimited (global) dispersal. The distance dispersed by the

propagules with local dispersal was governed by a modified Gaussian dispersal kernel (Clark et al. 1999; refer to Equation 1). The parameter values used within the dispersal kernel (see Table 2.2) generally resulted in each propagule colonizing communities adjacent to the community of the parent organism, but propagules could disperse a maximum distance of 7 communities. The dispersal kernel with these parameter values also yielded the frequency that propagules dispersed (rate of dispersal, u , see Table 2.1 and Table 2.2). The same rate of dispersal was used for global dispersal. Also, both local and global dispersal scenarios had the direction of propagule dispersal chosen at random. However, unlike with local dispersal, the distance of globally dispersed propagules was not dictated by a dispersal kernel, so propagules could potentially disperse anywhere in the landscape. In addition to inter-community dispersal (Step 4, Table 2.1), immigration and emigration (Step 2, Table 2.1) were dictated by dispersal capacity. The per capita immigration and emigration rates under the local and global dispersal scenarios differed; rates were lower for metacommunities with local dispersal than with global dispersal. The realized immigration and emigration rates were similar to the rates explored in other simulation studies (e.g., Bell 2005).

2.2.3. Sampling the Metacommunity

For each replicate metacommunity, I censused the communities located in the central 26 x 26 sites (676 sites) of the 40 x 40 lattice landscape. Avoiding the outer 7 communities reduced the potential impact of edge effects that could arise due to spatially random immigration into the metacommunity. A subset of the 676 central communities was selected for subsequent analyses, with the criterion being that the local

environmental conditions were not extreme, i.e., not less than or equal to -1.5, or greater than or equal to 1.5. This exclusion of extreme values avoided the potential confound of there being fewer species tolerant of extreme conditions; a potential problem arising because of the nature of the distinct preference fundamental niche model that was used (cf. Gravel et al. 2006).

2.2.4. Community Composition Predictability

To evaluate community composition predictability, I used the ‘vegan’ package in R (Oksanen et al. 2010), and code I wrote, to calculate among-replicate Bray-Curtis similarity (1 - Bray Curtis). This involved Bray-Curtis similarity comparisons of each focal site for each experimental treatment combination (a focal site is illustrated in Fig. 2.1d; there were n number of focal sites per metacommunity). Given 20 replicates, there were 190 pair-wise Bray-Curtis similarity comparisons per focal site. The mean of the 190 values was calculated for each focal site, resulting in the means for each experimental treatment combination. Bray-Curtis similarity values range between a minimum value of 0 (least predictable community composition) and a maximum value of 1 (most predictable community composition). Bray-Curtis similarity values approaching 1 indicated a high importance of deterministic relative to stochastic community assembly, or high community composition predictability.

I used Bray-Curtis similarity for the following reasons: it quantifies similarity of community composition based on species identity and abundance, it is commonly used for comparing community composition (see Anderson et al. 2010), and it has been used to assess among-replicate community similarity (e.g., Ruokolainen et al. 2009). Because

Bray-Curtis is sensitive to differences in alpha diversity, I also tested my results using measures that have been argued to be less dependent on alpha diversity. These were the numbers equivalents of Shannon beta diversity (see Jost 2007; for this measure I used the R package ‘vegetarian’ by Charney and Record 2010), and Morisita Horn similarity (Wolda 1981, 1 - Morisita-Horn, which I calculated with the R package ‘vegan’). These measures had trends similar those with Bray-Curtis similarity (Supplementary material).

2.2.5. Parameter Values and Analyses for Main Results and Supplementary Material

Table 2.2 gives the parameter values and analyses used for the simulations. See the simulation model section (Section 2.2.1) for further details on these parameters. In addition to the main experiment, the parameters and analyses used for additional simulations are provided (Supplementary material).

Table 2.2 Overview of model parameters for the main experiment and sensitivity analyses.

Simulation	Model parameters											Beta diversity resemblance measure	Maximum time-steps (reported)	Environment evenness
	S	K	L	u	d	p	v	b	z	q	σ			
Main results	25	50	40	0.1	1-7	6.5	5.225	0.5	0.3	0.1	0.75	1-Bray-Curtis	2001 (501)	High (Uniform distribution)
Supplementary material A	25	50, 500	40	0.1	1-7	6.5	5.225	0.5	0.3	0.1	0.75	1-Bray-Curtis	2001 (501)	Low (Gaussian distribution), High
Supplementary material B	25	50	40	0.1	1-7	6.5	5.225	0.5	0.3	0.1	0.75	1-Bray-Curtis, Numbers equivalents of Shannon beta diversity, 1-Jaccard, 1-Morisita Horn	2001 (1, 501, 2001)	High
Supplementary material C*	25	11-422	40	0.1	1-7	6.5	5.225	0.07 - 0.96	0.02 - 0.50	0.1	0.75	1-Bray-Curtis	501	High

*Provided here are the maximum and minimum values for the 19 sensitivity analyses that varied K , b , and z . See Bell (2005) for more details on the sensitivity analysis procedure.

N.B., This table only provides a brief summary; see Methods and Supplementary material sections for more details.

2.3. Results

Community composition predictability increased with increasing positive SAE when there was niche differentiation and local dispersal (Fig. 2.2d). In contrast, there was no affect in the absence of either spatially-restricted dispersal or niche differentiation (Fig. 2.2a-c). The pattern of increasing community predictability with increasing positive SAE was robust to variation in methods, generally occurring even when there was low environment evenness (Supplementary material A), different beta diversity resemblance measures (Supplementary material B), and various demographic parameter combinations (Supplementary material C). The positive relationship occurred early in succession, i.e., by 501 time-steps (Fig. 2.2d), and was evident at later time-steps, e.g., 2001 (Supplementary material B). Figure 2.3 plots the same values as Figure 2.2., but is included to illustrate how community composition predictability values varied in relation to the environmental conditions.

Additional findings are notable. First, the niche-differentiated and global dispersal scenario exhibited an intermediate level of community composition predictability compared to the niche-differentiated and local dispersal scenario (Fig. 2.2b). Second, neutral communities consistently exhibited the lowest community composition predictability (Fig. 2.2a, c, Supplementary material). Third, variation in Bray-Curtis values was generally much greater in magnitude for the niche-differentiated plus local dispersal scenario as compared to the other experimental treatment scenarios (compare the spread of the box plots among panels of Fig. 2.2).

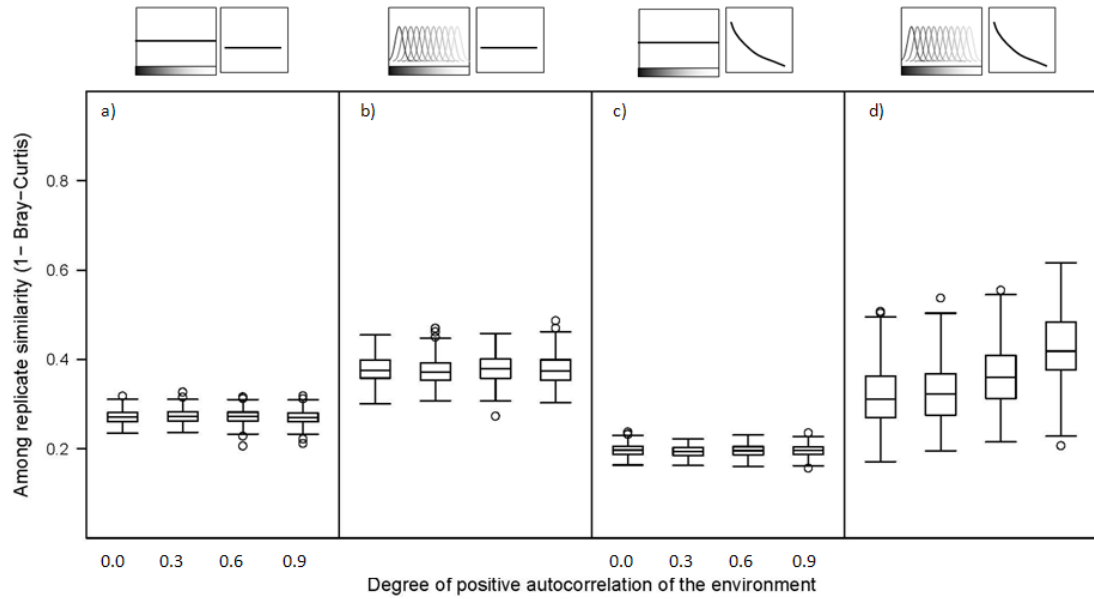


Figure 2.2 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment. Illustrated are box plots for the means of among-replicate similarity for neutral and global dispersal (a), niche-differentiated and global dispersal (b), neutral and local dispersal (c), and niche-differentiated and local dispersal (d). The results in each box plot are for the mean among-replicate similarity of the inner census with environmental condition values between -1.5 to 1.5. Each mean was calculated for each focal site by averaging among-replicate pair-wise comparisons (190 comparisons, given 20 replicate metacommunities). The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.6) to high positive spatial autocorrelation of the environment (0.9) as calculated using standardized environmental variance. This plot is at 501 time-steps.

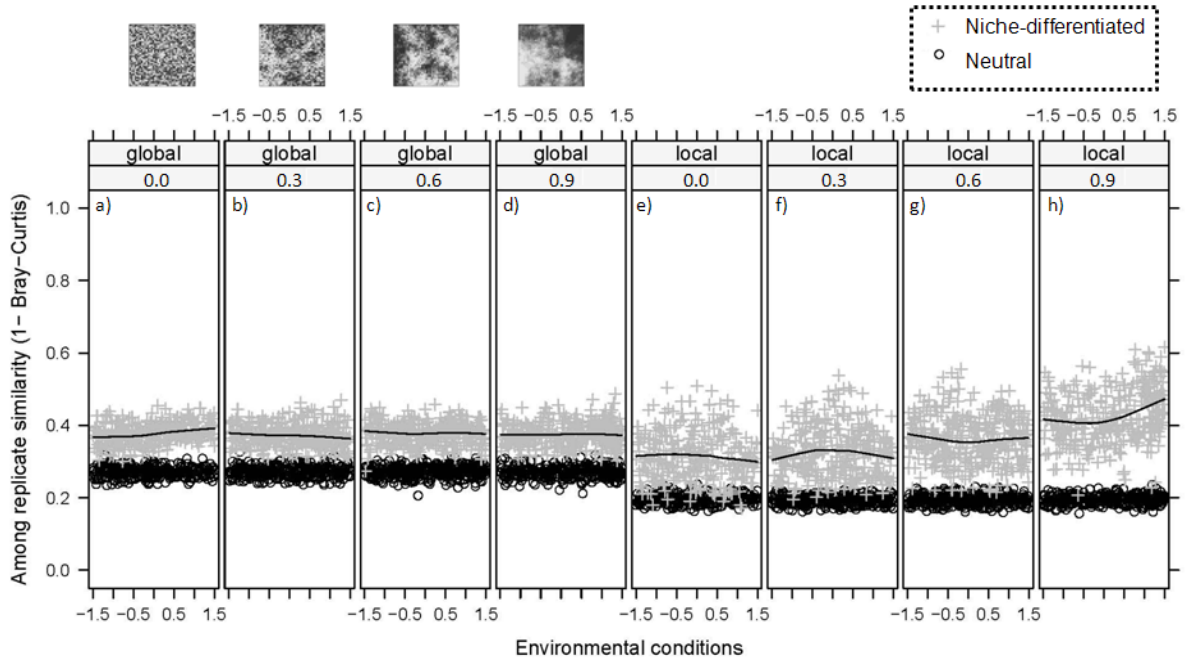


Figure 2.3 Among-replicate similarity (community composition predictability) at the same interval of environmental conditions. Illustrated are scatter plots for the means of among-replicate similarity for global dispersal (a-d), and local dispersal (e-h). Grey crosses show among-replicate similarity when the metacommunity has niche-differentiation, and black circles are for neutral metacommunities. The trend lines are locally weighted smoother lines. The results in each panel are for the mean among-replicate similarity of the inner census with environmental condition values between -1.5 to 1.5. Each mean was calculated for each focal site by averaging among-replicate pairwise comparisons (190 comparisons, given 20 replicate metacommunities). The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.6) to high positive spatial autocorrelation of the environment (0.9) as calculated using standardized environmental variance. This plot is at 501 time-steps.

2.4. Discussion

2.4.1. Take Home Message

This study highlights that the interaction of dispersal and the spatial configuration of the environmental conditions in the landscape can influence whether species composition is highly predictable in localities with similar environmental conditions. Specifically, this research shows that in the presence of both niche differentiation and local dispersal, community composition predictability increases with increasing positive SAE (Fig. 2.2d, Fig. 2.3e-h, Supplementary material).

2.4.2. Processes that Drive Community Composition Predictability

The increase in community composition predictability with increasing SAE (Fig. 2.2d, Fig. 2.3e-h, Supplementary material) can be attributed to increased landscape connectivity. Initially, species were seeded into all environmental conditions (see Step 1 of Methods). This ensured that priority effects, which arise due to initial colonization events, did not occur in the simulations. The degree to which offspring spread over generations from local communities into optimal environmental conditions in the broader landscape can be attributed to landscape facilitated movement: with increasing positive SAE, the landscape had more connected “stepping-stones” of optimal environmental conditions that would better facilitate across generation landscape-level dispersal. With increased landscape connectivity, species would more likely build up larger population sizes in their optimal environmental conditions, and subsequently there would be an

increased importance of deterministic species-environmental sorting (via differential survival probabilities; see Equation 2 of the Methods) relative to stochastic community assembly processes.

Various stochastic community assembly processes would have changed in strength with variation in SAE. To illustrate this, let us assume positive SAE in the landscape is the “norm,” which appears to be the case in many kinds of study systems (see Bell 1992, Bell et al. 1993, Bridges et al. 2007). First, with decreasing positive SAE, local stochastic extinction would increase. With decreasing positive SAE, optimal environmental conditions for each species would be more fragmented, and species would have had smaller populations because propagules were not be able to land in optimal environmental conditions as often. Thus, these smaller populations would have been prone to high rates of local stochastic extinction (Keitt 2003), producing more unpredictable local community composition than larger populations residing in landscapes with higher positive SAE. Second, mass-effect would have increased in prevalence with decreasing positive SAE; mass-effect involves the dispersal of species into suboptimal environmental conditions from optimal environmental conditions (Mouquet and Loreau 2003). Increased mass-effect would have decreased community composition predictability. Third, the action of demographic stochasticity very early on in succession, before large populations of species could arise, may have resulted in superior competitors being replaced by inferior competitors, subsequently leading to communities with higher abundances of inferior species than expected in later time-steps.

Given the local dispersal of propagules, local communities would have been constantly influenced by neighbor spill-over from its immediate neighbors (8 surrounding

communities). Neighbor spill-over in this situation is akin to matrix-to-patch edge effects described in habitat fragmentation studies (e.g., Davies et al. 2001), whereby the immigration of species from surrounding locations (matrix) influence the community composition of a local patch. With increasing positive SAE, on average, each local community would have resided in an environment that was on average more similar to the environmental conditions of its immediate neighbors, and this would have increased the likelihood that neighbor spill-over provided species that were well adapted to the environment in which each local community resided. Thus, with increasing positive SAE, neighbor spill-over would have increased the likelihood of deterministic species-environmental sorting relative to stochastic mass-effects. Compared to the other landscapes, in the random landscape, neighbor spill-over would have obscured composition-environment relationships the most via a local mass-effect.

In addition to the main effects of SAE, additional findings are noteworthy. First, the finding that global dispersal was an intermediate level of predictability (Fig 2.2b) can be explained with the results of Keitt's (2003) metapopulation model study that examined spatial autocorrelation of a suitable habitat, dispersal, and the maintenance of source-sink populations. Keitt found that passive long distance dispersal resulted in individuals often ending up in sink habitats, and thus gave rise to a low viability of populations. Translating this to the multiple species of my simulations, global dispersal prevented species from maintaining large population sizes — essentially dispersal into sinks consumed propagules — and thus increased local stochastic extinction, resulting in an intermediate level of community composition predictability. Second, the neutral community scenarios had the lowest community composition predictability due to the

composition of neutral communities arising from purely stochastic assembly processes (see Bell 2001, 2005), which would have produced low community composition predictability. Third, there was generally a greater magnitude of variation in Bray-Curtis values for the niche-differentiated plus local dispersal scenario in comparison to the other experimental treatment scenarios. Greater variability of this sort was found in a previous study that varied temporal autocorrelation (Ruokolainen et al. 2009). Such a result could be because the small-scale clustering of environmental conditions was not the same throughout a landscape, which would affect neighbor spill-over. Focal sites surrounded by more similar environmental conditions would have had neighbor spill-over that promoted more deterministic species-environmental sorting.

2.4.3. Composition-Environment Relationships Across Ecosystems

Different ecosystems vary in their spatial-environmental structure. Much research has focused on measuring spatial structure within ecosystems (e.g., Lechowicz and Bell 1991, Schlesinger et al. 1996, Robertson et al. 1997, Richard et al. 2000, Stoyan et al. 2000, Bekele and Hudnall 2006), but a comprehensive comparison of SAE among ecosystems that accounts for potential confounding factors (such as grain size and sampling effort) appears to be lacking. Given that inherent spatial structure of the environment varies among ecosystems (e.g., see Bell et al. 1993, Bridges et al. 2007), my research results can be generalized to the following prediction that appears untested: ecosystems with high positive SAE will have more predictable composition-environment relationships than ecosystems with less clustering of similar environmental conditions.

Experiments (field, simulation, and microcosm) and data mining of online databases (to do the aforementioned comprehensive comparison) can be used to assess this prediction. Furthermore, given my results, practitioners should keep in mind that the reliability of composition-environment correlations as tools for management (see Legendre 2005) might change depending upon the spatial attributes of the ecosystem of interest; these predictive tools may perform best in ecosystems with high positive SAE.

2.4.4. The Deterministic-Stochastic Community

Assembly Continuum

Communities are thought to lie along a deterministic-stochastic community assembly continuum, with niche and neutral models representing the extremes of this continuum (Gravel et al. 2006, Leibold and McPeck 2006, Cadotte 2007, Adler et al. 2007, Mutshinda et al. 2011). Understanding what influences where a community lies on this continuum is of key interest to ecologists studying plant community assembly. Ecologists often predict that plant species with spatially restricted dispersal capacity will, due to dispersal-limitation, assemble more stochastically in localities than plants with spatially unrestricted dispersal (see Tuomisto et al. 2003). However, species with spatially restricted dispersal capacities can also be predicted to deterministically sort if there is spatial clustering of similar environmental conditions because propagules encounter favorable environments nearby the parent plants (see Karst et al. 2005). My work illustrates that, all else being equal, the degree to which plant communities assemble stochastically in a particular locality is influenced by the interaction of dispersal with the spatial configuration of the environmental conditions in the broader landscape.

Practitioners would benefit from a better understanding the factors driving where communities lie along the deterministic-stochastic community assembly continuum because biodiversity conservation, ecosystem management, and ecological restoration decisions need to be tailored depending on the role of stochastic relative to deterministic community assembly (Legendre et al. 2005). My work highlights a key point that is often disregarded in field surveys conducted for management and conservation: even if representative environments are present, their spatial configuration can influence the predictability of community composition. If variation in SAE influences the predictability of community composition, then it is important for restoration workers to assess SAE when conducting risk-assessment surveys, and developing restoration plans designed to restore particular assemblages of plant species. My work also raises the concern that conducting reference environmental assessments without taking into consideration environmental configuration has the potential to lead to erroneous conservation planning. For example, if representative environments are present, then it might be assumed that predictable assemblages will arise, but if these representative environments are arranged in a random fashion — such that community assembly in the landscape is highly stochastic — taking measures to increase the movement of organisms among optimal habitat would be a better conservation strategy than solely protecting particular environmental conditions.

2.4.5. Conclusion

This study suggests that the degree of positive SAE in the landscape influences landscape connectivity, and other processes, and subsequently influences the

predictability of plant community composition. Given the results and that ecologists rarely study the influence of landscape geometry on plant community patterns and processes (see Dufour et al. 2006, McGlinn and Palmer 2011), I suggest ecologists should increasingly investigate the role of SAE on plant community patterns and processes. While ecologists often design sampling strategies to remove the effect of SAE (see Legendre et al. 2002), or use statistical methods that may not properly account for the ecological influence of SAE (Gilbert and Bennett 2010), statistical methods (see Keitt et al. 2002) and sampling strategies can be employed to quantify the unique influence of SAE on plant communities.

2.5. Supplementary Material

The supplementary material gives the results of additional simulations and analyses that complement the main experiment. The additional analyses use 50 sites randomly sampled in the inner 26 x 26 cells of the landscape. I used this type of sampling because it mimics common field approaches. Also, sampling the inner census between environmental values -1.5 and 1.5 gave results similar to the 50 site sampling. As well, note that time-step one is after a round of weighted lottery culling, which reduces the among-community similarity below 1.0 (Supplementary material B). The additional simulations were run using high performance computing on the WestGrid clusters, and on the UBCO SARAHS cluster.

2.5.1. Supplementary Material A: Environment Evenness

In nature, it is well known that the abundance of environmental conditions is unlikely to follow a uniform distribution. Instead, some environmental conditions will be

in higher abundance than others. Similarly, some species will have more optimal environmental conditions than the other species (low environment evenness).

Given that low environment evenness increases community composition predictability (see Gravel et al. 2006), it is important to see if SAE can still play a noticeable role in landscapes with low environment evenness. To this end, I ran simulation experiments similar to the main experiment, but with environment amount following a Gaussian frequency distribution (low environment evenness) rather than a uniform distribution (high environment evenness). The Gaussian distribution of environmental conditions was overlain on the same landscapes as the uniform distribution, creating a very similar pattern of SAE.

I examined composition predictability for the following: (i) low environment evenness, (ii) high versus low environment evenness for the niche-differentiated and local dispersal scenario, and (iii) high versus low environment evenness given higher average species richness in local communities. The third investigation was conducted because the main analyses showed a low average species richness in local communities for the niche-differentiated and local dispersal scenario (generally 3-6 species) at 501 and 2001 time-steps, so simulations were run that created communities with higher levels of species richness late in succession (generally 9-16 species). Higher richness is more realistic for understanding communities. However, these simulations increased processing time, so a limited number were run.

2.5.1.1. Results

Despite low habitat evenness, when positive SAE increased, community composition predictability increased for the niche-differentiated and local dispersal scenario (Fig. 2.4 -2.7). In general, the supplementary results were similar to the main results (Fig. 2.2 and Fig. 2.3e-h). However, the community composition predictability values were generally higher for the low environment evenness, i.e., shifted upward along the y-axis.

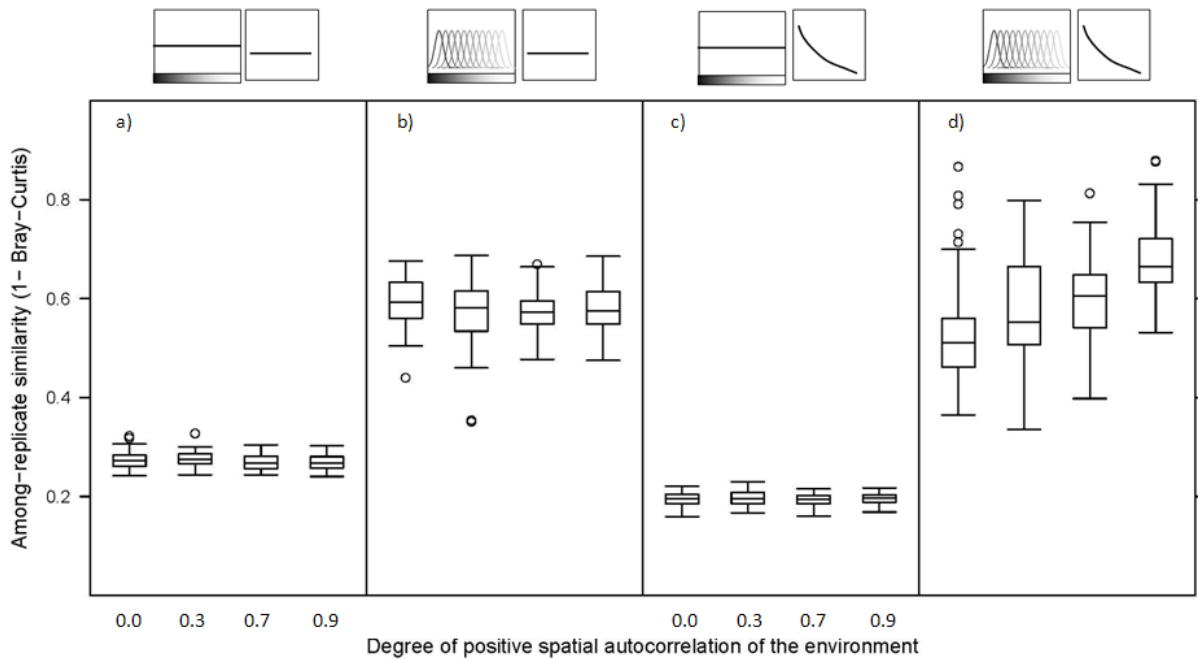


Figure 2.4 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment and low environment evenness. Illustrated are box plots for the means of among-replicate similarity for neutral and global dispersal (a), niche-differentiated and global dispersal (b), neutral and local dispersal (c), and niche-differentiated and local dispersal (d). The results in each box plot are for the mean among-replicate similarity of each focal site (n=50 focal site means). Each mean was calculated for each focal site by averaging among-replicate pair-wise comparisons (190 comparisons, given 20 replicate metacommunities). The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.7) to high autocorrelation (0.9) as calculated using standardized environmental variance. This plot is at 501 time-steps.

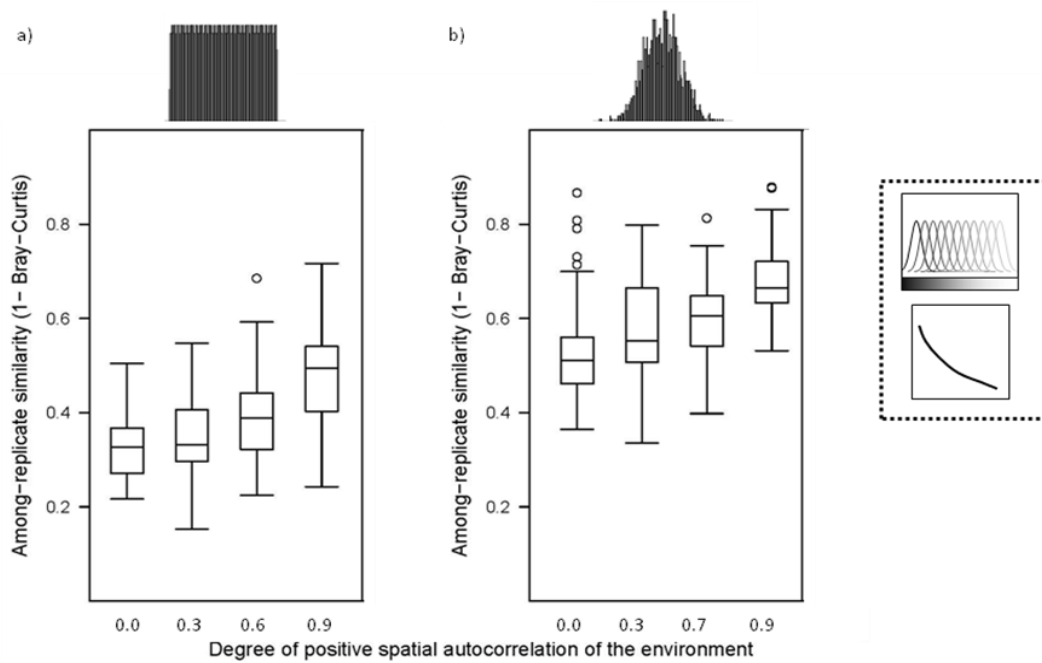
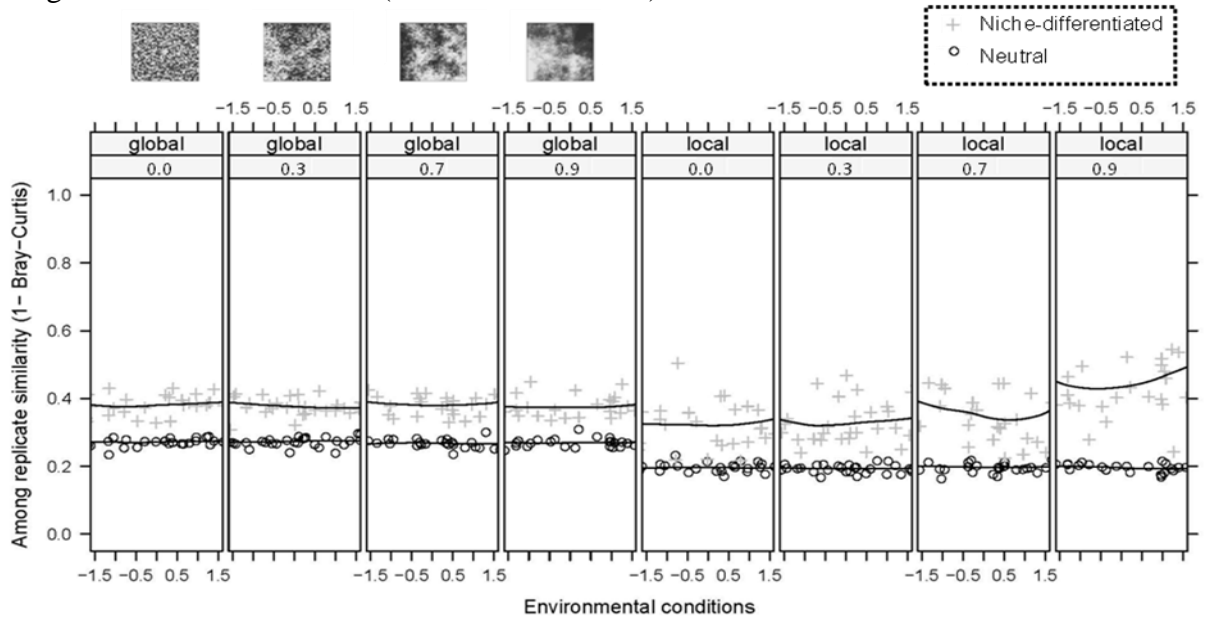


Figure 2.5 A comparison of the results given high and low environment evenness. Panel (a) is high environment and panel (b) is low evenness. Box plots are for the means of among-replicate similarity for the focal sites ($n=50$) in metacommunities with niche-differentiation and local dispersal. Means were calculated for each focal site by averaging among-replicate pair-wise comparisons ($n=190$). The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.6 or 0.7) to high autocorrelation (0.9). This plot is at 501 time-steps.

i) High environment evenness (uniform distribution)



ii) Low environment evenness (Gaussian distribution)

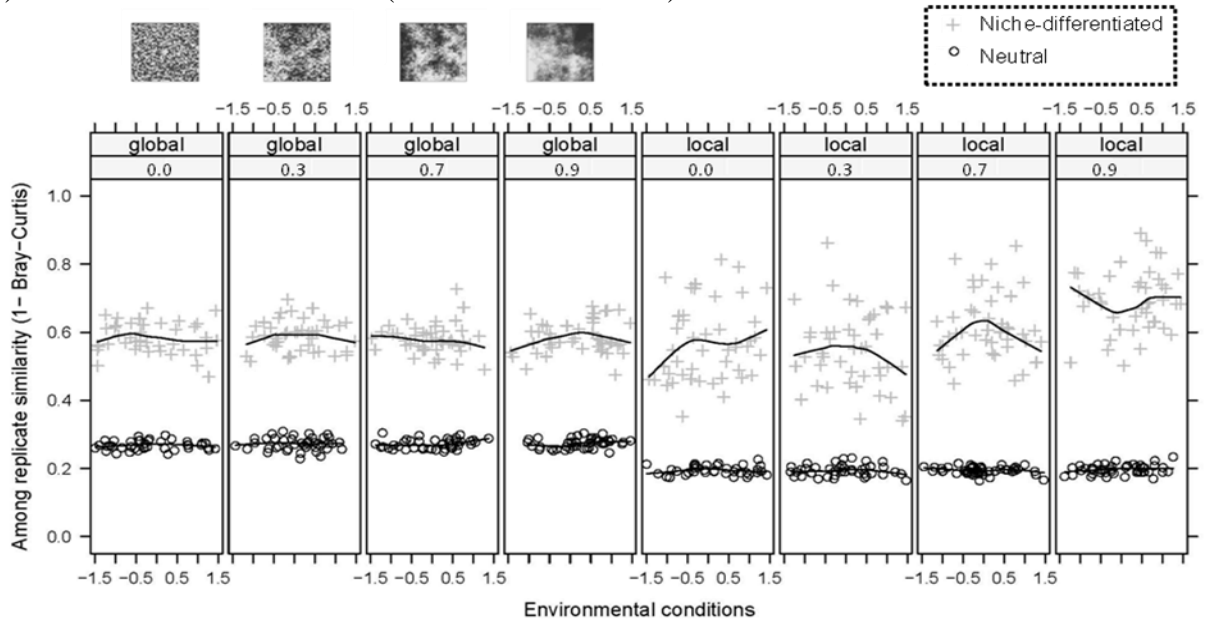


Figure 2.6 Among-replicate similarity (community composition predictability) at the same interval of environmental conditions given high and low environment evenness. Box plots are for the means of among-replicate similarity for the focal sites ($n=50$) in metacommunities with niche differentiation and local dispersal. Means were calculated for each focal site by averaging among-replicate pair-wise comparisons ($n=190$). Illustrated is high (i) and low (ii) environment evenness. The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.6 or 0.7) to high autocorrelation (0.9). This plot is at 501 time-steps.

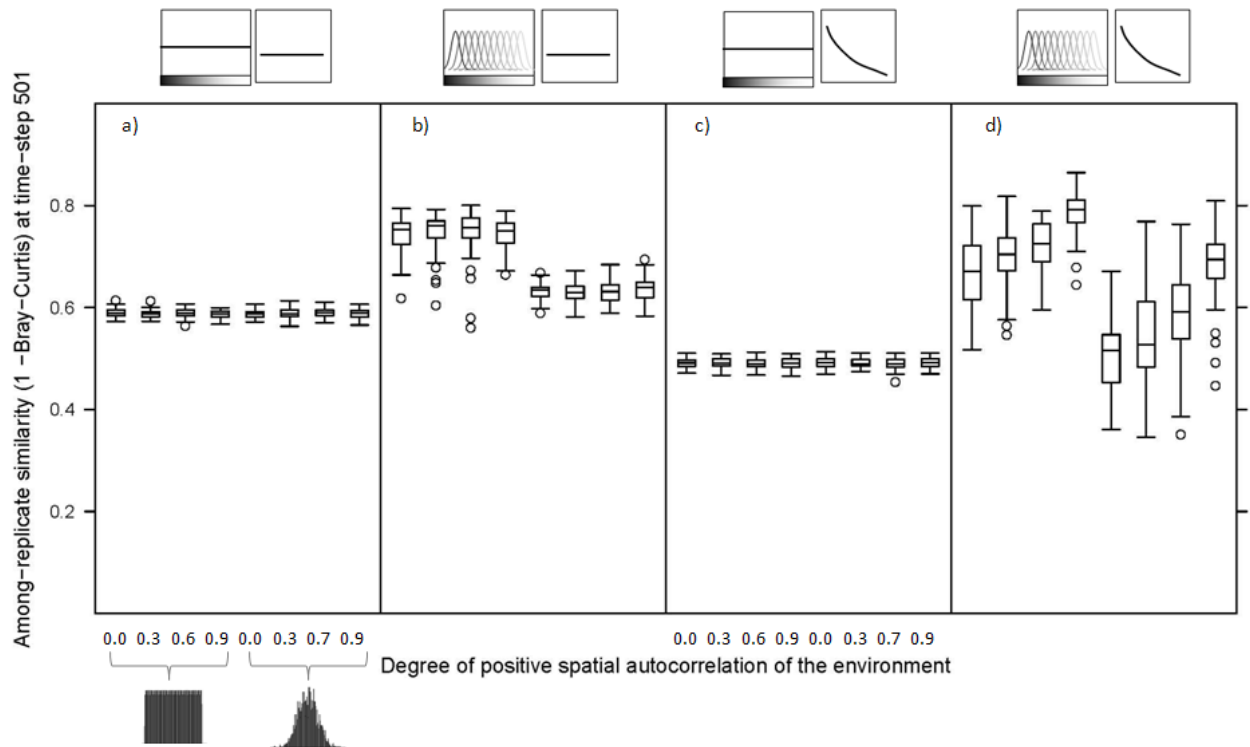


Figure 2.7 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment for higher local richness. For these simulations, the initial community carrying capacity (K) was 500, and the regional species pool (S) was 50. Box plots are of among-replicate similarity for the neutral and global dispersal (a), niche-differentiated and global dispersal (b), neutral and local dispersal (c), and niche-differentiated and local dispersal (d). The results in each box plot are for the mean among-replicate similarity of each focal site ($n=50$ focal site means). Each mean was calculated for each focal site by averaging among-replicate pairwise comparisons ($n=190$ comparisons). The first four plots in each panel are for high environment evenness, while the second set of plots is for low environment evenness. The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.6) to high autocorrelation (0.9) as calculated using standardized environmental variance. This plot is at 501 time-steps.

2.5.1.2. Discussion

There is debate about the relative importance of the spatial configuration versus environment amount as drivers of community assembly (Collinge 2009). My results support the notion that environment configuration can be an important factor influencing community assembly despite the influence of environment amount (see Krawchuk and

Taylor 2003). Indeed, the findings show that despite low environment evenness, there was still a detectable effect of increasing positive SAE on community composition predictability (Fig. 2.4d, Fig. 2.5b, Fig. 2.6, and Fig. 2.7).

Above a certain threshold of environment amount (see Flather and Bevers 2002) environment configuration will play an insignificant role in influencing community assembly. Predicting the presence of such a threshold will require understanding the scale at which organisms disperse and integrate environmental variables relative to the underlying environment configuration. Additional simulations suggested that the degree of fundamental niche-overlap will also influence this threshold: with decreasing niche width, the relationship between community composition predictability and the degree of positive SAE was more blurred for low compared to high environment evenness (data not shown).

This blurring arises because when niche width decreases, the degree of environment specialization increases, which increases the impact of oligarchic dominance (Macía and Svenning 2005) when there is low environment evenness (Gravel et al. 2006). In other words, when niche-specialization increases, species with the most optimal environment will tend to deterministically out-compete other species, which reduces the influence of SAE. Oligarchic dominance also led to the upward shift in the y-values for low environment evenness for the niche-differentiated and local dispersal scenario (Fig. 2.5b), and for the niche-differentiated and global dispersal scenario (Fig. 2.6 and Fig. 2.7).

2.5.2. Supplementary Material B: Beta Diversity

Measures and Time-Steps

I examined the sensitivity of my results to different beta diversity resemblance measures and time-steps because these different factors can influence among-replicate community similarity (Ruokolainen et al. 2009). The focus was on changes in composition due to relative abundance rather than presence/absence. However, 1-Jaccard (a presence/absence beta diversity resemblance measure) was included because ecological studies often use presence/absence data, and it has been used to assess stochastic versus deterministic assembly (Ruokolainen et al. 2009). The other measures consider abundance in the pair-wise comparison of community composition (Anderson et al. 2010). Morisita-Horn (Wolda 1981) and number equivalents (Jost 2007) have been argued to be less sensitive to alpha diversity. Plots were examined for time-steps 1, 501, and 2001 for Bray-Curtis similarity (1 - Bray-Curtis), Shannon beta diversity numbers equivalents, Jaccard similarity (1 - Jaccard), and Morisita-Horn similarity (1 - Morisita-Horn). Simulations were not run past 2001 time-steps because it was assumed pseudo-equilibrium had occurred; the same trend occurred much earlier (e.g., 501 time-steps).

2.5.2.1. Results

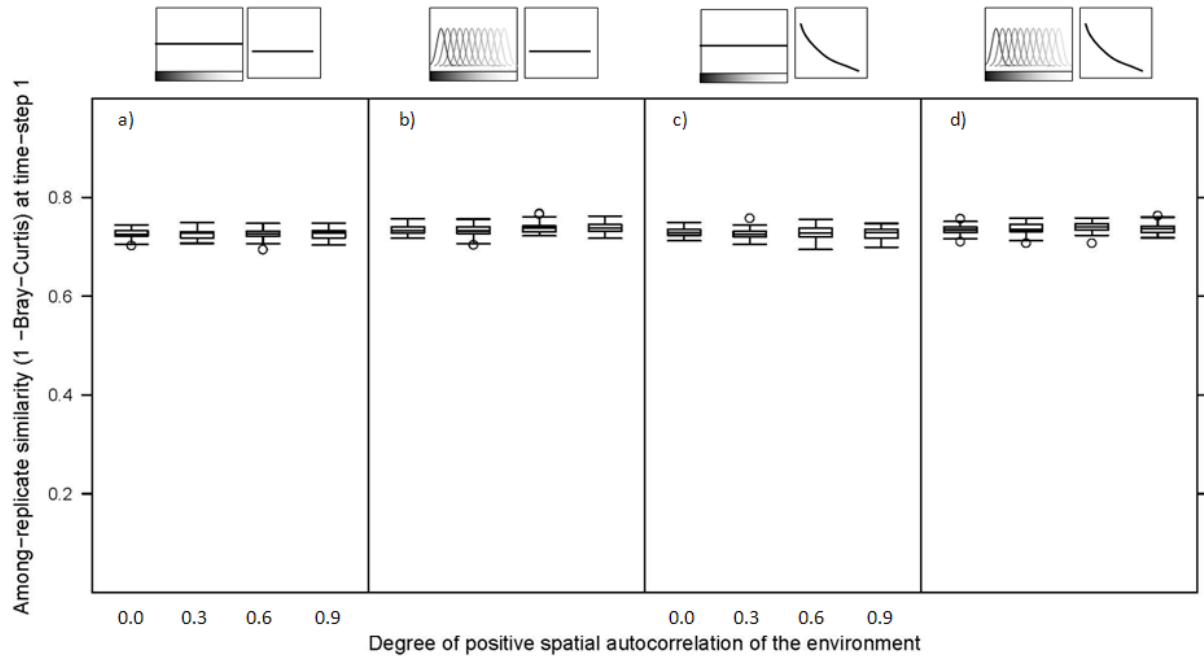
The trend of community composition predictability increased with increasing positive SAE only with niche differentiation and local dispersal was robust to variation in beta diversity resemblance measures and late succession time-steps (501 and 2001 time-

steps). Results are summarized below (Table 2.3). One set of plots (Fig. 2.8i-iii) are provided to give an example of the plots examined to create Table 2.3.

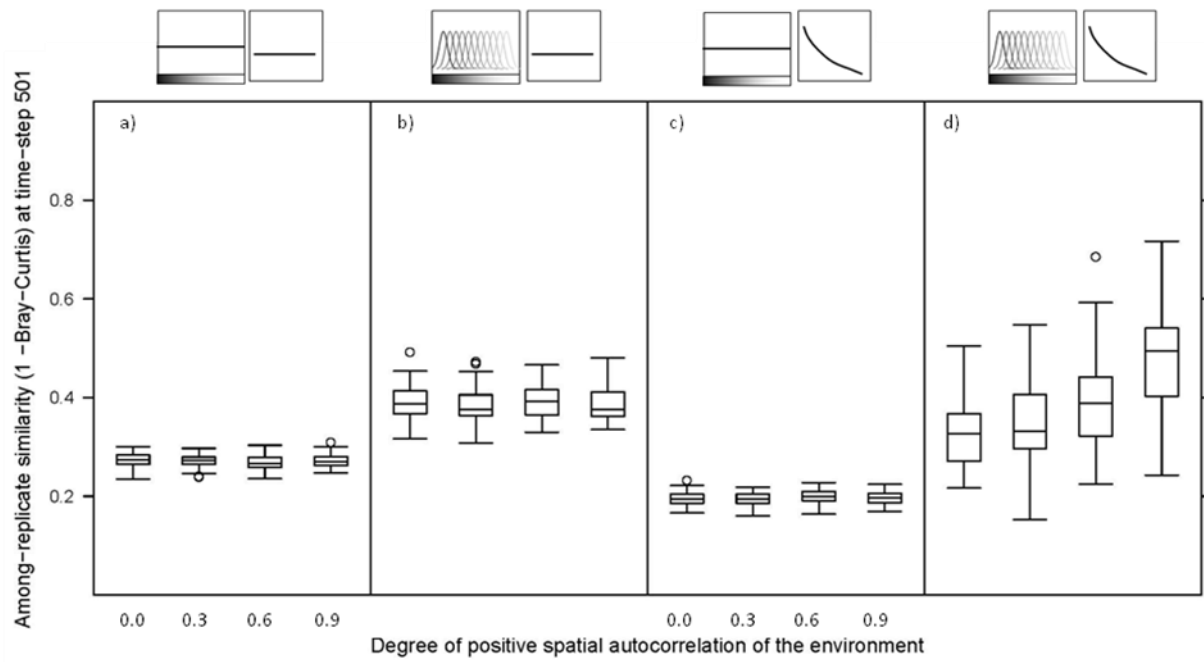
Table 2.3 Summary of the results from varying the beta diversity resemblance measure and number of time-steps. The trend of interest was increasing community composition with increasing positive spatial autocorrelation of the environment. At time-step 1 (not included in this table), there was no trend because it was too early in succession for a pattern to emerge.

Beta diversity resemblance measure	Time-step	Trend found
Bray-Curtis similarity (1- Bray Curtis)	501, 2001	Yes
Number equivalents for Shannon beta diversity	501, 2001	Yes
Jaccard similarity (1- Jaccard)	501, 2001	Yes
Morisita-Horn similarity (1- Morisita-Horn)	501, 2001	Yes

i) Bray-Curtis similarity, time-step 1



ii) Bray-Curtis similarity, time-step 501



iii) Bray-Curtis similarity, time-step 2001

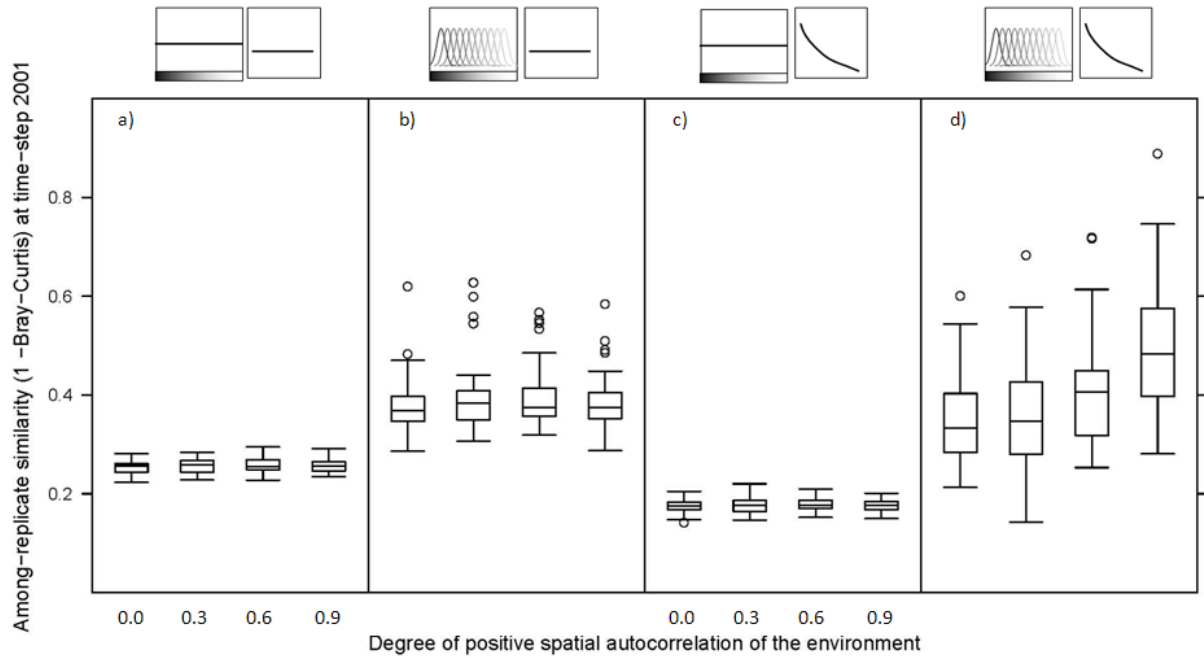


Figure 2.8 Among-replicate similarity (community composition predictability) with increasing positive spatial autocorrelation of the environment at multiple time-steps. The time-steps shown are: time-step 1 (i), 501 (ii), and 2001 (iii). Illustrated are box plots of among-replicate similarity for neutral and global dispersal (a), niche-differentiated and global dispersal (b), neutral and local dispersal (c), and niche-differentiated and local dispersal (d). The results in each box plot are for the mean among-replicate similarity of each focal site ($n=50$ focal site means). Each mean was calculated for each focal site by averaging among-replicate pair-wise comparisons (190 comparisons, given 20 replicate metacommunities). The degree of positive spatial autocorrelation of the environment ranges from random (0.0) to medium (0.3, 0.6) to high autocorrelation (0.9) as calculated using standardized environmental variance.

2.5.2.2. Discussion

The fact that multiple beta diversity resemblance measures gave the same trend (Table 2.3) is important in light of a recent synthesis paper arguing for the use of multiple resemblance measures to test hypotheses about beta diversity (Anderson et al. 2010). Ruokolainen et al. (2009) found a significant influence of late succession time-steps and beta diversity resemblance measures, but my results appeared robust to these factors.

2.5.3. Supplementary Material C: Demographic Parameter Sensitivity Analyses

It is important to check the sensitivity of model output to demographic parameters. I used an approach outlined in Bell (2005) to run 19 realizations. I varied K (community carrying capacity), b (per capita birth rate), and z (per capita death rate).

2.5.3.1. Results

In general, the results (Table 2.4) showed the same trend as the main experiment: with increasing positive SAE, community composition predictability increased for the niche-differentiated and local dispersal scenario (Fig. 2.2d, Fig. 2.3e-h). However, some of the demographic parameter combinations resulted in no trend.

Table 2.4 Summary of the results from varying demographic parameters. There were 19 realizations. The trend of interest was increasing community composition predictability with increasing positive spatial autocorrelation of the environment. Below is a tally of the number of simulations with the trend of interest, and the parameter range. See Bell (2005) for the procedure.

Number showing trend	Birth rate (b)	Death rate (z)	Community carry capacity (K)
17* out of 19	0.07 - 0.96	0.02 - 0.50	11- 422

*In a few instances, the first landscape (random) had a value close to, or just above, the second level of positive spatial autocorrelation of the environment.

2.5.3.2. Discussion

The expected trend was not found when birth and death rate were very similar. In this case, communities would have behaved in an essentially neutral fashion. This is because the species would not have produced large enough population sizes in optimal environmental conditions to enable effective deterministic species-environmental sorting.

3. CONCLUSION

3.1. Goal of Thesis

The goal of this thesis was to address on the following research question: does increasing the degree of positive spatial autocorrelation of the environment (SAE) in the broader landscape increase the predictability of local community composition? The simulations of this thesis showed a trend: community composition predictability increased with increasing positive SAE when there was niche differentiation and local dispersal. This trend was thought to be largely due to increasing positive SAE increasing landscape connectivity which, in turn, increased species-environmental sorting relative to stochastic community assembly processes. The trend of interest was robust to variation in environment evenness, beta diversity resemblance measures, number of time-steps, and demographic parameters.

3.2. Thesis Work in Light of Recent Research

3.2.1. Landscape Connectivity and Plant Community Patterns

The thesis work adds to recent research that seeks to understand the effect of landscape connectivity on plant community pattern (Minor et al. 2009, Flinn et al. 2010, e.g., Brudvig et al. 2009). For example, Brudvig et al (2009), with the world's largest corridor experiment, illustrated that the degree to which patches were connected influenced the degree of spill-over of reserve species into non-reserve areas. Their work

highlights the idea that there is limited space for conservation reserves, so conservation efforts need to increasingly take note of ways in which managing protected areas can facilitate the preservation of species richness outside of reserves. The thesis work does not focus on species richness, but it suggests that plant species composition-environment relationships are influenced by landscape connectivity. Minor et al. (2009) noted that landscape configuration was related to the likelihood that plant communities that were composed of native or invasive exotic species. They suggested that with increasing fragmentation of the environment, invasive species would spread more easily than native species, leading to homogenization of plant community composition. In contrast, the thesis research suggests that community homogenization is inversely related to fragmentation of optimal environments. However, the thesis research uses the simplifying assumption that species do not possess different invasion traits that would influence their species-specific rate of spread through the landscape.

3.2.2. Caution Regarding Variation Partitioning Analyses

Variation partitioning analyses have commonly used as predictive tools for applied ecology (Legendre et al. 2005). These analyses are meant to assess field data to estimate the relative importance of environmental determinism (environmental control) versus dispersal-based, stochastic assembly (ecological drift) (see citations in Legendre et al. 2005, Smith and Lundholm 2010). Because ecological drift can produce spatial patterns in the landscape, which can create the appearance of environmental structuring, variation partitioning analyses were crafted to deal with these spatial patterns and to parcel out the variation due to environmental control relative to ecological drift.

Variation partitioning analyses often treat SAE as a confounding factor. For example, Smith and Lundholm (2010) warn that variation partitioning is strongly influenced by SAE. They also discuss some caveats of variation partitioning; there has been much controversy over the usefulness of variation partitioning analyses.

Gilbert and Bennett (2010) provide evidence that several common uses of variation partitioning in conservation and ecology are inappropriate. Their simulation work employed a landscape with positive SAE and a random landscape, and they illustrated instances where common variation partitioning were not able to properly model the importance of stochastic relative to deterministic assembly of communities in these landscapes.

In light of such recent work, it is likely the role of SAE as a factor influencing the predictability of composition-environment relationships has been misrepresented previously by researchers using variation partitioning. Variation partitioning is not used in this thesis research. A potential implication of the thesis research is increasing the awareness of those using variation partitioning analyses (in the appropriate ways) that SAE is more than a nuisance; it has ecological significance (see Legendre 1993) as a factor influencing processes that shape community composition.

3.3. Potential Significance

3.3.1. Basic Ecology

The thesis research can potentially add to conceptual developments in metacommunity ecology. My work suggests that the importance of stochastic relative to deterministic community assembly is influenced by landscape configuration. This notion

adds to ideas previously expressed about metacommunities. For example, proponents of metacommunity theory have discussed how the distance between discrete patches, and *differences* in the dispersal capacities of the organisms, are expected to influence whether a metacommunity is influenced by mass-effect, species-sorting, or patch dynamics (Leibold et al. 2005). The results of this thesis suggest a shift between the relative importance of mass-effect and species-sorting depends on the spatial structure of the environment despite the organisms with the *same* dispersal capacity. Many plant species have spatially limited dispersal, and my research provides ideas about how these species may assemble in response to the spatial attributes of the ecosystems in which they reside.

This research is also potentially significant for advancing theoretical understanding of how metaecosystems could be influenced by landscape configuration. A metaecosystem is a set of ecosystems that are connected via flows of materials, energy, and organisms; it includes spatial flows among systems beyond just organism dispersal (Loreau et al. 2005). My results show that metacommunity dynamics were influenced by landscape configuration, and previous theory suggests that metacommunity dynamics can influence metaecosystem dynamics (Leibold et al. 2005). Indeed, the flow of organisms within the metacommunity of an ecosystem can influence its spatial properties, which in turn can influence among ecosystem spatial flows. Given my work, and all else being equal, I would expect that metacommunities would have increasingly predictable metaecosystem dynamics with increasing positive SAE. This increase in the predictability of metaecosystem dynamics could lead to more predictable ecosystem structure and function.

3.3.2. Applied Ecology

The thesis research supports the notion that the strength of composition-environment relationships are influenced by historical (e.g., initial demographic stochasticity) and regional-level (e.g., landscape configuration) factors. Brudvig (2011) stresses that a key step forward in restoration ecology is to understand how historical and landscape-level factors can influence restoration work at the site level. Restoration tends to focus on managing local scale abiotic factors with the aim of creating specific species assemblages (Matthews et al. 2009, Brudvig 2011). This local-scale approach may be useful for meeting certain restoration targets, but ignoring the influence of historical and regional factors can lead to undesirable outcomes.

Given that ecosystems vary in SAE (Bell et al. 1993, Bridges et al. 2007), it is important to evaluate if this variation influences composition-environment relationships. To this end, my research provides results that generate a prediction that appears untested: ecosystems characterized by higher positive SAE will have more repeatable composition-environment relationships than ecosystems characterized by less clustering of similar environmental conditions. As well, this study suggests that the use of composition-environment correlations as predictive tools for management (Legendre et al. 2005) will vary depending on the SAE of an ecosystem.

3.3.3. Research Strengths

The thesis research has several important strengths. First, the simulations had a continuous environmental gradient. As noted by Palmer (1992) and Murphy and Lovett-Doust (2004), plants likely experience continuous environmental conditions rather than

habitat patches. The thesis research also addresses the notion of Cushman et al. (2010) that it is important to understand landscape level processes by representing the environment as continuous gradients rather than discrete habitat patches. To date, research on species-environmental sorting in relation to landscape structure does not appear to address the influence of continuous environments on plant species, but instead takes a discrete habitat view (e.g., Brudvig et al. 2009, Minor et al. 2009, Flinn et al. 2010). Second, this study demonstrated the influence of landscape configuration without the confounding factor of landscape composition. It is well known that the number and relative abundance of environmental conditions will affect community patterns, but how landscape configuration on its own influences community patterns appears less well studied, especially given it is difficult to untangle the influence of landscape configuration from composition in the field (Fahrig and Nutton 2003). Third, a spatially explicit approach was used. A spatially explicit approach is important because the composition of plant communities, and other sessile organisms, is a spatially explicit phenomenon (Gardner and Enghardt 2008). Despite the critical information that can be gained from a spatially explicit approach (see Economo and Keitt 2010), it seems less common in metacommunity ecology than a spatially implicit approach perhaps because of the difficulties of quantifying spatially explicit dispersal in field studies (Jacobson and Peres-Neto 2010), and the increased processing time required for spatially explicit simulation modeling and analysis (Gravel et al. 2006). Fourth, this research integrates concepts from landscape ecology (e.g., landscape connectivity, landscape structure) into metacommunity ecology, which is becoming a trend in some other recent studies (see

Economo and Keitt 2008, 2010). It has been stressed that landscape and metacommunity ecology theory would benefit from integration (see Holyoak et al. 2005, Collinge 2009).

3.3.4. Research Limitations

There are several important limitations to keep in mind regarding the thesis research. First, not as much demographic parameter space was explored as some modeling studies. However, sufficient parameter space was explored to show that the results were generally robust to changes in demographic parameters. Second, because this research only examined the purely spatial effect of environment configuration, the simulations did not incorporate “habitat dynamics.” Although it is well known that “habitats” (or environmental conditions) have dynamics, fixed habitat heterogeneity is also common in nature, and the ecological implications of this type of heterogeneity are not well understood (Davies et al. 2009). However, future work could investigate habitat dynamics induced by plant resource foraging (see Tilman 1982, 2004). Third, the model used in the thesis, like all models, was simplistic. For example, in the model, many well known ecological processes, such as facilitation and predation, were not included. Some other factors not included were more realistic demography (e.g., demography according to age structure), intra-specific density-dependence, or species-specific traits besides differential mortality rate during culling. However, similar model simplicity has been used by others (e.g., Bell 2005), and it is likely that the results of this thesis are still relevant to better understanding community assembly. Fourth, alpha diversity may have influenced the results of Bray-Curtis similarity. However, community resemblance measures less sensitive to alpha diversity than Bray-Curtis similarity, i.e., Shannon beta

diversity (Jost 2007) and Morisita-Horn (Wolda 1981), showed outcomes similar to the Bray-Curtis similarity analyses. Fifth, the results are only relevant to plant (or other organisms with spatially restricted dispersal) assemblages, in nature if plant species are differentially adapted to different environments, and environmental determinism is a significant driver of species composition. However, field studies suggest that plant species are differentially adapted to environments, and environmental determinism can act as a significant driver of species composition depending on the dispersal capacities of the plant species relative to the scale of environmental heterogeneity (e.g., Lechowicz and Bell 1991, Bell et al. 1993, Richard et al. 2000, Karst et al. 2005, Pinto and MacDougall 2010).

3.3.5. Future Directions

Below are several possible future directions. First, future studies could use microcosm and field experiments to test if the predictability of community composition increases with increasing positive SAE. Although Pinto and MacDougall (2010) performed field experiments on one species, an endangered violet, to examine habitat occupancy in relation to SAE, they used variation partitioning analyses to infer community level effects, rather than community experiments. A study by Flinn et al. (2010) was inconclusive about the role of dispersal and landscape structure on the degree of species-environmental sorting. However, they did not use experiments, and also used variation partitioning methods. It seems no microcosm experiments have tested how SAE affects community assembly. Microbial experiments would be useful for testing hypotheses in relation to SAE that are virtually impossible to test with other organisms.

Second, future experiments could incorporate a habitat disturbance treatment in addition to the static SAE treatment. It is well known that disturbance influences the predictability of community composition by increasing local stochastic extinction (see Ruokolainen et al. 2009), but few studies have investigated how landscape configuration affects the response of communities to disturbance (Starzomski and Srivastava 2007, Büchi et al. 2009). Future experiments would complement previous research that examined the effect of temporal autocorrelation (Ruokolainen et al. 2009) and spatial autocorrelation of disturbance events (Brown et al. 2011) on community assembly.

Third, future research could study the effect of SAE on evolution in metacommunities. Previously, modelling showed that evolution in metacommunities was influenced by environment evenness (Hubbell 2006), and spatiotemporal environmental variation (Loeuille and Leibold 2008), but research is lacking on how SAE affects evolution in metacommunities. Environmental variability has been shown to affect the evolution of dispersal distance in single species populations (Murrell et al. 2002), but it would be useful to explore the evolution of dispersal distance in metacommunities in response to SAE. Also, in a future studies, metacommunity simulations could be used to test the prediction that increasing the degree of positive SAE decreases the tendency for organisms to evolve traits that promote phenotypic plasticity (Bell et al. 1993). Similarly, one could test the prediction that increasing positive SAE decreases the likelihood that generalists will evolve in communities (Hubbell and Foster 1986, Palmer 1992).

Fourth, future studies could examine the environmental texture hypothesis, which suggests that the rate of species accumulation during spatially explicit sampling of different environments is influenced by the geometry of the environment (McGlinn and

Palmer 2011); the lower the fractal dimension (associated with higher positive SAE), the more rapidly new species are accumulated. A recent field study by McGlinn and Palmer (2011) that tested the environmental texture hypothesis showed that a field site with higher positive SAE (low fractal dimension) had a greater accumulation of species than the other site. Presently, it appears work addressing the environmental texture hypothesis is still scarce, and data from the thesis research's simulation model could be gathered to evaluate this hypothesis.

Lastly, because the thesis research did not incorporate the influence of species on the SAE, or the process of facilitation, future simulations could have (i) species modify SAE, and (ii) a shift in the relative importance of facilitation and competition along a stress gradient. Field observations suggest that plant invasions into desert ecosystems may be influenced by the degree of positive SAE, whereby shrubs create "islands of fertility" (Schlesinger et al. 1996). Also, in desert ecosystems, facilitation can increase in importance relative to competition when environmental stress increases (Brooker et al. 2008).

3.3.6. Overall Conclusion

This thesis focused on a single research question: does increasing the degree of positive spatial autocorrelation of the environment (SAE) in the broader landscape increase the predictability of local community composition? The research results illustrate that the answer to this question is yes, and the positive trend can be attributed to increased landscape connectivity facilitating increased species-environmental sorting.

Despite the straightforward answer to the research question, the contributions of this thesis are potentially profound. As noted above, in addition to potentially important implications for basic and applied ecology, the results of the thesis research can be generalized to an important testable prediction that currently seems untested: ecosystems with high positive SAE will have more predictable community composition-environment associations than ecosystems with less clustering of similar environmental conditions.

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