DISSERTATION

EFFECTS OF SPATIAL HETEROGENEITY ON NATIVE AND NONNATIVE PLANT AND BUTTERFLY SPECIES RICHNESS IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO, USA

Submitted by
Sunil Kumar
Graduate Degree Program in Ecology

In partial fulfillment of the requirements
for the degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Spring 2007

COLORADO STATE UNIVERSITY

March 9th, 2007

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY SUNIL KUMAR ENTITLED "EFFECTS OF SPATIAL HETEROGENEITY ON NATIVE AND NONNATIVE PLANT AND BUTTERFLY SPECIES RICHNESS IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO, USA" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Barry R Noon

Member (Dr. Barry R. Noon)

Hariharan Iyer

Member (Dr. Hariharan K. Iyer)

Thomas J Stohlgren

Advisor (Dr. Thomas J. Stohlgren)

M Lefsky

Co-Advisor (Dr. Michael A. Lefsky)

Department Head/Director (Dr. William K. Lauenroth)

ABSTRACT OF DISSERTATION

EFFECTS OF SPATIAL HETEROGENEITY ON NATIVE AND NONNATIVE PLANT AND BUTTERFLY SPECIES RICHNESS IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO, USA

Spatial heterogeneity may have differential effects on the distribution of native and nonnative plant and butterfly species richness and their interactions. These effects may be scale dependent and may vary for different levels of biological organizations (e.g., landscape-level versus land cover type level native and nonnative plant species richness, or total versus family level butterfly species richness). I quantified spatial heterogeneity in vegetation, soil, topography, and landscape patterns (composition and configuration) in Rocky Mountain National Park, Colorado, and related it to native and nonnative plant and butterfly species richness. The landscape metrics represented five components of landscape heterogeneity and were measured at multiple spatial extents (within varying radii) around sample plots (20 x 50 m) using FRAGSTATS landscape pattern analysis program. Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to select the best models from a set of multiple linear regression models developed for native and nonnative plant and butterfly species richness at multiple spatial extents and different levels of biological organizations. For plant species, the best models explained 43% of the variation in native plant species richness and 70% of the variation in nonnative plant species richness at 240-m spatial extent. For butterfly species, the best model explained 62% of the variation in total butterfly species richness (2100-m spatial extent). Native and nonnative plant and butterfly species richness predictive models were significantly improved by including landscape metrics in addition to variables representing vegetation, soil and topographic heterogeneity. The role of spatial autocorrelation in native-exotic plant species richness relationships was also investigated. Principal coordinates of neighbor matrices (PCNM) approach and conditional autoregressive regression (CAR) were used to quantify broad-scale spatial dependence and fine-scale spatial autocorrelation, respectively. Modified variation partitioning showed that 'space' and 'spatially structured environmental processes' are relatively more important in shaping the native-exotic plant species richness relationships than native plant species richness alone. This study offers an approach to quantify spatial heterogeneity and spatial autocorrelation, and the results suggest that wider landscape context should be considered in managing native and nonnative plant and butterfly species.

Sunil Kumar
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Spring 2007

ACKNOWLEDGEMENTS

I am grateful to Ford Foundation International Fellowships Program (FF-IFP) for giving me an opportunity to pursue graduate studies and for generous financial and logistical support for the first three years of my studies (Aug. 2002- Aug. 2005). I also acknowledge support from NASA grant (NRA-03-OES-03) for remaining period of this research. I appreciate the logistical support provided by Natural Resource Ecology Laboratory (NREL) at Colorado State University.

I thank my major advisor, Thomas Stohlgren, for reading my numerous revisions and sometimes providing 'same day service', and for his continued encouragement, guidance, and support. I also thank my committee, Michael Lefsky, co-advisor, Barry Noon, and Hari Iyer for their time and energy and for agreeing to work with me.

My sincere thanks to Geneva Chong, Sara Simonson, and a number of field assistants who collected the data on plant and butterfly species, and many taxonomists from NREL at Colorado State University for species identification. Geneva Chong, Sara Simonson and Catherine Jarnevich provided helpful comments and suggestions on drafts of first, second and third Chapters, respectively; to all I am grateful. I also thank Robin Reich for his help with spatial statistical analyses, and Dan Kashian for comments on the draft of the first Chapter.

Thanks are also due to members of Stohlgren group for their support at different steps, and their friendship. I am also thankful to people at NREL, including faculty and students in Graduate Degree Program in Ecology (GDPE) and my office mates, who broadened my vision, enriched my knowledge and graduate experience through

numerous stimulating discussions, and provided very friendly environment for this research project. I also thank IFP New Delhi team and IFP fellows from the first cohort from India, and Tom Dragano and Karen Dragano for their support, affection and friendship.

Last but not the least; I thank my parents, grandfather, and my in-laws, for their emotional support. I especially thank my wife, Madhu, for putting up with late nights, and for her continued support, inspiration, patience, and most of all love.

TABLE OF CONTENTS

INTRODUCTION

The main premise of this dissertation is that all organisms live in a heterogeneous world and they are not only affected by the place in which they live (the study plot), but also by their surroundings (i.e., the landscape context). The degree of heterogeneity experienced by an organism may depend on the grain of its perception (Levins 1968), its natural history characteristics, and the grain of the landscape (Forman and Godron 1986). Therefore different organisms are expected to have differential responses to spatial heterogeneity.

Spatial heterogeneity can simply be thought of as the complexity in nature. It can be defined as the complexity and variability in ecological systems' properties of interest in space (Li and Reynolds 1994). Spatial heterogeneity in ecological systems is caused by spatial interactions between many biotic and abiotic factors and the differential responses of organisms to these factors (Milne 1991) and the organisms themselves (Huston 1994). The quantification of spatial heterogeneity and the decision at which scale to quantify it is a daunting task because spatial heterogeneity is a complex phenomenon and is highly scale dependent (Kolasa and Rollo 1991, Gustafson 1998, Fortin and Agrawal 2005, Wagner and Fortin 2005).

Why should we care about understanding the effects of spatial heterogeneity on species richness? Spatial heterogeneity is hypothesized as one of the major drivers of biological diversity (Wiens 1976, Milne 1991, Huston 1994). Spatial heterogeneity may change due to natural and anthropogenic disturbances such as fire, logging, grazing, flood, pollution and insect outbreak that may influence species distributions across the landscape. Therefore, if we know how spatial heterogeneity influences species diversity we might be able to predict future scenario in case of a change in the landscape spatial patterns. For example, if we understand how patch size or edges influence native and nonnative plant species across the landscape, we might be able to predict how plant species might respond to an altered landscape configuration due to fire or logging, or how an exotic species might spread.

Quantifying spatial heterogeneity

Quantification of spatial heterogeneity is prerequisite for understanding its effects on species distributions. For the sake of simplification, spatial heterogeneity in this study was divided in to different categories such as heterogeneity in soil characteristics, heterogeneity in topography, heterogeneity in landscape spatial patterns, and heterogeneity in vegetation, and was quantified at multiple spatial extents. Soil heterogeneity was quantified by measuring soil variables such as percent nitrogen, and texture (sand, silt and clay). Topographic heterogeneity was represented by elevation, slope, and aspect. Landscape metrics (McGarigal et al. 2002) were used to quantify landscape heterogeneity (composition and configuration of the landscape) and vegetation heterogeneity was included by considering average vegetation height and normalized difference vegetation index (NDVI).

Several approaches have been used to quantify spatial heterogeneity and develop predictive models for native and nonnative plant and butterfly species richness. However, most of these have included predictor variables representing environmental/topographic, soil, climatic and biotic heterogeneity (e.g., Stohlgren et al. 1998, 1999, 2000, 2005, Fleishman et al. 2002, Davies et al. 2005), and have largely neglected landscape heterogeneity. Only a few studies have included all five components (as per definition given by Li and Reynolds 1994) of landscape heterogeneity (e.g., Meyer et al. 1998, Kie et al. 2002) for other taxa, but rarely for plants and butterflies. Most studies only included one or two components of landscape heterogeneity such as patch characteristics (see review by Mazerolle and Villard 1999), however, considering one or two landscape metric(s) may not be adequate to capture all the aspects of landscape heterogeneity (Gustafson 1998).

Using landscape metrics to quantify landscape heterogeneity

In this study, I followed Li and Reynolds' (1994) definition of spatial heterogeneity in categorical maps (I called it "landscape heterogeneity") that they defined in terms of five compositional and configurational components: (1) number of patch types; (2) proportion of each patch type; (3) spatial arrangement of patches; (4) patch shape; and (5) contrast between neighboring patches (Li and Reynolds 1994). Landscape metrics, which are algorithms that quantify specific spatial characteristics of patches, classes of patches, or entire landscape mosaics (McGarigal et al. 2002) can be used to quantify different components of landscape heterogeneity (Gustafson 1998). Recently, landscape metrics have been successfully used to quantify different aspects of landscape heterogeneity and have helped in gaining ecological insights (e.g., Meyer et al. 1998, Mazerolle and Villard 1999, Kie et al. 2002).

Selection of spatial scale of analyses

The selection of spatial scale to quantify spatial heterogeneity is crucial as spatial heterogeneity is highly scale dependent (Wagner and Fortin 2005). Spatial scale may refer to both "grain" and "extent" (Turner et al. 1989). In this study, the grain size was fixed because I used the data from the sources with fixed grain size (30 x 30 m), but I varied the spatial extent of analyses.

Selecting spatial extent of analyses for the study that include single species may be relatively easier than community level studies. For example, ecologists studying the effects of spatial heterogeneity on taxa such as animals and insects generally use home range or territory size or area of an organism's activities (e.g., Kie et al. 2002, Steffan-Dewenter et al. 2002, Boyce et al. 2003) to assess spatial extent of analysis. However, for many species, such an extent is difficult to decide a priori because different species may have differential responses to multiple levels of spatial heterogeneity of resources and other covariates. One of the ways to confront this problem is to select multiple arbitrary spatial extents to quantify spatial heterogeneity in different environmental variables. Next, it is important to identify the dominant scale of community response by comparing the variation explained (coefficient of determination; R^2) at each spatial extent. This approach has been used in a number of studies on different taxa such as birds (Pearson 1993, Warren et al. 2005), animals (Kie et al. 2002, Maier et al. 2005), plants (Chapter 1), and insects including butterflies (Steffan-Dewenter et al. 2002, Thies et al. 2003, Chapter 2)). Also grouping different species based on their attributes (e.g., including conifers and grasses in two different groups, or dividing total butterfly species into broad taxonomic groups based on their families) might be helpful because species that share similar life history characteristics may respond to patch shape and patch size in a similar manner (Noon et al. 1997).

Spatial autocorrelation

Spatial autocorrelation in a variable can be defined as the lack of independence among observations (Legendre and Legendre 1998). For example, the distribution of species is often spatially autocorrelated (Legendre 1993, Lichstein et al. 2002). It can result from the spatial dependence (or broad-scale spatial trend) of the community on environmental factors or due to ecological processes (e.g., dispersal, growth, mortality, and competition; Legendre and Legendre 1998, Wagner and Fortin 2005). In any case, the presence of spatial autocorrelation in the response or predictor variables can pose a problem in applying parametric statistical methods because of the violation of the assumption of independence of observations (Legendre 1993, Wagner and Fortin 2005). To evaluate the magnitude of this problem, one can either remove the spatial dependency, or alternatively modify the statistical methods to take spatial autocorrelation into account (Legendre 1993), or acknowledge that in ecological variables spatial autocorrelation is the “fact of life” (Fortin and Dale 2005) and include it by incorporating spatial variables (a polynomial trend surface as a function of geographic coordinates of observations) to account for broad-scale spatial trend (Legendre 1993) and a spatial autoregressive term to model fine-scale spatial autocorrelation (Lichstein et al. 2002). In this study, I quantified the effects of spatial autocorrelation on native-exotic plant species richness relationships using spatially explicit conditional autoregressive regression (CAR; Cressie, 1993, Lichstein et al. 2002) models and variation partitioning.

Overview

This dissertation consists of three Chapters. The first Chapter investigates the effects of spatial heterogeneity in soil, topography and landscape patterns on native and nonnative plant species richness. The research questions addressed in this Chapter include: (1) Does spatial heterogeneity play an important role in the distribution of plant species richness? (2) Is this effect different for native and nonnative plant species richness? (3) How does this effect change with a change in (a) spatial extent of analysis, and (b) level of ecological hierarchy (i.e., landscape, land cover, and community)? Multi-level and multi-scale predictive models of native and nonnative plant species richness are presented in this Chapter. Chapter 2 includes an analysis of the effects of spatial heterogeneity in vegetation, topography and landscape patterns on butterfly species richness. My specific objectives in this Chapter were to: (1) Quantify spatial heterogeneity in vegetation, topography, and landscape patterns at multiple spatial extents, and relate it to butterfly species richness; (2) Test the null hypothesis of no effects of landscape heterogeneity on butterfly species richness; (3) Determine the spatial extent of the landscape at which butterflies have strongest responses to spatial heterogeneity; (4) Investigate whether spatial heterogeneity has differential effects on certain butterfly families; and (5) Develop predictive models for butterfly species richness in the study area. This Chapter contains total and family (five) level butterfly species richness models. The third Chapter provides new variance partitioning approaches in an analysis of the effects of spatial autocorrelation on native-exotic plant species richness relationships.

Literature cited

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience **10**: 421-431.

Cressie, N.A.C. 1993. Statistics for spatial data. Revised edition. John Wiley and Sons, New York, New York, USA.

Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology **86**: 1602-1910.

Fleishman, E., D. D. Murphy, and P. Sjogren-Gulve. 2002. Modeling species richness and habitat suitability for taxa of conservation interest. Pages 507-517 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of scale and accuracy. Island Press, Covelo, California, USA.

Forman, R. T. T., and M. Godron. 1986. Landscape Ecology, John Wiley and Sons, New York, New York, USA.

Fortin, M.-J., and A. A. Agrawal. 2005. Landscape ecology comes of age. Ecology **86**: 1965-1967.

Fortin M.-J., and M. R. T. Dale. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, UK.

Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems **1**: 143-156.

Huston, M. A. 1994. Biological Diversity: the coexistence of species in changing landscapes. Cambridge University Press, UK.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology **83**:530-544.

Kolasa, J., and C. D. Rollo. 1991. The heterogeneity of heterogeneity: a glossary. Pages 1-23 *in* J. Kolasa, and S. T. A Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Legendre, P. & Legendre, L. 1998. *Numerical ecology.* Second English edn. Elsevier Science, Amsterdam, The Netherlands.

Legendre, P. 1993. Spatial autocorrelation - trouble or new paradigm. Ecology **74**:1659-1673.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton.

Li, H., and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology **75**:2446-2455.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs **72**:445-463.

Maier, J. A. K., J. M. V. Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research **35**:2233-2243.

Mazerolle, M. J., and M. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience **6**:117-124.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS, version 3.0: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. [Online] <http://www.umass.edu/landeco/research/fragstats/fragstats.html>

Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs **139**: 1-51.

Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscape. Pages 69-84 *in* J. Kolasa, and S. T. A Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Noon, B. R., K. S., McKelvey, and D. D. Murphy. 1997. Developing an analytical context for multispecies conservation planning. Pages 43-59 *in* S. T. A. Pickett, Ostfeld, R. S., Shachak, M., and Likens, G. E. , editors. The ecological basis of conservation. Chapman & Hall, New York, NY, USA.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology **8**:3-18.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83**:1421-1432.

Stohlgren, T. J., A. J. Owen, and M. Lee. 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. Biodiversity and Conservation **9**:65-86.

Stohlgren, T. J., D. Barnett, C. Flather, J. Kartesz, and B. Peterjohn. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology **86**: 2298-2309.

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

Stohlgren, T. J., R. R. Bachnad, Y. Onami, and D. Binkley. 1998. Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. Plant Ecology **135**:215-228.

Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos **101**:18-25.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne 1989. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecology **3**: 153-162.

Wagner, H. H., and M. -J. Fortin 2005. Spatial analysis of landscapes: Concepts and statistics. Ecology **86**: 1975-1987.

Warren, T. L., M. G. Betts, A. W. Diamond, and G. J. Forbes. 2005. The influence of local habitat and landscape composition on cavity-nesting birds in a forested mosaic. Forest Ecology and Management **214**:331-343.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**:81- 120.

CHAPTER 1 EFFECTS OF SPATIAL HETEROGENEITY ON NATIVE AND NONNATIVE PLANT SPECIES RICHNESS

1.0 Abstract

Spatial heterogeneity may have differential effects on the distribution of native and nonnative plant species richness. I examined the effects of spatial heterogeneity on native and nonnative plant species richness distributions in the central part of Rocky Mountain National Park, Colorado, USA. Spatial heterogeneity around vegetation plots was characterized using landscape metrics, environmental/topographic variables (slope, aspect, elevation, and distance from stream or river), and soil variables (nitrogen, clay, and sand). The landscape metrics represented five components of landscape heterogeneity and were measured at four spatial extents (within varying radii of 120, 240, 480, and 960 m) using the FRAGSTATS landscape pattern analysis program. Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to select the best models from a set of multiple linear regression models developed for native and nonnative plant species richness at four spatial extents and three levels of ecological hierarchy (i.e., landscape, land cover, and community). Both native and nonnative plant species richness were positively correlated with edge density, Simpson's diversity index and interspersion/juxtaposition index, and were negatively correlated with mean patch size. The amount of variation explained at four spatial extents and three hierarchical levels ranged from 30% to 70%. At the landscape level, the best models explained 43% of the variation in native plant species richness and 70% of the variation in nonnative plant species richness (240-m extent). In general, the amount of variation explained was always higher for nonnative plant species richness, and the inclusion of landscape metrics always significantly improved the models. The best models explained 66% of the variation in nonnative plant species richness for both the conifer land cover type and lodgepole pine community. The relative influence of the components of spatial heterogeneity differed for native and nonnative plant species richness and varied with the spatial extent of analysis and levels of ecological hierarchy. The study offers an approach to quantify spatial heterogeneity to improve models of plant biodiversity. The results demonstrate that ecologists must recognize the importance of spatial heterogeneity in managing native and nonnative plant species.

Key words: AIC; FRAGSTATS; landscape metrics; model selection; native and nonnative plant species richness; Rocky Mountains; spatial autocorrelation; spatial heterogeneity; spatial scales.

1.1 Introduction

Most ecological studies prior to 1960 assumed spatial homogeneity to avoid the analytical difficulties posed by heterogeneity (Pickett and Cadenasso 1995, Wiens 1995). However, ecological systems are inherently heterogeneous at many scales, and ecologists realized the limitations to ecological understanding imposed by the assumption of homogeneity (Wiens 1995). Ecological studies conducted after 1960 more frequently acknowledged spatial heterogeneity. An early example is the study by MacArthur and MacArthur (1961), who related bird species diversity to the vertical heterogeneity of vegetation, followed by several other studies (e.g., Roth et al. 1976, Pearson 1993, Pearson et al. 1995, Meyer et al. 1998, Kie et al. 2002, Steffan-Dewenter et al. 2002, Davies et al. 2005, Kauffman and Jules 2006). Almost half a century after MacArthur and MacArthur (1961), the potential importance of the effects of spatial heterogeneity is well recognized (Turner 2005), but there is little agreement, and relatively few examples of how to accurately measure heterogeneity at multiple spatial scales (Fortin and Agarwal 2005).

Spatial heterogeneity is hypothesized as one of the major drivers of biological diversity (Wiens 1976, Milne 1991, Huston 1994), and a number of studies on different species (mostly native) support this hypothesis, however, empirical confirmation from nonnative or invasive species has been scarce (Kauffman and Jules 2006). Spatial heterogeneity results from the spatial interactions between a number of biotic and abiotic factors and the differential responses of organisms to these factors (Milne 1991) and the organisms themselves (Huston 1994). It can be manifest at multiple spatial scales and in many variables. Spatial heterogeneity may have significant influences on many ecosystem processes at multiple spatial scales (Turner 1989, Pearson et al. 1995, Pickett and Cadenasso 1995, Kie et al. 2002). Spatial heterogeneity of vegetation patterns (i.e., landscape heterogeneity) is a structural property of landscapes (Li and Reynolds 1994) that can be defined by the complexity and variability of ecological systems' properties in space (Li and Reynolds 1994). In this study, I considered effects of spatial heterogeneity in soil, topography and vegetation patterns on native and nonnative plant species diversity.

The distribution of plant species diversity from stand to landscape levels is determined by a number of factors such as climate, resource heterogeneity, habitat diversity, patch size and shape, connectivity, diversity of stands across the landscape, stand seral stage, vegetation structure and composition within stands, and disturbance

(Rosenzweig 1995, Szaro and Johnson 1996, Stohlgren et al. 1998a, Hunter 1999). Disturbances such as fire, flood, insect outbreaks, and grazing, which occur at multiple scales, affect the spatial and temporal heterogeneity of ecosystems, influence local and landscape level patterns of species diversity, and lead to a patchy vegetation structure (Pickett and Thompson 1978, Pickett and White 1985, Stohlgren et al. 1997a, b). However, the propagation of disturbance in an area may depend on the interplay between disturbance intensity and frequency and the amount of spatial heterogeneity because spatial heterogeneity may enhance or retard the spread of disturbance (Risser 1987, Turner et al. 1989a). Therefore, it is important to investigate the effects of spatial heterogeneity on plant diversity patterns, especially in areas threatened by habitat loss and invasive species (Stohlgren et al. 1999).

Several authors have attempted to define spatial heterogeneity (Kolasa and Rollo 1991, Dutilleul and Legendre 1993, Wiens 1995). Li and Reynolds (1994) operationally defined spatial heterogeneity in categorical and numerical maps. In this study, I followed their definition of spatial heterogeneity in categorical maps (I called it "landscape heterogeneity") that they defined in terms of five compositional and configurational components: (1) number of patch types; (2) proportion of each patch type; (3) spatial arrangement of patches; (4) patch shape; and (5) contrast between neighboring patches (Li and Reynolds 1994). Quantification of landscape heterogeneity is needed to investigate its effects on ecosystem processes. Different components of landscape heterogeneity can be quantified in terms of landscape metrics (Gustafson 1998), which are algorithms that quantify specific spatial characteristics of patches, classes of patches, or entire landscape mosaics (McGarigal et al. 2002). Recently, landscape metrics have been successfully used to quantify different aspects of landscape heterogeneity (e.g., Meyer et al. 1998, Mazerolle and Villard 1999, Kie et al. 2002).

Because of economic and time constraints, it is affordable only to measure a small portion (usually, 1%) of any landscape, but resource managers need species distribution information across the entire landscape for planning biodiversity conservation and monitoring. Therefore, predictive distribution models are needed, both for native and nonnative plant species, which can accurately and reliably provide information over the remainder of the landscape (Stohlgren et al. 1997a). A number of approaches have been used to develop predictive models for native and nonnative plant species richness at different spatial scales. However, most of these have included predictor variables representing environmental/topographic, soil, and biotic heterogeneity (e.g., Stohlgren et al. 1998a, 1999, 2000, 2005, Davies et al. 2005), and have largely neglected landscape heterogeneity. Only a few studies have included all five components (as per definition given by Li and Reynolds 1994) of landscape heterogeneity (e.g., Meyer et al. 1998, Kie et al. 2002) for other taxa, but rarely for plants. Most studies only included one or two components of landscape heterogeneity such as patch characteristics (see review by Mazerolle and Villard 1999).

Why should ecologists care about the effects of landscape heterogeneity on plant species diversity? There are a number of factors that influence plant species' ability to disperse, establish, survive and reproduce successfully that may be influenced by configuration and composition of the landscape. For example, the dispersal of plant propagules across the landscape might be affected by the spatial arrangement of patches (e.g., distance between patches, structural contrast among patches, juxtaposition, patch size and shape). Even if a plant species is able to disperse to a site, its reproduction, survival, and establishment will depend on resources available at that site including a number of biotic and abiotic conditions. Edges may facilitate or inhibit species' dispersal depending on their structural characteristics and microenvironment, and the flow of propagules. For example, most nonnative plant species are great dispersers and edges may trap their airborne propagules and facilitate invasion (Brothers and Spingarn 1992, Harrison et al. 2001). Therefore, areas with many small patches or high edge density are expected to be more prone to invasion by nonnative plant species.

I propose a general methodology that can be used to investigate the role of spatial heterogeneity in influencing patterns of biodiversity. In addition to variables representing environmental/topographic (slope, aspect, elevation, distance from stream or water) and soil (nitrogen, clay, and sand) heterogeneity, I used composition and configuration landscape metrics to characterize heterogeneity in vegetation patterns. The broad research questions I addressed were: (1) Does spatial heterogeneity play an important role in the distribution of plant species richness? (2) Is this effect different for native and nonnative plant species richness? (3) How does this effect change with a change in (a) spatial extent of analysis, and (b) level of ecological hierarchy (i.e., landscape, land cover, and community)?

1.2 Study area

The study area comprised ~ 80 000 ha in the central portion of Rocky Mountain National Park, Colorado, USA. Rocky Mountain National Park extends from $40^0 10^0$ N to 40^0 34' N latitude and 105^0 30' W to 105^0 55' W longitude, covers ~107 500 ha with an elevation ranging from 2300 m to over 4300 m above mean sea level, and lies on the

Front Range of the southern Rocky Mountains in Colorado (Fig. 1.1). The average annual minimum and maximum temperatures are -1.5^0 and 14.0^{0}C (taken near Estes Park, 105^0 30’ W, 40^0 24’ N; at 2390 m elevation at the east side entrance of the park). The mean annual precipitation is 36 cm, with the highest proportion in May and July (Ehle and Baker 2003). The latitudinal and elevation arrangements of species distributions have been attributed to temperature and precipitation, as typically influenced by elevation and topographic position (Peet 1981, 1988, Allen et al. 1991). The area exhibits a variety of vegetation communities from prairie to tundra (see Plate 1). Dominant vegetation types and plant species include: prairie vegetation dominated by short grasses (*Bouteloua gracilis* Vasey in Rothr., *Buchloe dactyloides* Engelm.) and sage brush (*Artemisia tridentata* Nutt.); ponderosa pine (*Pinus ponderosa* Douglas ex. C. Lawson; 2320– 3170 m); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; 2370–3213 m); lodgepole pine (*Pinus contorta* Doug. ex. Loud; 2380–3480 m); aspen (*Populus tremuloides* Mich.; 2350–3500 m); limber pine (*Pinus flexilis* James; 2620–3560 m); and spruce (*Picea engelmannii* Perry ex. Engel.; 2530–3710 m) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.; 2530–3710 m; Peet 1988).

1.3 Methods

1.3.1 Landscape mapping/classification

The landscape heterogeneity was represented by an existing digital land cover type map prepared by the Rocky Mountain National Park Geographical Information Systems Program (RMNP GIS Program 1995). The map was developed using a series of 1:15 840 scale color aerial photographs acquired in September 1987 and September 1988.

The accuracy of the map is estimated to be 80–85%. This was the best available map for the area that was close to the period (1995–1999) of vegetation and soil sampling. There were no major disturbances in the area since the acquisition of the aerial photographs and the field sampling. I grouped original map's classes into seven land cover types: conifer, deciduous, grasses, shrub, tundra, willows, and non-vegetated. For example, Douglas-fir, limber pine, lodgepole pine, ponderosa pine, and Engelmann spruce/subalpine fir were grouped into the conifer class; and aspen, cottonwood, alder/aspen were grouped into the deciduous class.

Based on the concept of hierarchical structuring of biological systems (Urban et al. 1987, O'Neill et al. 1989) I developed plant species richness prediction models at three levels of ecological hierarchy, assuming that measures of spatial heterogeneity may have differential effects at each level of the hierarchy. I classified the highest level in the hierarchy as the landscape level, which is a mosaic of patches of all the land cover types in the study area. The intermediate level of organization was defined as the land cover, which included relatively homogenous cover types, defined by their broad botanical composition (Cherrill et al. 1995) and defined the six classes as conifer, deciduous, grasses, shrub, tundra, and willows. The lowest level in the hierarchy, the community level, included the dominant species-based communities within a land cover type (e.g., ponderosa pine, lodgepole pine, and Engelmann spruce/Douglas-fir, communities within the conifer land cover type).

1.3.2 Vegetation and soil sampling

Plant species richness data were collected from 180 20 x 50 m (1000-m^2) Modified-Whittaker, multi-scale plots with the long axis parallel to the environmental gradient (Stohlgren et al. 1998b) between 1995 and 1999. Sample points were located based on stratified random sampling in different vegetation types identified on the color aerial photographs (1:15 840 scale). Each site was sampled as close to peak biomass as possible. Plant species that could not be identified in the field were collected and identified in the herbarium at Colorado State University (Department of Biology, Fort Collins, Colorado, USA). Fewer than 5% of the specimens encountered could not be identified to species due to phenological stage or missing flower parts. In these cases, plants were identified to genus and treated as individual species. Native and nonnative species were classified using local and regional floras. Ancillary data recorded for each plot included location, elevation, slope, and aspect. Plot locations and elevation were recorded using the global positioning system (GPS; Trimble Navigation Limited, Westminster, Colorado, USA), and coordinates were taken using the Universal Transverse Mercator (UTM) system, which provides x, y coordinates in meters from a regional reference point.

Five soil samples were taken in each Modified-Whittaker plot (one in each corner and one in the plot center) and pooled into one sample (see Stohlgren et al. [1999] for details). The surface litter, if present, was removed, and the top 15 cm of soil was sampled. Samples were air dried for 48 h, sieved with a standard number 10 (2-mm pore size) sieve, ground in a standard three-ball grinder, and then oven-dried at 55^0C for 24 h. Samples were analyzed for percentage total carbon and nitrogen using a LECO-1000 CHN analyzer (LECO Corporation, Saint Joseph, Missouri, USA; following the methods of Carter 1993), and for particle size (clay, silt, and sand fractions) based on the standard hydrometer method (Gee and Bauder 1986).

1.3.3 Environmental/topographic variables

The environmental/topographic heterogeneity in the area was represented by elevation, slope, aspect, and distance from stream or river. Digital elevation model (DEM) data for the area were downloaded from the National Elevation Data set, U.S. Geological Survey website, to sample elevation (m) for the centroid of each 0.1-ha plot. Subsequently, the DEM grid (30 x 30 m) was used to generate slope (in degrees), and aspect (in degrees) using Environmental Systems Research Institute's (ESRI, Redlands, California, USA) ARC GIS, version 9.0, surface analysis functions. For statistical analyses, I transformed the circular variable aspect into a linear north-south gradient (northness) and an east-west gradient (eastness) by performing cosine and sine transformations, respectively (Guisan et al. 1999, Gutierrez et al. 2005). Northness varies from -1 (south-facing) to 1 (north-facing), and eastness from -1 (west-facing) to 1 (east-facing). Both of these variables can be used to define the relative position of a location in two orthogonal aspect gradients (Gutierrez et al. 2005). Streams or rivers may affect the distribution and establishment of plant species by influencing seed dispersal and moisture availability. Also riparian zones often contain more nonnative plant species than nearby upland areas (Stohlgren et al. 1998c). Therefore, I included distance from stream or river as one of the environmental variables in my models. A stream or river network shapefile was acquired from the Colorado Department of Water Resources. After converting it into a raster layer of 30 x 30 m cell size, Euclidean distance for the centroid of each 0.1-ha plot from the nearest stream or river was calculated using Map Calculator in Arc Map of ARC GIS version 9.0.

1.3.4 Quantifying landscape heterogeneity

Landscape heterogeneity was quantified by measuring landscape metrics at four spatial extents. I measured 13 commonly used configuration metrics (landscape level) including mean edge contrast, edge density, mean patch size, patch size coefficient of variation, mean fractal dimension, mean nearest neighbor distance (in m), mean shape index, contagion, cohesion, interspersion/juxtaposition index, patch richness density, Shannon's diversity index, Simpson's diversity index; and one composition metric (class level, PLAND- proportion of the area occupied by each land cover type; McGarigal et al. 2002) representing five components of landscape heterogeneity (Li and Reynolds 1994). The definitions and formulas for these metrics are given elsewhere (McGarigal et al. 2002). These metrics were chosen based on their potential biological relevance to plant species richness, and quantifiable definition of landscape heterogeneity in categorical maps (Li and Reynolds 1994) and their successful use in past studies (e.g., Meyer 1998, Kie et al. 2002).

The land cover type map in raster format (ESRI GRID; projection, UTM; datum, NAD 1927; and cell size, 30 m) was used as a basic input data layer for measuring landscape metrics. I used the raster version of the FRAGSTATS, version 3.0, landscape pattern analysis program (McGarigal et al. 2002) to calculate the landscape metrics. Four nested spatial extents were considered by measuring landscape metrics within varying radii (120, 240, 480, and 960 m) windows. I chose to use circular windows over square assuming that the zone of influence of landscape heterogeneity around vegetation plots may be better approximated by a circle than a square.

The selection of spatial scale to quantify spatial heterogeneity may be critical as spatial heterogeneity is highly scale dependent (Wagner and Fortin 2005). Spatial scale may refer to both “grain” and “extent” (Turner et al. 1989b). In this study, the grain size was fixed because I used the data from the sources with fixed grain size (30 x 30 m) but I varied the spatial extent of analyses. Ecologists studying the effects of spatial heterogeneity on other taxa such as animals and insects generally use home range or territory size or area of an organism’s activities (e.g., Kie et al. 2002, Steffan-Dewenter et al. 2002, Boyce et al. 2003) to assess spatial scale of analysis to quantify spatial heterogeneity. However, for plants, such scale is difficult to decide a priori because different plant species may have differential responses to multiple levels of spatial heterogeneity of resources and other covariates. Therefore, the spatial extents of analysis were selected based on the expected dispersal and establishment abilities of the plant species in the area and their expected response to adjacent spatial heterogeneity of soil, topography, and vegetation. I started with the smallest scale as 120 m, assuming that most of the species in the area were at least influenced by spatial heterogeneity within 120 m of their surrounding, and so, considered it to be the smallest zone of influence of spatial heterogeneity. Successive radii were determined by doubling the previous radius. Corresponding areas were 4.5, 18, 72, and 290 ha, respectively. I also conducted spatial analyses at the next successive higher scale (1920 m) but excluded it from the models due to the edge effect from losing many samples at that scale. For each of the four spatial extents, mean values of the environmental/topographic covariates were also calculated.

1.3.5 Statistical analyses

The estimates of landscape metrics obtained in landscape analyses were used to develop the native and nonnative plant species richness prediction models. In addition, elevation, slope, northness, eastness, and distance from stream or river were used as surrogate variables for topographical heterogeneity. Soil heterogeneity in the models was considered by including the total soil N and percentages of sand and clay (to reduce multicollinearity, percentage silt was not added into the models). Before conducting regression analyses, I tested all the variables for multicollinearity (Neter et al. 1996) by examining cross-correlations among variables (Table 1.1). I also calculated variance inflation factors (VIF; Neter et al. 1996). Since Neter et al. (1996) suggested that multicollinearity is only severe at VIFs > 10, the variables with high VIF (in my models VIF > 2.5) and cross-correlation > $\pm$ 0.75 were not included in the same model. I conducted stepwise forward multiple regressions to eliminate insignificant predictors. In all the models I used plant species richness (i.e., number of species per 0.1-ha plot) as a measure of plant diversity. Data distributions that were strongly skewed were transformed prior to analysis. For example, $\log_{10}$ transformations were performed on total soil N and nonnative plant species richness. Univariate regression was used to identify relationships between various independent variables and native and nonnative plant species richness. Regression analyses were conducted using the PROC REG procedure in SAS software (SAS Institute 2004) and alpha = 0.05 was used to determine significance level in all cases.

Response variables for the landscape-level models included native and nonnative plant species richness data from 79 plots (0.1 ha) out of the 180 Modified-Whittaker plots. Since I wanted to consider soil heterogeneity in this study; 80 plots with missing soil data were excluded from the analysis. Further, to account for edge influence in landscape analysis (McGarigal et al. 2002), 21 plots falling on the edges were also removed from analysis. For models at the level of land cover type, 79 plots were divided into six land cover types based on their spatial distribution. For example, plots falling on conifer land cover type (i.e., 49 plots) were used as response variables to develop the conifer land cover type's native and nonnative plant species richness models. A similar approach was followed for community-level models. For example, for community-level models, the conifer land cover type plots (49) were further divided into lodgepole pine (24), ponderosa pine (13), and Engelmann spruce/subalpine fir (12). However, because of the inadequate number of samples I could only develop models for the conifer land cover type and the lodgpole pine community.

I used Akaike's Information Criteria (AIC) and the information-theoretic approach (Burnham and Anderson 2002) to evaluate multiple regression models and select the "best" models for native and nonnative plant species richness at three levels of ecological hierarchy from a set of candidate models developed at four spatial extents. I assumed normally distributed errors with a constant variance for least-squares regressions, and computed AIC as

$$\mathrm{AIC} = \mathrm{n} \log (\mathrm{RSS/n}) + 2K \qquad (1)$$

where n is the sample size; RSS is the residual sum of squares in the model; RSS/n is the maximum likelihood estimator (MLE); and K is the total number of estimable parameters in the model (including the intercept and residual variance; Burnham and Anderson

2002). Since the number of samples was small (n = 79) relative to K, I calculated AIC adjusted for small sample size (AIC_c) as follows:

$$AIC_c = AIC + 2K(K+1) / (n - K - 1) \tag{2}$$

Since AIC_c is on a relative scale, I calculated differences in AIC_c values as

$$\Delta AIC_{ci} = AIC_{ci} - \text{minimum } AIC_c \tag{3}$$

across all candidate models in the set. The best model has $\Delta AIC_{ci} = 0$ and only the models with $\Delta AIC_{ci} \leq 2$ have substantial support (Burnham and Anderson 2002).

1.3.6 Spatial autocorrelation

Native and nonnative plant species richness data and residuals from the regression models were tested for spatial autocorrelation using Moran's I (Legendre and Legendre 1998). Since the original Moran's I does not vary exactly between -1 and +1, it was standardized (I_{std}) by dividing by its maximum attainable value (Haining 1990, Lichstein et al. 2002). Spatial correlograms were constructed using I_{std} at 20 distance classes. Each lag distance class was 150 m wide to a maximum distance of 3100 m. However, to ensure the adequate number of site pairs (Fortin 1999); the first lag distance interval was extended to 250 m (containing 30 site pairs). Randomization tests (999 permutations) were used to determine the probability of observing a value of Moran's I as large as the observed value (Lichstein et al. 2002). Each correlogram was tested for global significance using a Bonferroni-corrected α^* of 0.05/20 =0.0025 ($\alpha = 0.05$, 20 lags; Legendre and Legendre 1998, Lichstein et al. 2002). The significance of I_{std} at each lag distance class was assessed using progressive Bonferroni correction (Legendre and Legendre 1998, Lichstein et al. 2002). Explanatory variables in the native and nonnative plant species richness models were also tested for spatial autocorrelation. All spatial statistical analyses were performed using S-PLUS (version 7.0) statistical software (Insightful Corporation, Seattle, Washington, USA) and the spatial library written by R. M. Reich and R. A. Davis (Reich and Davis 2006).

1.4 Results

1.4.1 Relationship between measures of spatial heterogeneity and native and nonnative plant species richness

Both native and nonnative plant species richness were significantly correlated with different measures of spatial heterogeneity at four spatial extents. At the landscape level, nonnative plant species richness was significantly negatively correlated with elevation ($r = -0.67$, $P < 0.0001$, 120-m spatial extent), slope ($r = -0.47$, $P < 0.0001$, 960-m extent), and distance from stream or river ($r = -0.43$, $P < 0.0001$, 480-m extent). This suggests that nonnative species are more prevalent in lower elevations and resource-rich riverine areas (Stohlgren et al. 1998c). No relationship was found between native plant species and elevation, slope, and distance from stream or river. However, native plant species richness showed a positive relationship with eastness ($r = 0.29$, $P = 0.011$, 120-m extent).

Most of the landscape metrics were correlated with native and nonnative plant species richness. For example, both native and nonnative plant species richness were positively correlated with edge density, Simpson's diversity index, and interspersion/juxtaposition index (Figs. 1.2 and 1.3). A significant negative relationship was found between mean patch size and native and nonnative plant species richness (the correlation coefficient, r, varied from - 0.23 to - 0.42) at all four spatial extents (Figs. 1.2

and 1.3). Most of these relationships were relatively stronger for nonnative plant species richness.

1.4.2 Predictive models of native and nonnative plant species richness

Predictive models of native and nonnative plant species richness were developed separately at four spatial extents for each of the three levels of ecological hierarchy using landscape metrics, environmental/topographic, and soil variables. Most of the models included at least one or more landscape metric(s), and were highly statistically significant ($P < 0.0001$). The amount of variation explained by the best models (based on AIC_c) varied from 30% to 70%, and, in general, more nonnative plant species richness variation was explained (Table 1.2).

At the landscape level, the best model (lowest $AIC_c = 366.76$, $\Delta AIC_c = 0$) explained 43% of the variation in native plant species richness at the 240-m spatial extent (model 1, Table 1.3) and included predictors from all three groups of variables: environmental/topographic, soil, and landscape metrics. Patch richness density (partial $R^2 = 0.125$) and soil nitrogen (partial $R^2 = 0.110$) were among the best redictors of native plant species richness (Table 1.2). Other models explained 18–31% of the variation in native plant species richness (models 2-6, Table 1.3). Landscape metrics alone explained little variation (adjusted $R^2 = 0.18$) in native plant species richness (model 6, $\Delta AIC_c = 24.41$, Table 1.3). However, when coupled with other groups of variables (i.e., environmental/topographic or soil), they significantly improved the models (models 1–3, Table 1.3).

Of the six models evaluated for nonnative plant species richness at the landscape level, the best model (lowest $AIC_c = -260.50$, $\Delta AIC_c = 0$) explained 70% of the variation in nonnative plant species richness (model 7, Table 1.4). In addition to three groups of variables, this model also included native plant species richness as one of the predictors (Table 1.2). Mean elevation (partial $R^2 = 0.440$) and native plant species richness (partial $R^2 = 0.208$) were the two best predictors of nonnative plant species richness (Table 1.2). Other candidate models explained 30–56% of the variation in nonnative plant species richness (models 8–12, Table 1.4). A model that included only landscape metrics (model 12, $\Delta AIC_c = 66.05$, Table 1.4) explained 30% of the variation in nonnative plant species richness. However, inclusion of landscape metrics with other groups of variables significantly improved model performance (models 7, 8, and 10, Table 1.4).

At the land cover level, the best models explained 30% of the variation in native plant species richness and 66% of the variation in nonnative plant species richness for the conifer land cover type at the 120-m spatial extent (Table 1.2). Edge density (partial $R^2 = 0.222$) was one of the best predictors of native plant species richness, and elevation (partial $R^2 = 0.486$) was the best predictor of nonnative plant species richness in conifer land cover type models (Table 1.2). At the community level, the best models explained 41% and 66% of the variation in native and nonnative species richness, respectively, for the lodgepole pine community. Edge density (partial $R^2 = 0.299$) was the best predictor of native species richness, and fractal dimension (partial $R^2 = 0.144$) was one of the best predictors of nonnative plant species richness for the lodgepole pine community.

At the landscape level, positive spatial autocorrelation was detected in nonnative plant species richness (n = 79, log-transformed; $I_{std} = 0.0955$, $P < 0.0001$, global Bonferroni test significant at $\alpha^* = 0.0025$). However, native plant species richness did not exhibit any significant spatial autocorrelation (n = 79, $I_{std} = -0.0247$, $P = 0.70$, not significant at $\alpha^* = 0.0025$). The spatial autocorrelation observed in nonnative plant species richness may be a result of their seed dispersal (by wind, water, birds, and animals) pattern or spatially structured ecological processes. The Moran's I_{std} spatial correlogram for nonnative plant species richness (Fig. 1.5) showed some significant positive spatial pattern only at two lag distances (i.e., 550 and 1150 m). However, the native plant species correlogram did not show any significant spatial pattern at any of the lag distances (Fig. 1.5). Some of the predictors (e.g., elevation, slope, and interspersion/juxtaposition) also exhibited positive spatial autocorrelation. Residuals from native and nonnative plant species richness models (landscape level) did not show any significant spatial autocorrelation ($I_{std} = 0.0172$, $P = 0.27$ for native, and $I_{std} = - 0.0132$, $P = 0.91$ for nonnative). The correlogram for nonnative plant species richness model residuals showed significant autocorrelation only at 250-m and 400-m lag intervals, whereas the correlogram for native plant species richness model residuals did not show any spatial pattern at any of the lag distances. No significant spatial autocorrelation was detected in residuals from the conifer land cover type native ($I_{std} = - 0.0008$, $P = 0.56$) and nonnative ($I_{std} = - 0.0385$, $P = 0.61$) plant species richness models, nor for the lodgepole pine community native ($I_{std} = - 0.0094$, $P = 0.58$) and nonnative ($I_{std} = - 0.0953$, $P = 0.21$) plant species richness models. The absence of spatial autocorrelation in the nonnative plant species richness model residuals suggest that the spatial pattern in the raw data (i.e., log-transformed nonnative plant species richness) was explained by the spatial autocorrelation observed in some of the predictor variables (Legendre and Legendre 1998).

1.5 Discussion

In this paper, I offer a general approach to quantify spatial heterogeneity to improve models of plant biodiversity patterns. My approach combined the power of field data, remotely sensed data, and easy-to-calculate landscape metrics that are readily available to many plant ecologists. The methodology presented here is not entirely new to ecologists, as the role of landscape heterogeneity has been recognized in other taxa, especially birds, animals, and insects (e.g., Pearson 1993, Pearson et al. 1995, Meyer et al. 1998, Kie et al. 2002, Steffan-Dewenter et al. 2002, Boyce et al. 2003), but somehow is relatively less recognized by plant ecologists.

My results suggest that spatial heterogeneity plays an important role in the distribution of native and nonnative plant species richness across this landscape, and that nonnative plant species are more sensitive to spatial heterogeneity (Table 1.2, Figs. 1.2-1.4). This is consistent with the idea that landscapes with greater heterogeneity can support more native and nonnative species; however, my results suggest that there may be a threshold to the effect of spatial heterogeneity to which plant species are more sensitive (Fig. 1.4). The inclusion of landscape metrics as predictor variables along with environmental/topographic and soil variables greatly improved the predictive ability of plant species richness models (Tables 1.3 and 1.4, Fig. 1.4). This suggests that landscape configuration and composition are important determinants of native and nonnative plant species diversity in this study area. However, the relative importance of the components of spatial heterogeneity predicting native and nonnative species richness varied with the spatial extent of measurements and the level of ecological hierarchy (Table 1.2, Fig. 1.4). My results demonstrated that the effect of spatial heterogeneity on the distribution of native and nonnative plant species richness was highly scale dependent (Fig. 1.4), which is consistent with what researchers have found for other taxa (Pearson 1993, Pearson et al. 1995, Kie et al. 2002, Steffan-Dewenter et al. 2002). This may be partly due to (1) ''local determinism,'' where species richness at large spatial scales is determined by optimal environmental conditions or local site history and evolutionary history (Ricklefs 2004); and (2) current ecological processes operating at various spatial scales.

The stronger response of nonnative plant species to spatial heterogeneity suggests that they may be affected by different measures of spatial heterogeneity than native plant species. This may be because they have not yet had enough time to disperse across the landscape whereas native species have had a long time to establish. The stronger relationship between nonnative plant species richness and edge density and mean patch size (Fig. 1.3) suggests that their rates of propagule dispersal and potential for establishment and spread may be influenced by edges or disturbances (Harrison et al. 2001).

Some ecological processes affecting plant species richness operate at small spatial scales (e.g., neighborhood competition, gap dynamics), while others operate at intermediate and larger scales (e.g., fires, climate change). The change in predictive abilities of regression models with the change in levels of ecological hierarchy could be attributed to the changes in plant physiology or morphology (such as conifer or deciduous trees), plant size, and climatic limitations (e.g., tundra vs. forest species), varied light availability to the understory plants, moisture and nutrient availability, or varied levels of dominance of different species in different patches. In any case, I believe that landscape metrics may integrate complex environmental conditions that influence vegetation plots, and, thus, landscape metrics may be important for understanding species composition, invasion, coexistence, and persistence.

1.5.1 Appropriately scaling landscape metrics analyses

In this case study, measures of spatial heterogeneity at an intermediate spatial extent (240 m, i.e., 18 ha) provided the best models that explained the highest variation in native and nonnative plant species richness at the landscape level. The models at successively smaller (120-m) and larger (480- and 960-m) spatial extents explained relatively less variation at the landscape level. For general applications, this suggests that the spatial analyses should be conducted at multiple spatial extents (Pearson 1993, Pearson et al. 1995, Kie et al. 2002, Steffan-Dewenter et al. 2002) and that the identification of an appropriate scale is an important first step in understanding the effects of spatial heterogeneity on ecological processes across multiple spatial scales (Turner et al. 1989b). The strongest influence of the 240-m spatial extent (Fig. 1.4) on native and nonnative plant species richness in this study may be related to the relatively coarse grain of the Rocky Mountain National Park landscape. Given the range of variation in topographic relief in the study area, the most effective extent may also be related to the coarseness of the environmental variation in this landscape. However, other landscapes with lower topographic variability, different degrees of patchiness of the vegetation, different disturbance regimes, or different species composition may exhibit different spatial extents at which surrogates of spatial heterogeneity will show the strongest influence on patterns of plant species diversity. Therefore, the specific model results developed in this study cannot be directly applied to other regions. Models developed for other regions, or smaller or larger areas in a region, may vary in the intensity of influence of landscape metrics at various spatial extents. In my species richness models, I varied only spatial extent and kept the grain size constant (i.e., 30 m); however, most landscape metrics are also sensitive to changes in grain size and thematic resolution of the input map (Benson and MacKenzie 1995, O'Neill et al. 1996, Baldwin et al. 2004). In addition, the models developed in this study may also be sensitive to the "resolution" at which plant species richness data were sampled (i.e., 0.1-ha plot size used in this field survey). Therefore, more research is needed to investigate the effects of changing grain size, thematic resolution, and sampling resolution on these models.

1.5.2 Improving multi-scale metrics and models in plant diversity studies

Since it is affordable to measure only a small portion of a landscape, predictive models of plant species diversity are necessary for estimating diversity for the remaining parts of a landscape (Stohlgren et al. 1997a). Advances in modeling complex patterns of plant diversity may require more sophisticated field measurements and landscape metrics than I used. In this study, I only considered between-patch heterogeneity and ignored the fine-scale, within-patch, spatial heterogeneity, which is one of the dominant characteristics of vegetation structure (Lertzman and Fall 1998) that may have strong effects on plant species distributions, specifically on the establishment and spread of invasive plant species (Jurena and Archer 2003). I considered horizontal (two-dimensional) spatial heterogeneity effects on plant species diversity. However, vertical spatial heterogeneity generated by vertical vegetation stratification also affects plant species diversity. For example, the spatial structure of canopy trees in a forest greatly influences understory plant regeneration and succession patterns (Clark et al. 1996, Moeur 1997) and may affect community structure and biodiversity patterns. Sunlight penetration through the canopy is directly related to the three-dimensional spatial pattern of vegetation and influences the interactions between organisms and their physical environments (Stohlgren et al. 2000). Although it is difficult to characterize the vertical spatial heterogeneity at the landscape level with commonly used techniques, recently developed lidar (light detection and ranging) remote sensing techniques hold the potential to characterize the fine-scale, within-patch spatial pattern and heterogeneity of canopy structure (Frazer et al. 2005) at the landscape level (Lefsky et al. 2002a, b, Frazer et al. 2005). The addition of vertical spatial heterogeneity might greatly improve the present models.

1.6 Conclusions

I showed that spatial heterogeneity may play an important role in determining the distribution of native and nonnative plant species richness. I recognize the importance of landscape heterogeneity when developing species distribution models at landscape or regional scales. Quantitative data on spatial heterogeneity should come from analysis at the scale that most influences plant species composition. Therefore, I also suggest that predictive models need to be developed at multiple spatial scales to determine which scales are the most influential. We are in our infancy in developing generalized theories and methods in quantifying habitat heterogeneity, and I recommend that an experimental approach be taken in further landscape ecology studies including:

1) testing multiple types of remote sensing data (vertical and horizontal imaging) in developing landscape metrics;

2) testing the landscape metrics at several scales (i.e., grain, extent, and thematic resolution) with continuous scaling being most desirable (although it is difficult and computer intensive now);

3) developing separate models for native and nonnative species to gain a better understanding of invasion patterns;

4) using vegetation and landscape hierarchy schemes to produce general models (i.e., for other species at other sites); and

5) merging the types of multivariate models described here with spatial analysis models (e.g., kriging, cokriging) to evaluate the role of spatial autocorrelation in the data.

Finally, I draw attention to the urgency associated with predicting nonnative species invasions to improve understanding and conservation of native plant diversity.

1.7 Acknowledgements

Discussions with Barry Noon, and comments on an earlier draft by Geneva Chong and Dan Kashian improved this Chapter. Thanks to Robin Reich for assistance with spatial statistical analyses. The data used in this study were collected by a number of field technicians assisted by many excellent taxonomists from the Natural Resource Ecology Laboratory at Colorado State University, and the U. S. Geological Survey Fort Collins Science Center. The staff at Rocky Mountain National Park provided housing and logistical support. I also acknowledge the support of the Ford Foundation International Fellowships Program for Ph.D. studies at Colorado State University. To all I am grateful.

1.8 Literature cited

Allen, R. B., R. K. Peet, and W. L. Baker. 1991. Gradient analysis of latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography **18**:123-139.

Baldwin, D. J. B., K. Weaver, F. Schnekenburger, and A. H. Perera. 2004. Sensitivity of landscape pattern indices to input data characteristics on real landscapes: implications for their use in natural disturbance emulation. Landscape Ecology **19**: 255-271.

Benson, B. J., and M. D. MacKenzie. 1995. Effects of sensor spatial resolution on landscape structure parameters. Landscape Ecology **10**:113-120.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience **10**: 421-431.

Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6**:91-100.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretical approach. Second edition. Springer, New York, New York, USA.

Carter, M. R., editor. 1993. Soil sampling and methods of analysis. Lewis, Boca Raton, Florida, USA.

Cherrill, A. J., C. McClean, P. Watson, K. Tucker, S. P. Rushton, and R. Sanderson. 1995. Predicting the distribution of plant species at the regional scale: a hierarchical matrix model. Landscape Ecology **10**:197-207.

Clark, D. B., D. A. Clark, P. M. Rich, S. Weiss, and S. F. Oberbaur. 1996. Landscape–scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. Canadian Journal of Forest Research **26**:747-757.

Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology **86**: 1602-1910.

Dutilleul, P., and P. Legendre. 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. Oikos **66**: 152-171.

Ehle, D. S., and W. L. Baker. 2003. Disturbance and stand dynamics in Ponderosa pine forests in Rocky Mountain National Park, USA. Ecological Monographs **73**:543-566.

ESRI. 2004. Environmental Systems Research Institute, Inc., 380 New York St., Redlands, CA 97373, USA.

Forman, R. T. T., and M. Godron. 1986. Landscape Ecology, John Wiley and Sons, New York, New York, USA.

Fortin, M.-J. 1999. Spatial statistics in landscape ecology. Pages 253-279 *in* R. H. Gardner, and J. M. Klopatek, editors. Landscape ecological analysis: issues and applications. Springer-Verlag, New York.

Fortin, M.-J., and A. A. Agarwal. 2005. Landscape ecology comes of age. Ecology **86**: 1965-1967.

Frazer, G. W., M. A., Wulder, and K. O. Niemann. 2005. Simulation and quantification of the fine-scale spatial pattern and heterogeneity of forest canopy structure: a lacunarity-based method designed for analysis of continuous canopy heights. Forest Ecology and Management **214**: 65-90.

Gee, G. W., and J. W. Bauder. 1986. Particle size analysis. Pages 383-411 *in* A. Klute, editor. Methods of soil analysis. Part I. Physical and mineralogical methods. Second edition. American Society of Agronomy, Madison, Wisconsin, USA.

Guisan, A., S. B., Weiss, and A.D. Weiss. 1999. GLM versus CCA spatial modeling of plant species distribution. Plant Ecology **143**:107-122.

Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems **1**: 143-156.

Gutierrez, D., Fernandez, P., Seymour, A.S., and D. Jordano. 2005. Habitat distribution models: are mutualist distributions good predictors of their associates? Ecological Applications **15**:3-18.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University press, Cambridge, UK.

Hargis, C. D., J. A. Bisonette, and J. L. David. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecology **13**:167-186.

Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. Biological Conservation **100**:45-53.

Hunter, M., editor. 1999. Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, New York.

Huston, M. A. 1994. Biological Diversity: the coexistence of species in changing landscapes. Cambridge University Press, UK.

Jurena, P. N., and S. Archer. 2003. Woody plant establishment and spatial heterogeneity in grasslands. Ecology **84**: 907-919.

Kauffman, M. J., and E. S. Jules. 2006. Heterogeneity shapes invasion: host size and environment influence susceptibility to a nonnative pathogen. Ecological Application **16**: 166-175.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology **83**:530-544.

Kolasa, J., and C. D. Rollo. 1991. The heterogeneity of heterogeneity: a glossary. Pages 1-23 *in* J. Kolasa, and S. T. A Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Legendre, P., and Legendre, L. 1998. Numerical ecology. Second English edition. Elsevier Science, Amsterdam, The Netherlands.

Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. Harding. 2002a. Lidar remote sensing for ecosystem studies. Bioscience **52**:19-30.

Lefsky, M. A., W. B. Cohen, D. J. Harding, G. G. Parker, S. A. Acker, and S. T. Gower. 2002b. Lidar remote sensing of aboveground biomass in three biomes. Global Ecology and Biogeography **11**:393-400.

Lertzman, K. P., and J. G., Fall. 1998. From forest stands to landscapes: spatial scales and the roles of disturbance. Pages 339-367 *in* D. L. Peterson, and V. T., editors. Ecological scale: theory and applications. Columbia University Press, New York.

Li, H., and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology **75**:2446-2455.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs **72**:445-463.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology **42**: 594-598.

Mazerolle, M. J., and M. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience **6**:117-124.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS, version 3.0: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>

Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs **139**: 1-51.

Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscape. Pages 69-84 *in* J. Kolasa, and S. T. A Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Moeur, M. 1997. Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla/Thuja plicata* forests. Forest Ecology and Management **34**:70-78.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models: regression, analysis of variance, and experimental designs. Fourth edition. Irwin, Chicago, Illinois, USA.

O'Neill, R. V., C. T. Hunsaker, S. P. Timmins, B. L. Jackson, K. B. Jones, K. H. Riitters, and J. D. Wickham. 1996. Scale problems in reporting landscape patterns at the regional scale. Landscape Ecology **11**:169-180.

O'Neill, R.V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology **3**:193-205.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology **8**:3-18.

Pearson, S. M., M. G. Turner, L. L. Wallace, and W. H. Romme.1995. Winter habitat use by large ungulates following fires in northern Yellowstone National Park. Ecological Applications **5**:744-55.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio **45**: 3-75.

Peet, R. K. 1988. Forests of the Rocky Mountains. Pages 64-101 *in* M. G. Barbour, and W. D. Billings, editors. North American Terrestrial Vegetation, Cambridge University Press, New York.

Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation **13**:27-37.

Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: a synthesis. Pages 371-384 *in* S. T. A. Pickett, and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science **269**: 331-334.

Reich, R. M., and R. A. Davis. 2006. Online spatial library for the S-PLUS 7.0 statistical software package. Colorado State University, Fort Collins, CO, USA.

< http://www.warnercnr.colostate.edu/~robin/>

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters **7**: 1-15.

Risser, P.G. 1987. Landscape ecology: state-of-the-art. Pages 3-14 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

RMNP GIS Program. 1995. Cover types of Rocky Mountain National Park, Rocky Mountain National Park GIS Program, Estes Park, Colorado, 80517, USA.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology **57**: 773-782.

SAS Institute. 2004. SAS for Windows, version 9.1. SAS Institute, Cary, NC.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83**: 1421-1432.

Stohlgren, T. J., G. W. Chong, M. A. Kalkhan, and L. D. Schell. 1997a. Rapid assessment of plant diversity patterns: a methodology for landscapes. Environmental Monitoring and Assessment **48**:25-43.

Stohlgren, T. J., M. B. Coughenour, G. W. Chong, D. Binkley, M. A. Kalkhan, L. D. Schell, D. J. Buckley, and J. K. Berry. 1997b. Landscape analysis of plant diversity. Landscape Ecology **12**:155-170.

Stohlgren, T. J., R. R. Bachnad, Y. Onami, and D. Binkley. 1998a. Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. Plant Ecology **135**:215-228.

Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998b. Comparison of rangeland vegetation sampling techniques in the central grasslands. Journal of Range Management **51**:164-172.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998c. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology **138**: 113-125.

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

Stohlgren, T. J., A. J. Owen, and M. Lee. 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. Biodiversity and Conservation **9**:65-86.

Stohlgren, T. J., T. T. Veblen, K. C. Kendall, W. L. Baker, C. D. Allen, J. A. Logan, and K. C. Ryan. 2002. The heart of the Rockies: montane and subalpine ecosystems. Pages 203-218 *in* J. S. Baron, editor. Rocky Mountain futures: an ecological perspective, Island Press, Washington, USA.

Stohlgren, T. J., D. Barnett, C. Flather, J. Kartesz, and B. Peterjohn. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology **86**: 2298-2309.

Szaro, R. C., and D. W. Johnson, editors. 1996. Biodiversity in Managed Landscapes: Theory and Practice. Oxford University Press, New York.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on processes. Annual Review of Ecology and Systematics **20**:171-197.

Turner, M. G. 2005. Landscape ecology in North America: past, present, and future. Ecology **86**: 1967-1974

Turner, M. G., R. H. Gardner, V. H. Dale, and R. V. O'Neill. 1989a. Predicting the spread of disturbance across heterogeneous landscapes. Oikos **55**: 121-129.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne 1989b. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecology **3**: 153-162.

Urban, D. L., R. V. O'Neill, and H. H. Shugart. 1987. Landscape Ecology. Bioscience **37**:119-127.

Wagner, H. H., and M. -J. Fortin 2005. Spatial analysis of landscapes: Concepts and statistics. Ecology **86**: 1975-1987.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**:81- 120.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1-26 *in* L. Hansson, L. Fahrig, and G. Merriam, editor. Mosaic landscapes and ecological processes. Chapman and Hall, London, UK.

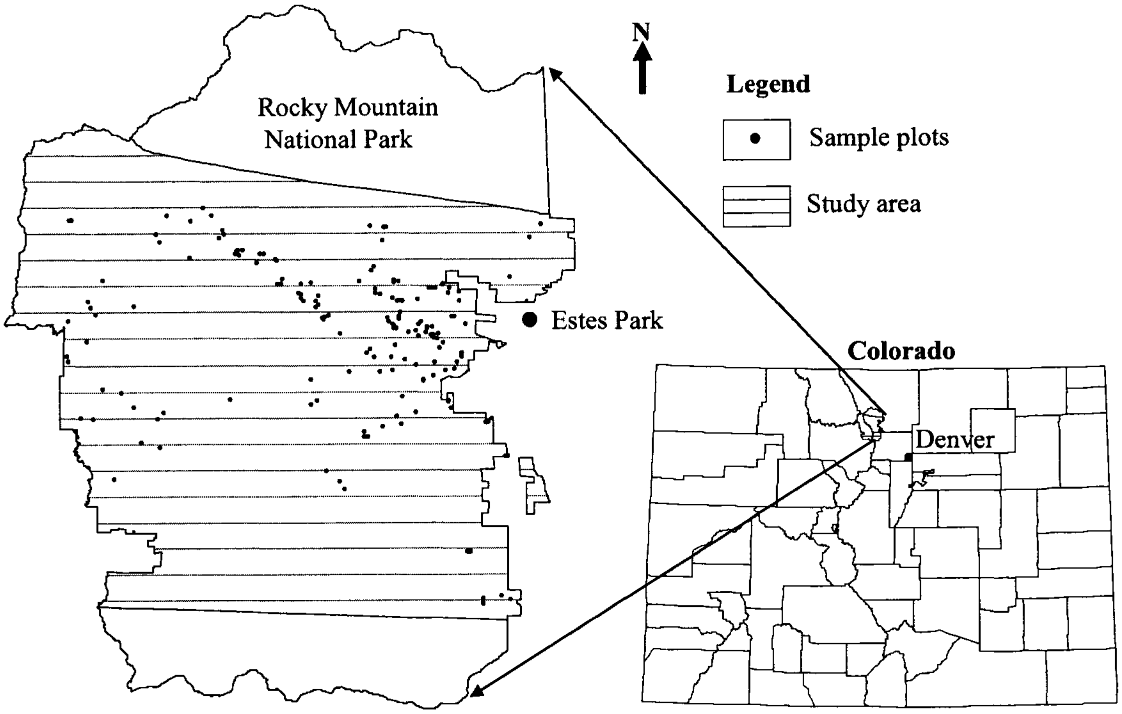

Figure 1.1: Map of study area.

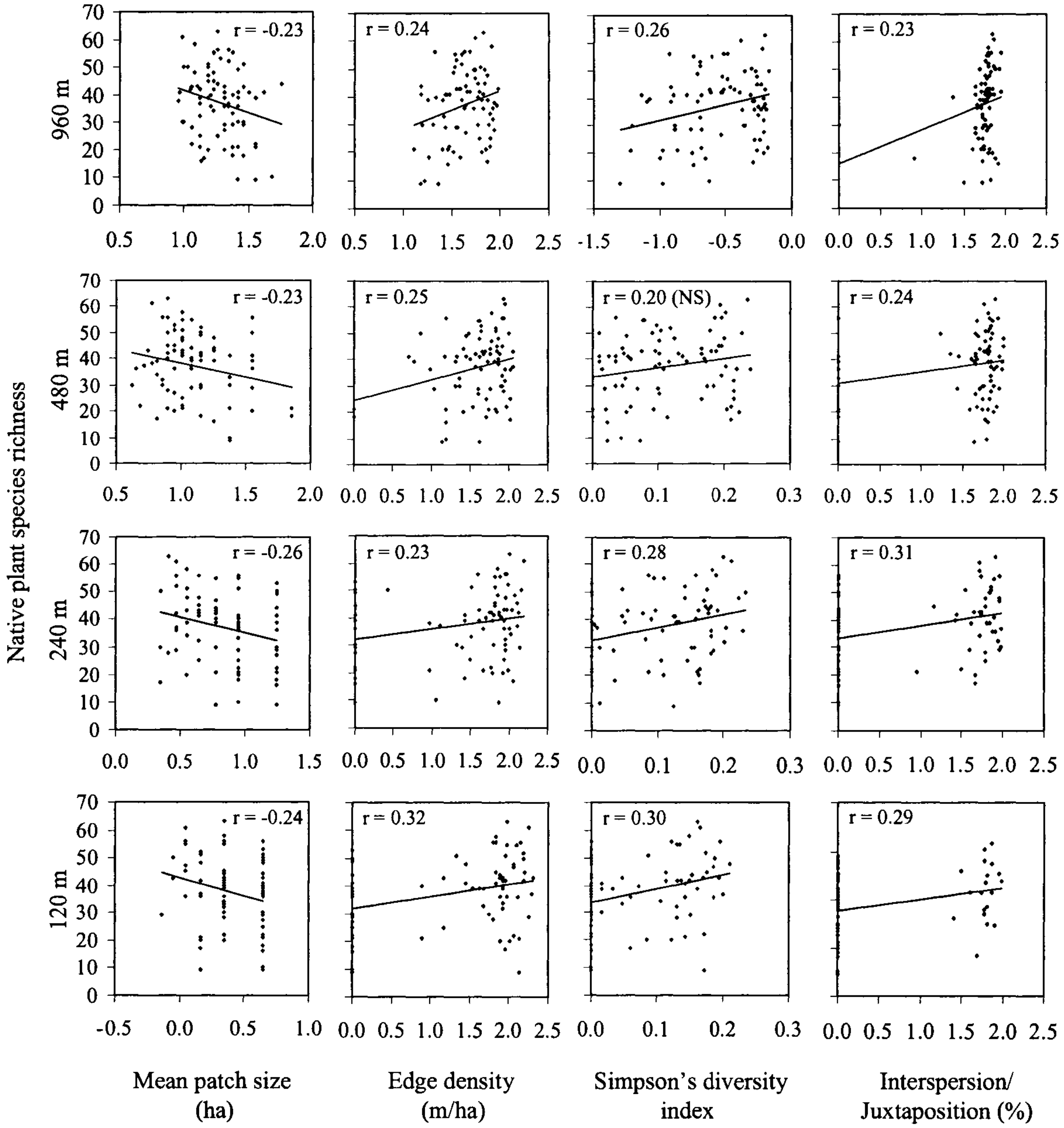

Figure 1.2: Relationships between native plant species richness and four measures of spatial heterogeneity in vegetation patterns (mean patch size, edge density, Simpson's diversity index, and interspersion/juxtaposition) at four spatial extents (radii of 120, 240, 480, and 960 m, shown from bottom to top rows, respectively). Transformed data were used where it was appropriate. Relationships were significant at alpha = 0.05, except where noted; r is the correlation coefficient; NS indicates nonsignificant (alpha > 0.05) (landscape level, n = 79, 0.1-ha plots).

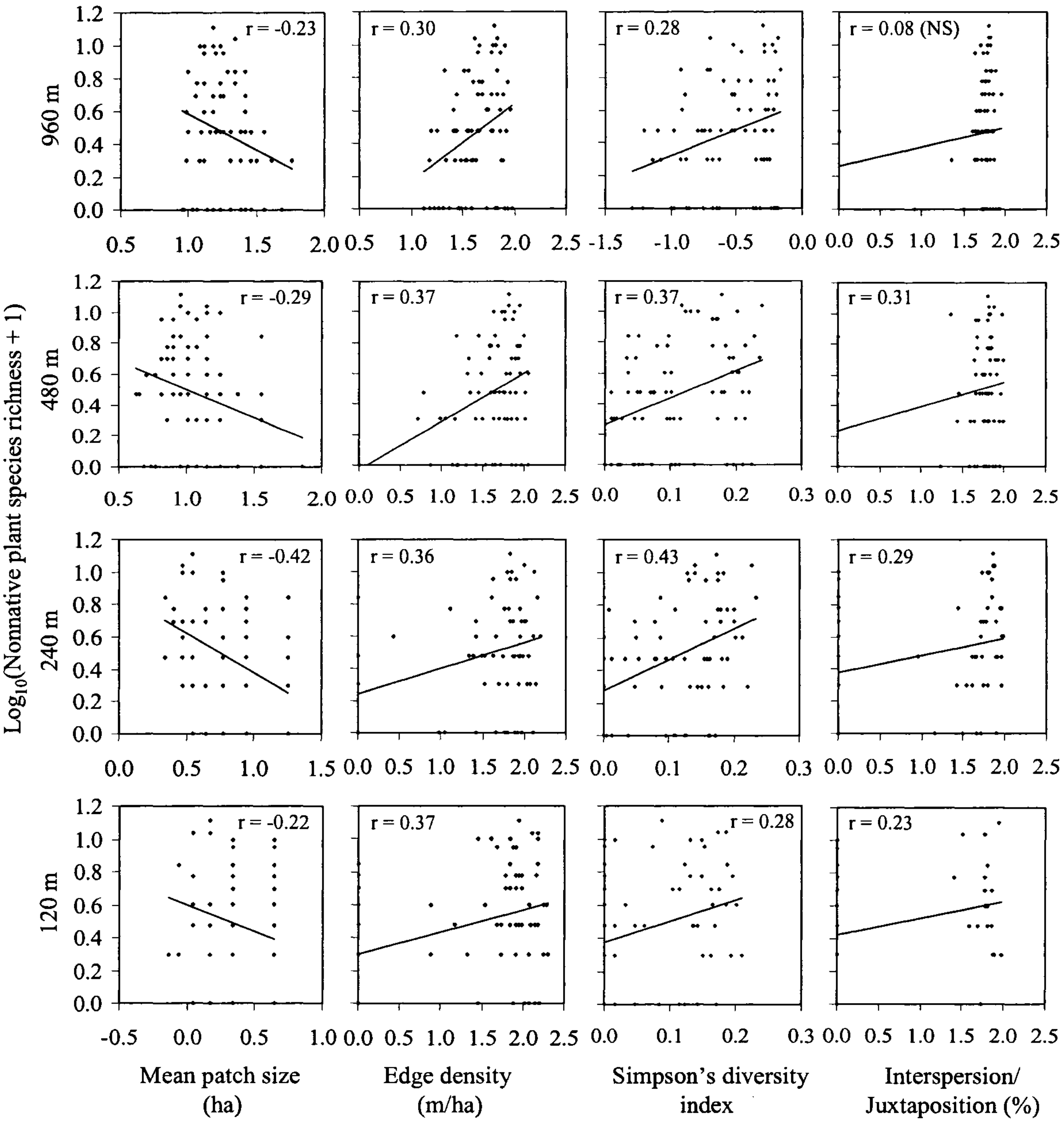

Figure 1.3: Relationships between nonnative plant species richness and four measures of spatial heterogeneity in vegetation patterns (mean patch size, edge density, Simpson's diversity index, and interspersion/juxtaposition) at four spatial extents (radii of 120, 240, 480, and 960 m, shown from bottom to top rows, respectively). Transformed data were used where it was appropriate. Relationships were significant at alpha = 0.05, except where noted; r is the correlation coefficient; NS indicates nonsignificant (alpha > 0.05) (landscape level, n = 79, 0.1-ha plots).

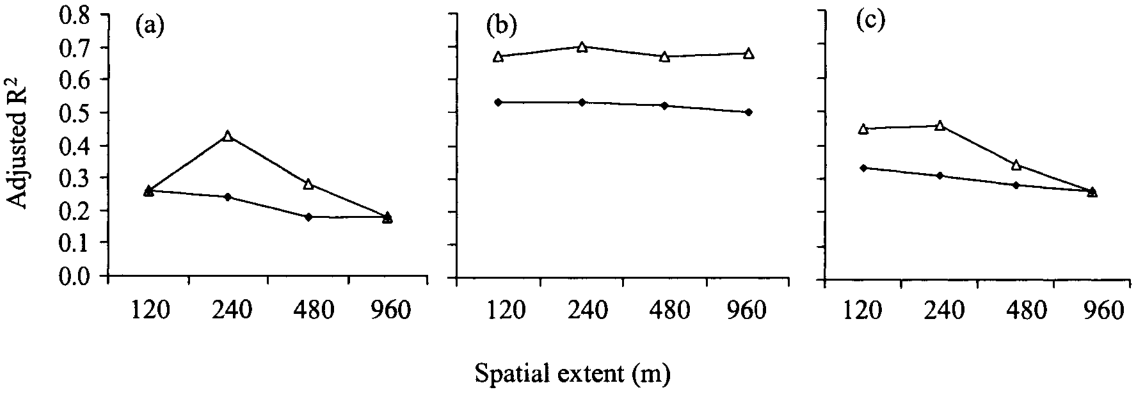

Figure 1.4: Explained variation (adjusted R^2) in "landscape-level" (a) native, (b) nonnative, and (c) total plant species richness as a function of spatial extent of analysis, with (open triangles) and without (solid diamonds) the inclusion of landscape metrics in the models (n = 79, 0.1-ha plots).

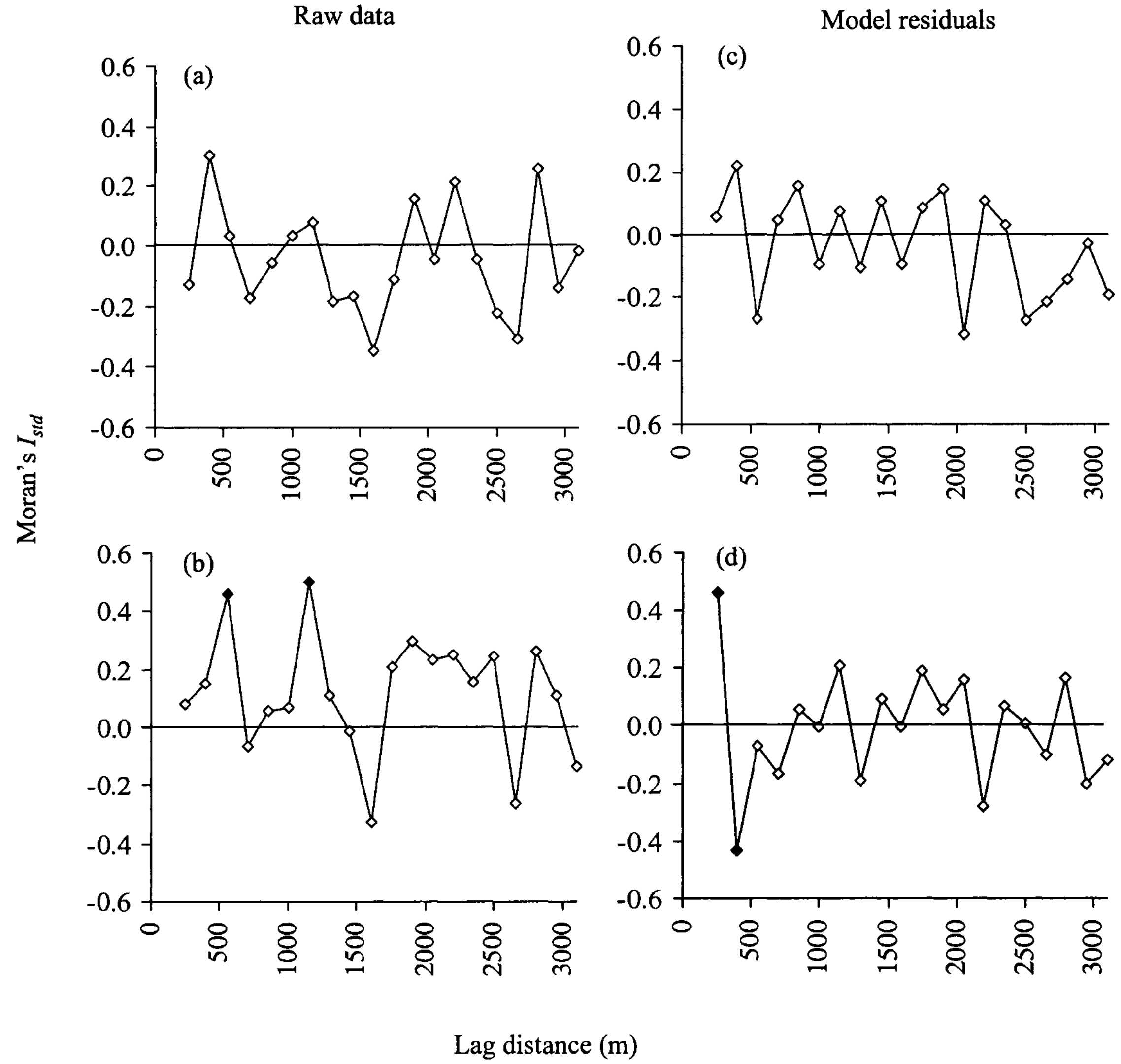

Figure 1.5: Landscape level (n = 79, 0.1-ha plots) Moran's I_{std} correlograms of (a) native and (b) nonnative (log-transformed) plant species richness, and residuals from (c) native and (d) nonnative plant species richness models (240 m spatial extent). Open diamonds represent nonsignificance, and closed diamonds indicate significance (one-tailed test ($\alpha = 0.05$) for positive spatial autocorrelation adjusted using progressive Bonferroni correction [Legendre and Legendre 1998, Lichstein et al. 2002]). Lag distance 150 m, except first lag distance that was extended to 250 m to accommodate an adequate number of site pairs.

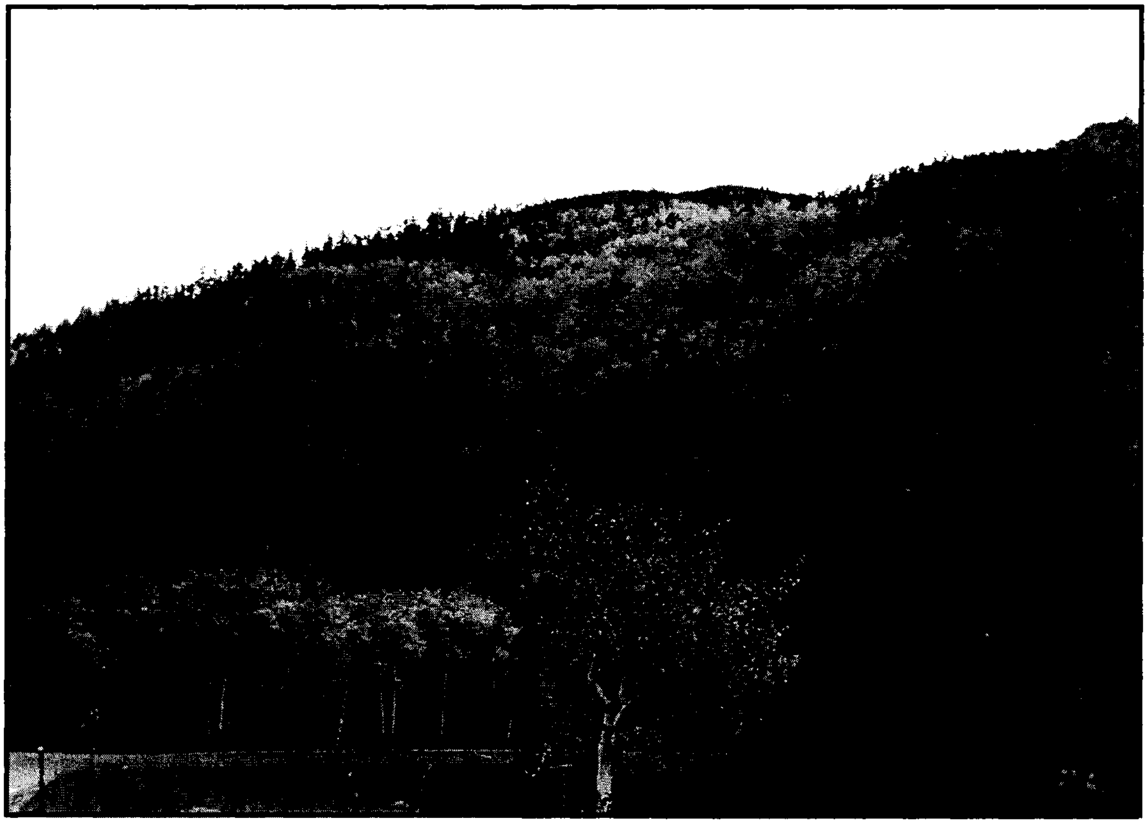

Plate 1. A heterogeneous mosaic of aspen and conifer patches in Rocky Mountain National Park, Colorado, USA. Photo Credit: S. Kumar.

Table 1.1: Cross-correlations (Pearson correlation coefficients; r) among selected variables that were a part of the best models of native and nonnative plant species richness at the 'landscape level' (n = 79, 0.1 ha plots, 240 m spatial extent).

	Native species richness	Non-native species richness	Patch richness density	Nitrogen	Percent tundra	Sand
Native species richness	1.00					
Nonnative species richness	0.56	1.00				
Patch richness density	0.35	0.40	1.00			
Nitrogen	NS	NS	NS	1.00		
Percent tundra	NS	-0.31	NS	NS	1.00	
Sand	0.23	NS	NS	-0.74	NS	1.00
Mean slope	NS	-0.24	-0.29	NS	NS	NS
Mean elevation	NS	-0.66	-0.31	NS	0.64	NS
Interspersion/ Juxtaposition	0.31	0.29	0.84	NS	NS	NS
Simpson's diversity index	0.28	0.43	0.83	0.25	NS	NS

Table 1.1 continued.

	Mean slope	Mean elevation	Interspersion/ Juxtaposition	Simpson's diversity index
Mean slope	1.00			
Mean elevation	0.31	1.00		
Interspersion/ Juxtaposition	-0.28	-0.29	1.00	
Simpson's diversity index	-0.35	-0.28	0.74	1.00

Note: Variables with $r > \pm 0.75$, and variance inflation factors > 2.5, were not included in the same model. Transformed data were used where it was appropriate. Correlations are significant at alpha = 0.05, except where noted; NS is nonsignificant at alpha > 0.05.

Table 1.2: Best models for native and nonnative plant species richness at three levels of ecological hierarchy (i.e. landscape, land cover, and community; 0.1 ha plots).

Dependent variable	Predictor	Parameter estimate	P	Partial R^2	Model Adj. R^2, F, P
I. Landscape level (n = 79, spatial extent = 240 m)					
Native species richness	Patch richness density	0.646	0.0041	0.125	$R^2 = 0.43$, $F_{6,72} = 10.63$, $P < 0.0001$
	Total soil nitrogen	72.129	0.0002	0.110	
	Percent tundra	13.018	0.0014	0.082	
	Sand	24.764	< 0.0001	0.075	
	Mean slope	0.688	0.0002	0.049	
	Mean elevation	-156.110	0.0003	0.029	
Nonnative species richness	Mean elevation	-4.813	< 0.0001	0.440	$R^2 = 0.70$, $F_{5,73} = 37.85$, $P < 0.0001$
	Native species richness	0.012	< 0.0001	0.208	
	Total soil nitrogen	0.549	0.0272	0.034	
	Interspersion/Juxtaposition	-0.099	0.0070	0.029	
	Simpson's diversity index	1.308	0.0026	0.011	
II. Land cover level					
Conifer (n = 49, spatial extent = 120 m)					
Native species richness	Edge density	5.376	0.0023	0.222	$R^2 = 0.30$, $F_{2,46} = 11.36$, $P < 0.0001$
	Eastness	42.062	0.0088	0.109	
Nonnative species richness	Mean elevation	-4.516	<0.0001	0.486	$R^2 = 0.66$, $F_{3,45} = 31.36$, $P < 0.0001$
	Native species richness	0.012	<0.0001	0.153	
	Sand	-0.219	0.0260	0.038	
III. Community level					
Lodgepole pine (n = 24, spatial extent = 120 m)					
Native species richness	Edge density	8.773	0.0009	0.299	$R^2 = 0.41$, $F_{2,21} = 8.87$, $P < 0.0016$
	Sand	13.682	0.0217	0.159	
Nonnative species richness	Native species richness	0.012	0.0001	0.384	$R^2 = 0.66$, $F_{4,19} = 11.99$, $P < 0.0001$
	Mean Fractal dimension	26.857	0.0050	0.144	
	Clay	-0.249	0.0188	0.106	
	Percent tundra	-0.184	0.0299	0.082	

Note: Transformed data were used where it was appropriate.

Table 1.3: Models evaluated for native plant species richness (S, landscape level, n = 79, 240-m spatial extent).

Model No.	Native plant species richness (S) models	AIC$_c$	Δ AIC$_c$	Adjusted R^2	K
1	S = Environmental/topographic, landscape metrics, soil variables	366.76	0.00	0.43	7
2	S = Environmental/topographic variables, landscape metrics	379.70	12.94	0.31	6
3	S = Landscape metrics, soil variables	380.57	13.81	0.28	4
4	S = Environmental/topographic, soil variables	385.89	19.13	0.24	5
5	S = Soil variables	390.29	23.53	0.18	3
6	S = Landscape metrics	391.17	24.41	0.18	4

Note: AIC$_c$ is the Akaike's Information Criterion corrected for small samples; K is the number of estimable parameters in the model (including the intercept).

Table 1.4: Models evaluated for nonnative (or non-indigenous) plant species richness (S, landscape level, n = 79, 240-m spatial extent).

Model No.	Nonnative plant species richness (S) models	AIC_c	ΔAIC_c	Adjusted R^2	*K*
7	S = Environmental/topographic, landscape metrics, native species richness, soil variables	-260.50	0.00	0.70	6
8	S = Environmental/topographic, landscape metrics, soil variables	-230.77	29.73	0.56	5
9	S = Environmental/topographic, soil variables	-225.50	35.0	0.53	4
10	S = Environmental/topographic variables, landscape metrics	-219.64	40.86	0.48	3
11	S = Environmental/topographic variables	-213.30	47.20	0.43	2
12	S = Landscape metrics	-194.45	66.05	0.30	4

Note: AIC_c is the Akaike's Information Criterion corrected for small samples; *K* is the number of estimable parameters in the model (including the intercept).

CHAPTER 2 EFFECTS OF SPATIAL HETEROGENEITY ON BUTTERFLY SPECIES RICHNESS

2.0 Abstract

The way that an organism responds to spatial heterogeneity depends on the grain of the landscape, the grain of organism's perception, and the interaction between its life history characteristics and the environment. I hypothesized that spatial heterogeneity may affect butterfly species richness and that this effect may vary for different butterfly families. I quantified spatial heterogeneity in vegetation (plant species richness, vegetation height, and NDVI range), topography (elevation, slope, aspect, and distance from stream/river), and landscape patterns (composition and configuration) in Rocky Mountain National Park, Colorado, USA, and related it to measured butterfly species richness. Stratified random sampling was used to collect butterfly species richness from seventy six 20 x 50 m plots. The species recorded from each plot (total 68 species) were divided into broad taxonomic groups based on the five families of butterflies (Hesperiidae, Lycaenidae, Nymphalidae, Paplionidae, and Pieridae). The plant species richness and average vegetation height were collected from 76 Modified-Whittaker plots (20 x 50 m) overlaid on 76 butterfly plots. The spatial heterogeneity in landscape patterns around sample plots was quantified by measuring landscape metrics using FRAGSTATS landscape analysis program at eight spatial extents (radii of 300, 600, 900 to 2400 m). The total butterfly species richness was strongly positively correlated with total plant species richness, proportion of shrubland, mean patch size of shrubland, and negatively correlated with mean patch size (landscape level), average vegetation height, elevation, and range in NDVI. The regression models were developed for total butterfly species richness and five butterfly family species richness. The best predictive model selected using Akaike's Information Criterion corrected for small sample size (AIC_c), explained 62% of the variation in total butterfly species richness at the 2100 m spatial extent. Average vegetation height and mean patch size were among the best predictors of total butterfly species richness. The models that included topographic and vegetation heterogeneity explained relatively less variation in butterfly species richness and were improved significantly after including measures of landscape heterogeneity. The results from this study suggest that spatial heterogeneity greatly influences patterns in butterfly species richness and that management activities should consider wider landscape context.

Keywords: Akaike's Information Criterion, AIC, butterfly species richness, FRAGSTATS, landscape metrics, model selection, plant species richness, spatial autocorrelation, spatial heterogeneity, spatial scales.

2.1 Introduction

Understanding how spatial heterogeneity affects ecological patterns and processes is one of the major focuses of landscape ecology (Risser et al. 1984, Pickett and Cadenasso 1995, Turner et al. 2001, Fortin and Agrawal 2005, Turner 2005). Spatial heterogeneity can be defined as the complexity and variability in ecological systems' properties of interest in space (Li and Reynolds 1994). Quantifying spatial heterogeneity is needed to understanding its effects on the diversity and distributions of different organisms and their species-specific responses (Gustafson 1998, Turner et al. 2001, Thies et al. 2003, Chapter 1). However, the decision at which scale to quantify spatial heterogeneity is one of the challenging questions that ecologists face because spatial heterogeneity is a complex phenomenon and is highly scale dependent (Kolasa and Rollo 1991, Gustafson 1998, Fortin and Agrawal 2005, Wagner and Fortin 2005).

Spatial heterogeneity in ecological systems is caused by spatial interactions between many biotic and abiotic factors and the differential responses of organisms to these factors (Milne 1991) and the organisms themselves (Huston 1994). Different organisms may have differential responses to spatial heterogeneity at multiple scales depending on their grain of perception (Levins 1968), the grain of the landscape (Forman and Godron 1986) and their natural history; therefore, identification of the factors that most influence species diversity, and the dominant scale (i.e., the scale that explains highest variation in the diversity and abundance of organisms) of response of species to these factors is important (Turner 2005) for maintaining and managing biodiversity.

Among insects, butterflies are well-studied, relatively easy to monitor, and have relatively short generation periods (Fleishman et al. 2002, Thomas 2005); and they are also relatively more sensitive to changes in their environment including climate and land-use (Wood and Samways 1991, Parmesan 1996, Smallidge and Leopold 1997, Fleishman et al. 2002, Luoto et al. 2006) and carry information about ecosystem properties of management interest, and thus, may be used as indicator species for other taxa (Kremen 1992, Fleishman et al. 2002, Thomas 2005). For example, butterflies have diverse and strong trophic links to other taxa (Gilbert and Singer 1975) such as plants, ants, and birds. Butterflies and plants have long coevolutionary history and the diversity and distribution of plants may influence butterfly species diversity by affecting their movement and searching behavior (Kareiva 1983, Simonson et al. 2001). Butterflies' sensitivity to changes in climate and sunlight levels, due to habitat loss, fragmentation and climate change, could be used as an indicator to local habitat loss or degradation (Murphy and Weiss 1992, Kremen 1992, Pollard and Yates 1993, Parmesan 1996).

The diversity and distribution of butterflies may be influenced by many other biotic and abiotic factors such as topography, moisture availability, disturbance, climate, local weather, species diversity and spatial distribution of host and larval plants, irradiance, successional stages of vegetation, and landscape composition and configuration (Thomas and Mallorie 1985, Wood and Samways 1991, Kremen 1992, Pollard and Yates 1993, Parmesan 1996, Simonson et al. 2001, Fleishman et al. 2002, Krauss et al. 2003, Bergman et al. 2004, Hogsden and Hutchinson 2004).

The responses of butterflies to spatial heterogeneity will depend on the interaction between their life histories and environment. Spatial arrangement of habitat patches in a landscape can affect various butterfly activities such as foraging, mate-location, predator avoidance, and finding oviposition sites (Rabasa et al. 2005). Therefore, butterflies' ability to locate suitable resource patches and perform these activities in a complex mosaic of vegetation may be an important determinant of their abundance and distribution across the landscape because species movement can be facilitated or impeded where one part of the landscape is relatively homogeneous with low degree of structural contrast and another part heterogeneous with high contrast (Forman and Godron 1986). Spatial heterogeneity can also influence butterfly population structure (Dyck and Matthysen 1999, Thomas et al. 2000). For example, increasing patch isolation can alter the exchange rate (emigration and immigration) of individuals between local populations (Thomas et al. 2000).

An alteration in spatial heterogeneity due to natural and anthropogenic disturbances such as fire, logging, grazing, flood, pollution and insect outbreak can influence butterfly species diversity and distribution across the landscape (Smallidge and Leopold 1997), because spatial heterogeneity may enhance or retard the spread of disturbances (Risser 1987, Turner et al. 1989) depending on intensity and frequency of the disturbance and the existing level of spatial heterogeneity. A change in composition and configuration of the landscape can influence butterfly species richness by changing patch size, patch shape, distance between the habitat patches, edge density, spatial variation of host and larval plant species, variation in prevailing winds, temperature and moisture across the landscape. Therefore, it is important to understand how butterflies respond to spatial heterogeneity. Based on the heterogeneity in dispersal behavior among individuals of different butterfly species (Ehrlich 1961), it is expected that relatively sedentary (less mobile) or habitat specialist species may respond to small scale spatial heterogeneity whereas more vagile or habitat generalist species may respond to large scale spatial heterogeneity. Sedentary butterflies can be more sensitive to loss of habitat than relatively more vagile butterflies (Murphy and Weiss 1992).

Knowledge about the factors which influence butterfly species richness across the landscape is a prerequisite for their conservation, monitoring, and management. In addition, land managers also need information about the spatial distribution of different species in surveyed as well as unsurveyed areas to focus their conservation or restoration activities; therefore, predictive models are required because we can only survey a very small portion of the landscape (generally < 1%; Stohlgren 2006). Some land managers may be interested in knowing the spatial distribution of a particular group of species (e.g., butterfly species belonging to Nymphalidae family); therefore, predictive models may be required not only for total butterfly species richness but also for different butterfly families or species. Moreover, different groups of butterflies may have differential responses to various environmental factors, and hence may require different management strategies. In this study, I developed predictive models for both total butterfly species richness and family level species richness.

A number of observational and experimental studies have investigated the effects of spatial heterogeneity in climate, soil, topography, vegetation and landscape on insects including butterflies (e.g., Kremen 1992, Golden and Crist 1999, Wettstein and Schmid 1999, Fleishman et al. 2002, Steffan-Dewenter et al. 2002, Summerville et al. 2002, Collinge et al. 2003, Krauss et al. 2003, Thies et al. 2003, Stefanescu et al. 2004, Strathmann 2005, Luoto et al. 2006). However, only a few of these studies on butterflies quantified spatial heterogeneity at multiple spatial scales (e.g., Fleishman et al. 2002, Collinge et al. 2003, Krauss et al. 2003) and none of them fully integrated landscape spatial heterogeneity (i.e., composition and configuration) with other types of spatial heterogeneity. Moreover, the studies that considered the effects of landscape heterogeneity included only a few of its measures such as composition, patch size or isolation (Collinge et al. 2003, Bergman et al. 2004, Rabasa et al. 2005, Strathmann 2005). In this study I considered all five components of landscape heterogeneity: (1) number of patch types; (2) proportion of each type; (3) spatial arrangement of patches; (4) patch shape; and (5) contrast between neighboring patches (Li and Reynolds 1994), because one or two indices of landscape pattern can not capture all the aspects of landscape heterogeneity (Gustafson 1998). In addition, I also included spatial heterogeneity in topography (elevation, slope, aspect, and distance from stream/river) and vegetation (plant species richness, vegetation height and range in Normalized Difference Vegetation Index (NDVI)).

The purpose of this study was to explore a methodology for developing butterfly species richness predictive models at multiple levels (i.e., total species richness and family species richness) using surrogates for spatial heterogeneity in vegetation, topography, and landscape patterns as predictor variables which were quantified at multiple spatial extents (within radii of 300, 600, 900 to 2400 m). I tested the null hypothesis that different measures of spatial heterogeneity do not affect butterfly species richness in the study area. My specific objectives were to:

1. Quantify spatial heterogeneity in vegetation, topography, and landscape patterns at multiple spatial extents, and relate it to butterfly species richness.
2. Test the null hypothesis of no effects of landscape heterogeneity on butterfly species richness.
3. Determine the spatial extent of the landscape at which butterflies have strongest responses to spatial heterogeneity.
4. Investigate whether spatial heterogeneity has differential effects on certain butterfly families.
5. Develop predictive models for butterfly species richness in the study area.

2.2 Study area

The study was conducted in central portion of Rocky Mountain National Park, Colorado, USA, located between 40^0 10' - 40^0 34' N latitude and 105^0 30' - 105^0 55' W longitude, covers approximately 107,500 ha. The elevation in the area varies from 2,300 m to over 4,300 m above mean sea level and lies on the Front Range of the southern Rocky Mountains in Colorado (Fig. 2.1). The average annual temperature varies from –1.5 ^{0}C to 14.0 ^{0}C. The mean annual precipitation is 36 cm. The temperature and precipitation have been suggested as strong determinants of latitudinal and elevation arrangements of species distributions, as typically influenced by elevation and topographic position (Peet 1981, 1988, Allen et al. 1991).

A number of vegetation communities varying from prairie to tundra are found in the area. Dominant vegetation types and plant species include: prairie vegetation dominated by short grasses (*Bouteloua gracilis* Vasey in Rothr., *Buchloe dactyloides* Engelm.) and sage brush (*Artemisia tridentate* Nutt.); ponderosa pine (*Pinus ponderosa* Douglas ex. C. Lawson; 2320-3170 m); douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; 2370-3213 m); lodgepole pine (*Pinus contorta* Doug. ex. Loud; 2380-3480 m); aspen (*Populus tremuloides* Mich.; 2350-3500 m); limber pine (*Pinus flexilis* James; 2620-3560 m); and spruce (*Picea Engelmannnii* Perry ex. Engel.; 2530-3710 m) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.; 2530-3710 m; Peet 1988). Aspen forest provides critical habitat for many species of plants, butterflies, and birds (Stohlgren et al. 2002, Simonson et al. 2001).

2.3. Methods

2.3.1 Butterfly survey and ecological classification

Stratified-random sampling design was used to measure butterfly species richness in the study area. The number of each butterfly species was recorded from seventy-six 20 x 50 m plots that were overlaid directly on the 0.1 ha Modified-Whittaker vegetation plots (Stohlgren et al. 1998). Established guidelines were followed for butterfly monitoring during the survey to minimize observer bias and any effects of environmental variation (Pollard and Yates 1993).

Observations were made during systematic walking surveys (44 minute per plot visit) only in sunny conditions (temperature >17^0 C) and under calm to light winds. The survey was done between 09.30 and 16.00 hrs and repeated four times during June, July, and August 1996 (Simonson et al. 2001). The surveys were restricted to the times when weather was favorable for butterfly flights. The species recorded from each plot (total 68 species; Appendix A) were divided into broad taxonomic groups based on the five families of butterflies: Hesperiidae (11), Lycaenidae (15), Nymphalidae (25), Paplionidae (6), and Pieridae (11).

2.3.2 Quantifying spatial heterogeneity

Since spatial heterogeneity is a complex phenomenon and is a multidimensional concept (Kolasa and Rollo 1991), for the sake of simplification, in this study I divided it into three major categories: heterogeneity in vegetation (hereafter referred to as 'vegetation heterogeneity'), heterogeneity in topography (hereafter referred to as 'topographic heterogeneity') and heterogeneity in landscape patterns (hereafter referred to as ‘landscape heterogeneity’). Vegetation heterogeneity was represented by total plant species richness, average vegetation height, and range in NDVI. Topographic heterogeneity was quantified in terms of elevation, slope, aspect, topographic exposure, and distance from stream/river. Landscape metrics (representing both composition and configuration; McGarigal and Marks 1995) were used to quantify five components of landscape heterogeneity (Li and Reynolds 1994).

2.3.2.1 Selection of spatial scales

Selection of spatial scale(s) at which to quantify spatial heterogeneity is a daunting task because spatial heterogeneity is a highly scale-dependent phenomenon (Kolasa and Rollo 1991, Wagner and Fortin 2005). The spatial scale may refer to both ‘grain’ and ‘extent’ (Turner 1989). In this study, I did not change the grain size (fixed it to 30 x 30 m); however, I varied the spatial extents of analyses.

Most ecologists, who study single species, use home range size or territory size or area of an organism’s activity to select spatial extent(s) at which they quantify spatial heterogeneity. However, for community level studies, such as this, the scale for quantifying spatial heterogeneity is difficult to know a priori because different species may have differential responses to spatial heterogeneity depending on their dispersal abilities, life history characteristics, and habitat requirements. One of the ways to deal with this problem is to select multiple arbitrary spatial extents to quantify spatial heterogeneity in different environmental variables. Next, identify the dominant scale of organisms’ response by comparing the variation explained (coefficient of determination; R^2) at each spatial extent. This approach has been used in a number of studies on different taxa such as birds (Pearson 1993, Warren et al. 2005), animals (Kie et al. 2002, Maier et al. 2005), plants (Chapter 1), and insects including butterflies (Steffan-Dewenter et al. 2002, Thies et al. 2003, Krauss et al. 2003, Bergman et al. 2004).

In general, information about the dispersal or home ranges of most butterfly species is limited. With the exception of a few long-distance migrants such as monarchs (*Danaus plexippus*), most butterflies move small distances (up to a few hundred meters; Wahlberg et al. 2002), while a few species move much larger distances between 1.0 - 2.25 km (Wahlberg et al. 2002; see review by Schneider 2003). However, there is an uncertainty in these estimates because these movement distances are based on mark-release-recapture studies, which may be biased due to the extent of the study area (Schneider 2003). Moreover, the movement distances of different butterflies may also vary spatially and temporally (Wahlberg et al. 2002). Based on this information I quantified vegetation heterogeneity at plot level (0.1-ha extent; except NDVI), and topographic and landscape heterogeneity at eight radii of 300, 600, 900, 1200, 1500, 1800, 2100, and 2400 m, representing a nested set of spatial extents. Corresponding areas were 28, 113, 255, 453, 707, 1018, 1386, and 1810 ha, respectively.

2.3.2.2 Quantifying vegetation heterogeneity

Plant species richness data were collected from 20 X 50 m (0.1 ha) modified-Whittaker, multi-scale plots with the long axis parallel to the environmental gradient (Stohlgren et al. 1998). These plots were located based on stratified random sampling in different vegetation types. Each site was sampled as close to peak biomass as possible. Plant species that could not be identified in the field were collected and identified at the herbarium at Colorado State University (Department of Biology, Fort Collins, Colorado). Some of the specimens could not be identified to species due to phenological stage or missing flower parts. In these cases, plants were identified to genus and treated as individual species. Plot locations were recorded using the global positioning system (GPS; Trimble Navigation Ltd., Westminster, Colorado, USA.), and coordinates were taken using the universal transverse mercator (UTM) system, which provides x, y coordinates in meters from a regional reference point. The average vegetation height (cm) by species was recorded in the ten 1-m^2 subplots in each modified-Whittaker plot (Stohlgren et al. 1998).

The range in NDVI, 250 m spatial resolution, around the center of the sample plot was extracted using a discrete Fourier transform (Moody and Johnson 2001) from the National Aeronautics and Space Administration's (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) instrument data, and were provided by researchers at NASA's Goddard Space Flight Center, Greenbelt, MD, USA. The MODIS data were acquired from February 2000 through February 2004; see Morisette et al. (2006) for more details. The range in NDVI contains information on vegetation as a measure of photosynthetic activity and biomass.

2.3.2.3 Quantifying topographic heterogeneity

The topographic heterogeneity was quantified in terms of elevation, slope, aspect, topographic exposure and distance from stream or river. Digital Elevation Model (DEM) data for the area were downloaded from the National Elevation Dataset, United States Geological Survey (USGS) website, to sample elevation (m) around the center of each 0.1-ha plot. Subsequently, the DEM grid (30 x 30 m) was used to generate slope (in degrees), and aspect (in degrees) using Environmental Systems Research Institute's (ESRI) ARC GIS, version 9.0, surface analysis functions (ESRI 2004).

For statistical analyses, the circular variable aspect was transformed into a linear north-south gradient (northness) and an east-west gradient (eastness) by performing cosine and sine transformations, respectively (Guisan et al. 1999, Fleishman et al. 2002, Gutierrez et al. 2005). Northness varies from -1 (south-facing) to 1 (north-facing), and eastness from -1 (west-facing) to 1 (east-facing). Both of these variables can be used to define the relative position of a location in two orthogonal aspect gradients (Gutierrez et al. 2005). Mean topographic exposure within a specified spatial extent was calculated by subtracting elevation at the center of the plot from the mean elevation of the specified spatial extent (Fleishman et al. 2002). A stream or river network shapefile was acquired from the Colorado Department of Water Resources. After converting it into a raster layer of 30 x 30 m cell size, Euclidean distance around the center of each 0.1 ha plot from the nearest stream or river was calculated using Map Calculator in Arc Map of ARC GIS version 9.0 (ESRI 2004). All of these topographic variables were quantified at eight spatial extents (radii of 300 m, 600 m, 900 m to 2400 m) around the center of the sample plots, and their summary statistics (mean, minimum, maximum and standard deviation) were calculated (Appendix B). In all analyses, an extended area, 3 km outside the park boundary, was included to account for the edge effects.

2.3.2.4 Quantifying landscape heterogeneity

Landscape heterogeneity was quantified by measuring a number of landscape metrics representing both landscape composition and configuration using the raster version of the FRAGSTATS (version 3.3) landscape pattern analysis program (McGarigal and Marks 1995). National Land Cover Dataset (NLCD; Vogelmann et al. 1998) for Colorado was obtained from USGS. The original land cover map was reclassified into five broad land cover types: conifer, deciduous, grasslands, shrubland, and non-vegetated (bare rocks, water, and ice/snow). The land cover map for the study area was clipped with an extended area, 3 km outside the park boundary, to account for the edge effects in landscape metrics calculations (McGarigal and Marks 1995). This map in raster format (ESRI GRID; projection: UTM, Zone 13, datum: NAD 1983, and cell size: 30 m) was used as a basic input data layer for calculating landscape metrics (e.g., proportion of each land cover type, mean patch size, patch richness density, edge density, mean edge contrast index, cohesion, interspersion and juxtaposition index, Euclidean nearest neighbor distance, and Simpson diversity index; Appendix B) at eight spatial extents (radii of 300 m, 600 m, 900 m to 2400 m). I also calculated "area weighted mean patch size," at both landscape level and class level (Appendix B), because it contains information about number of patches and patch size, and is considered more robust (Li and Archer 1997) than "mean patch size" alone. These landscape metrics represented five components of landscape heterogeneity (Li and Reynolds 1994); and were chosen based on their potential biological relevance to butterfly species richness and their use in a number of previous studies on butterflies and other taxa (e.g., Mazerolle and Villard 1999, Kie et al. 2002, Collinge et al. 2003, Thies et al. 2003, Krauss et al. 2003, Maier et al. 2005, Chapter 1). The detailed information (definitions and formulas) about these metrics is given elsewhere (McGarigal and Mark 1995). I assigned arbitrary structural contrast between different land cover types based on information in Peet (1981) and Stohlgren et al. (2002) to measure mean edge contrast using FRAGSTATS (McGarigal and Marks 1995, Kie et al. 2002; Table 2.1).

2.3.3 Statistical analyses

The variables representing spatial heterogeneity in vegetation, topography, and landscape patterns were used as predictor variables. Total butterfly species richness recorded from each of the 76 plots was divided into broad taxonomic groups based on the five families (Hesperiidae, Lycaenidae, Nymphalidae, Paplionidae, and Pieridae; Appendix A). The total butterfly species richness and the species richness for each of the five butterfly families were used as response variables. Since eight nested spatial extents were not independent of each other, separate models were developed at each spatial extent for total butterfly species richness and five butterfly family species richness. All the variables were tested for normality and the strongly skewed variables were transformed prior to analyses. For example, total butterfly species and the five butterfly families' species richness data were square root transformed. Pearson correlation coefficient (r) was used to investigate associations between total butterfly species richness and measures of spatial heterogeneity.

Prior to regression analyses, all the predictors were tested for multicollinearity (Neter et al. 1996) by examining cross-correlations among them (e.g., see Table 2.2). Only one variable from a set of highly cross-correlated (correlation coefficient > $\pm$ 0.75) variables was included in the regression models. The biological relevance of each predictor variable to butterfly species richness, and the ease of interpretation were used as criteria to select or drop the highly cross-correlated predictors. For example, at 2100 m spatial extent, cohesion, edge density, mean patch size, Shannon-diversity index and Simpson-diversity index were highly cross-correlated; I excluded others and included mean patch size because it is easily understood and interpreted. I conducted stepwise forward multiple regressions to eliminate insignificant predictors ($P > 0.05$). In all analyses, residuals were examined for deviations from normality and homogeneity of variances (Zar 1974). Regression analyses were conducted using the PROC REG procedure in SAS software (SAS Institute 2004) and alpha = 0.05 was used to determine significance level in all cases.

I used Akaike's Information Criteria (AIC) and the information-theoretic approach (Burnham and Anderson 2002) to evaluate multiple regression models and select the "best" models for butterfly species richness from a set of candidate models developed at eight spatial extents. I assumed normally distributed errors with a constant variance for least-squares regressions, and computed AIC as

$$\mathrm{AIC} = \mathrm{n} \log (\mathrm{RSS}/\mathrm{n}) + 2K \tag{1}$$

where n is the sample size; RSS is the residual sum of squares in the model, RSS/n is the maximum likelihood estimator (MLE); and K is the total number of estimable parameters in the model (including the intercept and residual variance; Burnham and Anderson 2002). Since the number of samples was small ($n = 79$), I calculated AIC adjusted for small sample ($\mathrm{AIC_c}$) as follows:

$$\mathrm{AIC_c} = \mathrm{AIC} + 2K(K+1) / (\mathrm{n} - K - 1) \tag{2}$$

Since $\mathrm{AIC_c}$ is on a relative scale, I calculated differences in $\mathrm{AIC_c}$ values as

$$\Delta\mathrm{AIC}_{\mathrm{c\,i}} = \mathrm{AIC_{ci}} - \text{minimum } \mathrm{AIC_c} \tag{3}$$

across all candidate models in the set. The best model has $\Delta\mathrm{AIC_{ci}} = 0$ and only the models with $\Delta\mathrm{AIC_{ci}} \leq 2$ have substantial support (Burnham and Anderson 2002).

2.3.4 Spatial autocorrelation

For quantitative or continuous variables (e.g., species richness), the Moran's I coefficient is the most commonly used coefficient to test for spatial autocorrelation (Legendre and Legendre 1998). Response variables, total butterfly species richness and five family's butterfly species richness, and the residuals from their respective best regression models were tested for spatial autocorrelation using Moran's I. The response variables were transformed (square root transformation) before calculating Moran's I because skewed distribution can induce bias in the estimation of spatial autocorrelation (Fortin and Dale 2005). Since original Moran's I does not vary exactly between -1 and +1, it was standardized (I_{std}) by dividing by its maximum attainable value (Haining 1990, Lichstein et al. 2002, Reich and Davis 2006). Also, since this global Moran's I is the average value of spatial autocorrelation for the entire study area (Fortin and Dale 2005) and does not reveal any local spatial pattern, I constructed spatial correlograms.

Spatial correlograms are a way to quantify spatial dependence along multiple distance classes and are obtained by plotting autocorrelation values against distances among different locations (Legendre 1993, Legendre and Fortin 1989). The interpretation of the shape of a correlogram can reveal the underlying spatial pattern in the data, for example, alteration of positive and negative values can indicate patchiness (Legendre and Fortin 1989). All directional spatial correlograms were constructed using I_{std} at 20 distance classes. Each lag distance class was 150 m wide to a maximum distance of 3150 m, however, to include the adequate number of site pairs (Fortin 1999); the first lag distance interval was extended to 300 m (contained 32 site pairs). Global significance of each correlogram was tested using a Bonferroni corrected α^* of $0.05/20 = 0.0025$ ($\alpha =$

0.05; 20 lags, Legendre and Legendre 1998, Lichstein et al. 2002). The significance of I_{std} at each lag distance class was assessed using the progressive Bonferroni correction (Legendre and Legendre 1998, Lichstein et al. 2002). In all cases, randomization tests (999 permutations) were used to determine the probability of observing a value of Moran's I as large as the observed value (Lichstein et al. 2002).

All spatial statistical analyses were performed using S-PLUS (version 7.0) statistical software (Insightful Corp., Seattle, Washington), and the spatial library written by Reich and Davis (2006).

2.4. Results

2.4.1 Butterflies' responses to spatial heterogeneity

There was a strong positive relationship between total butterfly species richness and total plant species richness ($r = 0.42$, $P < 0.0001$; Fig. 2.2a) in my study area. I found highly significant negative relationships between total butterfly species richness and average vegetation height ($r = -0.44$, $P < 0.0001$; Fig. 2.2b); elevation (plot level) ($r = -0.42$, $P < 0.0001$; Fig. 2.2c); and range in NDVI ($r = -0.36$, $P = 0.001$; Fig. 2.2d). However, at family level, only Hesperiidae and Pieridae species richness were significantly negatively correlated with average vegetation height ($r = -0.26$, $P = 0.024$; and $r = -0.52$, $P < 0.0001$; respectively). Species richness of three other families viz. Lycaenidae, Nymphalidae and Papilionidae, did not show any significant relationships with average vegetation height. Hesperiidae, Lycaenidae, and Papilionidae species richness were significantly negatively correlated with elevation (plot level) ($r = -0.32$, $P = 0.005$; $r = -0.23$, $P = 0.046$; and $r = -0.25$, $P = 0.029$; respectively) but Nymphalidae and Pieridae species richness showed weaker relationships with elevation (plot level) ($r = -0.21$, $P = 0.067$; $r = -0.20$, $P = 0.090$; respectively).

Total butterfly species richness was significantly negatively correlated with mean patch size at all spatial extents (Table 2.3; $r = -0.53$, $P < 0.0001$, at 300 m extent; Fig. 2.3a). However, there were strong positive relationships between total butterfly species richness and mean patch size of shrubland (e.g., $r = 0.34$, $P = 0.003$, at 300 m extent; Table 2.3), and the proportion of shrubland (e.g., $r = 0.40$, $P < 0.0001$, at 300 m extent; Fig. 2.3b) at all spatial extents (Table 2.3). Also, there were positive correlations between total butterfly species richness and proportion of grasslands (significant at 300, 600, 1800, and 2400 m extents; Table 2.3) and proportion of deciduous land cover type (significant only at 300 and 600 m extents; Table 2.3). In contrast, total butterfly species richness was mostly negatively correlated with mean patch size of conifer and proportion of conifer at all spatial extents (significant at smaller extents, but insignificant at larger extents; Table 2.3). No significant relationships were detected between total butterfly species richness and mean patch area of non-vegetated and proportion of non-vegetated land cover type at any of the spatial extents (Table 2.3).

Overall, across eight spatial extents, different measures of spatial heterogeneity showed complex patterns of relationships with total butterfly species richness (Table 2.3). Some of them were consistently positively correlated with total butterfly species richness (e.g., proportion of shrubland, mean patch size of shrubland, and edge density; Table 2.3) and some were consistently negatively correlated (e.g., mean patch size, mean elevation, and mean exposure; Table 2.3). A few of them exhibited inconsistent relationships with total butterfly species richness (Table 2.3), negative at some spatial extents and positive at others, and insignificant at some spatial extents and significant at others. For example, total butterfly species richness did not show any significant correlation with distance from stream/river at smaller spatial extents (Table 2.3), however, it showed strong positive correlations at higher spatial extents (1500 to 2400 m extents; Table 2.3; e.g., $r = 0.41$, $P < 0.0001$ at 2400 m extent; Fig. 2.3c).

At family level, Hesperiidae species richness showed significant positive relationships with area weighted mean patch size of grasslands ($r = 0.33$; $P = 0.003$, at 300 m extent) and shrubland ($r = 0.31$; $P = 0.006$, at 300 m extent) at smaller spatial extents (up to 1500 m extent), but no significant relationships at larger spatial extents (e.g., $r = 0.04$; $P = 0.76$ for grasslands, and $r = - 0.05$; $P = 0.68$, for shrubland, at 2400 m extent). Lycaenidae species richness was strongly positively correlated with area weighted mean patch size of grasslands and shrubland at all spatial extents (e.g., $r = 0.49$; $P < 0.0001$, and $r = 0.43$; $P < 0.0001$, respectively, at 2100 m extent). In contrast, Nymphalidae species richness and Paplionidae species richness did not exhibit any significant relationships with area weighted mean patch size of grasslands and shrubland at any of the spatial extents. Pieridae species richness showed significant positive relationships with area weighted mean patch size of grasslands and shrubland ($r = 0.28$; $P = 0.013$, and $r = 0.25$; $P = 0.033$, respectively) at only 300 m extent, but no significant relationships at higher extents.

Hesperiidae and Paplionidae species richness were significantly positively correlated with edge density at all spatial extents ($r > 0.25$ and $P < 0.05$, for both families). However, Nymphalidae species richness did not show significant relationship with edge density at any of the spatial extents. Pieridae species richness showed significant positive correlation ($r = 0.35$; $P = 0.002$) with edge density at only the smallest spatial extent (i.e. 300 m) and no significant correlations at larger spatial extents (i.e. > 300 m). Strong positive relationships were found between Lycaenidae species richness and edge density at larger spatial extents (> 1200 m; e.g., $r = 0.33$, $P = 0.003$ at 2400 m), but no significant relationships were found at smaller spatial extents (i.e. 300, 600 and 900 m).

2.4.2 Predictive models of butterfly species richness

The best model explained 62% of the variation in total butterfly species richness at 2100 m spatial extent and included variables representing all three categories of spatial heterogeneity: vegetation, topographic and landscape (Table 2.4, model 1; Table 2.5). This model was highly significant ($F_{6, 69} = 21.57$, $P < 0.0001$), and average vegetation height (partial $R^2 = 0.20$), mean patch size (partial $R^2 = 0.17$), and total plant species richness (partial $R^2 = 0.15$) were the three best predictors of total butterfly species richness (Table 2.4). Patch richness density, interspersion and juxtaposition index, and standard deviation of elevation were three other predictors of total butterfly species richness (Tables 2.4-2.5).

Six other models explained 29-59% of the variation in total butterfly species richness (models 2-7; Table 2.5; $\Delta AIC_c > 5.0$). The models that included only landscape (model 7; Table 2.5) or only topographic (model 6; Table 2.5) heterogeneity variables as predictors performed worse ($\Delta AIC_c = 43.21$ and 43.85, respectively) than the model that included only vegetation heterogeneity variables (model 4; $\Delta AIC_c = 23.64$; Table 2.5). However, the models based on the combinations of predictor variables representing three categories of heterogeneity performed better than the models based only on predictors from one type of heterogeneity (models 2-3, except model 5; Table 2.5). For example, the model based on the combination of landscape and vegetation heterogeneity predictors was the second best model (model 2; $\Delta AIC_c = 5.25$; Table 2.5) and explained 59% of the variation in total butterfly species richness (Table 2.5). The third best model (model 3; $\Delta AIC_c = 13.09$; Table 2.5) explained 54% of the variation in total butterfly species richness and included predictors from topographic and vegetation heterogeneity. It is clear from the model evaluation exercise (Table 2.5) that considering predictor variables representing landscape heterogeneity in addition to the predictors representing the other two types of heterogeneity improved the models significantly (Table 2.5).

Among family-level models, the best model for Hesperiidae family explained 42% of the variation in Hesperiidae species richness at 2100 m spatial extent (Table 2.4). Distance from stream/river was one of the best predictors of Hesperiidae species richness (partial $R^2 = 0.26$; Table 2.4). The best models for four other families explained 40%, 39%, 25%, and 39% of the variation in species richness of Lycaenidae (2400 m extent), Nymphalidae (2100 m extent), Paplionidae (300 m extent), and Pieridae (600 m extent) family, respectively (Table 2.4). Area weighted mean patch size of grasslands was one of the best predictors of Lycaenidae species richness (partial $R^2 = 0.23$; Table 2.4). However, total plant species richness was the best predictor of Nymphalidae species richness (partial $R^2 = 0.26$; Table 2), mean nearest neighbor distance was the best predictor of Paplionidae species richness (partial $R^2 = 0.25$; Table 2.4), and average vegetation height was the best predictor of Pieridae species richness, respectively (partial $R^2 = 0.27$; Table 2.4).

Spatial autocorrelation analyses using Moran's I_{std} for both total butterfly species richness (raw data) and the best model residuals indicated that there was a significant positive spatial autocorrelation ($I_{std} = 0.121$, $P < 0.0001$) in the raw data (Table 2.6), but no significant spatial autocorrelation in the model residuals ($I_{std} = - 0.016$, $P = 0.997$; Table 2.6), which indicates that the best regression model (model 1; Table 2.5) was effective in modeling spatial autocorrelation in the raw data. This may be due to the fact that spatial autocorrelation in the raw data was explained by the significant spatial autocorrelation observed in some of the independent variables in the best model (Legendre and Legendre 1998). Three of the five butterfly families' species richness (raw data) exhibited significant positive spatial autocorrelation, but their respective best models' residuals did not show any significant spatial autocorrelation (Table 2.6).

The significant positive spatial autocorrelation in total butterfly species richness (raw data) at smaller lag distances and the periodicity in spatial autocorrelation (i.e., positive and negative values) at successive lag distances indicated patchiness in butterflies' distributions across the landscape (Fig. 2.4a). Reduced number of significant peaks in correlogram for the best model's residuals of total butterfly species richness showed that the best regression model was also effective in modeling local spatial autocorrelation (Fig. 2.4b). Similar trends were observed in family level butterfly species richness (raw data) and the residuals from their respective best models' residuals (Fig. 2.5). Differences in spatial pattern exhibited by shapes of correlograms for different butterfly family species richness (Fig. 2.5) indicate their patchy distributions and differential responses to spatial heterogeneity.

2.4.3 Responses of butterflies to spatial heterogeneity at multiple scales

The consideration of landscape context with plot level measures of spatial heterogeneity always improved the variation explained in butterfly species richness (Fig. 2.6; notice the change in adjusted R^2 values on the left and right sides of the vertical dotted line). The response of total butterfly species richness was strongest (adj. $R^2 = 0.62$) at 2100 m spatial extent (Fig. 2.5). However, across the scales, no continuous trend in the amount of variation explained in total butterfly species richness was observed (Fig. 2.5). It may be because some of the butterfly species are responding to small scale spatial heterogeneity (adj. $R^2 = 0.60$; 300 m), while others respond to intermediate (adj. $R^2 = 0.60$; 1200 m) or larger scale (adj. $R^2 = 0.62$; 2100 m) spatial heterogeneity. Family-level butterfly species richness models supported this hypothesis, as different butterfly families had differential responses to spatial heterogeneity at eight spatial extents (Fig. 2.6). For example, butterfly species in Papilionidae family responded strongly to 300 m spatial extent whereas butterfly species in Lycaenidae family showed strongest response at 2400 m extent (Table 2.4, Fig. 2.6).

2.5 Discussion

In this study, I presented a general approach to quantify spatial heterogeneity in vegetation, topography, and landscape; related it to butterfly species richness; and developed predictive models for total butterfly species richness and five butterfly families' species richness, at landscape level. The results from this study show that butterfly species richness in Rocky Mountain National Park was strongly influenced by spatial heterogeneity in vegetation, topography, and landscape patterns at different spatial extents. This is consistent with several studies on butterflies that have related different types of spatial heterogeneity to butterfly species diversity (e.g., Kremen 1992, Wettstein and Schmid 1999, Fleishman et al. 2002, Summerville et al. 2002, Collinge et al. 2003, Krauss et al. 2003, Stefanescu et al. 2004, Strathmann 2005, Luoto et al. 2006). However, my models contained much more information of different aspects of spatial heterogeneity, and thus, were more explanatory than previous studies. My best model explained 62% of the variation in total butterfly species richness at 2100 m spatial extent (Tables 2.4-2.5) and included predictors representing all three categories of spatial heterogeneity. Five butterfly families had differential responses to spatial heterogeneity at different spatial extents (Fig. 2.6). Addition of landscape metrics with other measures of spatial heterogeneity always helped improve the predictive models (Table 2.5).

2.5.1 Effects of vegetation heterogeneity on butterfly species richness

I found a strong positive relationship between total butterfly species richness and total plant species richness (Fig. 2.2a). These results are consistent with previous studies on butterflies (e.g., Thomas and Mallorie 1985, Simonson et al. 2001, Fleishman et al. 2005). This positive association may be because plants provide nectar resources, serve as host plants and provide shelter to butterflies (Wood and Samways 1991). Higher plant species diversity may be an indicator of better habitat quality, and therefore would fulfill habitat requirements of more butterfly species.

Total butterfly species richness was negatively associated with average vegetation height (Fig. 2.2b). This suggests that vegetation height act as a barrier to butterfly movements. This pattern agrees with the earlier studies (e.g., Thomas and Mallorie 1985, Wettstein and Schmid 1999) that reported negative relationships between butterfly diversity and vegetation height. However, positive relationships between butterfly diversity and average plant height have also been reported (e.g., Dennis 2004, Strathmann 2005). This discrepancy in relationships may be explained by the range of variation in vegetation height included in the analyses. For example, my study included more variation in vegetation height (range 0.29 to 30.41 m) than study conducted by Strathmann (2005) (range 0.10 to 0.37 m) and Dennis (2004). This suggests that most butterflies prefer moderately high vegetation (e.g., grasslands and shrubland land cover types) strata and avoid completely flat or bare grounds (Wood and Samways 1991, Dennis 2004) or higher vegetation. This could be due to the high risk of predation that may be associated with higher flights. Moreover, in my study, majority of the sample plots that showed higher butterfly species richness had an average vegetation height less than 5 m (Fig. 2.2b).

Different families had differential responses to vegetation height. For example, Hesperiidae and Pieridae species richness were negatively correlated with vegetation height whereas no such relationships were detected for Lycaenidae, Nymphalidae and Papilionidae. This suggests that butterfly species in Hesperiidae and Pieridae families are low-flying species (e.g., *Colias philodice*; Summerville et al. 2002) whereas Lycaenidae, Nymphalidae and Papilionidae families include high-flying butterfly species (e.g., *Celastrina ladon*, and *Vanessa cardui*; Summerville et al. 2002). The negative responses of some of the butterfly species to vegetation height may also be related to varying degree of shaded areas created by vegetation height that could directly influence butterfly species richness and abundance (Warren 1985, Greatorex-Davies et al. 1993).

I found a negative relationship between range in NDVI and total butterfly species richness (Fig. 2.2d). This could be because my study area is dominated by conifer land cover type which is relatively more productive than other land cover types; and also conifer appears to be acting as a matrix for butterflies' movements (Ricketts 2001) because of the relatively taller vegetation.

2.5.2 Effects of topographic heterogeneity on butterfly species richness

Total butterfly species richness was negatively correlated with elevation (Fig. 2.2c). This pattern is not unexpected as insect species richness may decrease, increase, or show no trends relative to elevational gradients, depending on the biology of the insect species and the range of variation in the altitude (Hodkinson 2005). Some studies reported positive relationships between elevation and butterfly diversity (e.g., Wettstein and Schmid 1999, Stefanescu et al. 2004, Strathmann 2005), while others have reported negative relationships (e.g., Fleishman et al. 1998). These contrasting relationships may be because of the range in elevation at the study location and regional climate. For example, the elevation at the sample plots in my study varied from 2400 to 3200 m, whereas the elevation in other studies was less than 2400 m (e.g., 800-1400; Wettstein and Schmid 1999, and 850-2300 m; Strathmann 2005). The negative relationship observed in my study may be because of the decrease in temperature with an increase in elevation in the area that in turn may be affecting butterfly species richness as butterflies are thermoregulated (Clench 1966). It may also be due to a decrease in flight time at higher elevations (e.g., studies of *Colias philodice* by Kingsolver 1983a, b). It appears that butterflies are positively correlated with elevation at lower elevations (< 2300 m) and negatively associated with elevation at higher elevations (> 2300 m). Butterflies showed a positive response to distance from stream/river at higher spatial extents (e.g., Fig. 2.3c), which may be because at larger distances from streams or rivers, there is a high probability of finding ridges or hill tops in mountainous areas, which are preferred by the butterflies for different activities such as basking and mate locating (Scott 1975).

2.5.3 Effects of landscape heterogeneity on butterfly species richness

Mean patch size negatively affected total butterfly species richness (Table 2.3) and was one of the best predictors of total butterfly species richness (Table 2.4-2.5) which indicates that butterflies in the area prefer smaller patches. I suggest the following explanations for the pattern found: (1) it may be because butterflies prefer edges, which provide resources for thermoregulation (Dennis et al. 2006), and many small patches will have more edges than a large patch of the same area; (2) small patches may also serve as 'stepping stones' (Dennis et al. 2006) for different individuals (especially sedentary species) during their movement across the landscape; (3) several small patches may have high density of host plants (Nieminen et al. 2004), and may be more dissimilar in species composition than a bigger patch with same area and may provide diverse resources for butterflies; and (4) this could also be because of the dominance of conifer land cover type in the area that has relatively larger patches and taller vegetation because of which it might be acting as a barrier to butterfly movements (Ricketts 2001).

Total butterfly species richness was strongly positively correlated with the proportion of shrubland and mean patch size of shrubland at all spatial extents (Table 2.3). This could be because shrublands may provide better quality habitats and contain relatively higher plant species diversity or a greater number of important functional groups; and larger patches of shrublands may have more heterogeneous resources (e.g., host plants, nectar plants, oviposition sites and microhabitats) than the smaller patches (Thomas and Hanski 1997, Golden and Crist 1999). This pattern is supported by previous studies that reported butterflies' preferences to shrub vegetation (e.g., Bergman et al. 2004, Dennis 2004). Positive associations between total butterfly species richness and the proportion of deciduous land cover type at smaller spatial extents (Table 2.3) suggest that butterflies also like deciduous plant species such as aspen, a dominant tree in deciduous land cover type, which is also very high in native species richness (Simonson et al. 2001).

Total butterfly species richness was positively correlated with edge density (Table 2.3). This may be because edges may have greater abundance and diversity of host and nectar plants. For example, in Chapter 1 I found a positive relationship between plant species richness and the edge density in the same study area. Edges may also have different microclimatic conditions than the interior of a patch and may provide warmth and shelter for butterflies (Wood and Samways 1991). Higher butterfly species richness on the edges may also be attributed to the preferences of some female butterflies to oviposit on the plants protruding from the surrounding vegetation (Warren 1984, Dennis 2004) patches that have relatively taller vegetation.

2.5.4 Multi-scale responses of butterflies to spatial heterogeneity

The strongest response of total butterfly species richness to 2100 m spatial extent (Table 2.4; Fig. 2.6) suggests that the butterfly community in my study area perceive the landscape primarily within 2100 m radius (i.e., 1386 ha) of their surrounding area. This may be because of the collective responses of different butterfly species, resulting from their differential dispersal behavior, to available resources and the relatively coarse grain of the landscape. Range in elevation and coarseness of the environmental variation in the study area could also have contributed to butterflies' responses to spatial heterogeneity at 2100 m spatial extent. Less variation in total butterfly species richness was explained at larger spatial extents (> 2100 m) because dominant processes may change at larger extents (O'Neill and King 1998). In this case, regional climate may play as a dominant force in determining the butterfly species distribution. The dominant scale of response of butterfly communities to spatial heterogeneity would be different in other areas with relatively lower topographic heterogeneity (e.g., Krauss et al. 2003, Bergman et al. 2004). Differential responses of different butterfly families to spatial heterogeneity (Fig. 2.6) could be attributed to their varying dispersal abilities (Ehrlich 1961, Wahlberg et al. 2002, Schneider 2003), spatial distribution of their host and larval plants, their ability to use the matrix (non-vegetated or conifer areas in my study area), specialist versus generalist species (Krauss et al. 2003), their ability to cross structural barriers created by vegetation height (e.g., low-flying versus high-flying species; Summerville et al. 2002) or composition and configuration of the landscape. However, in relatively homogenous landscapes, different butterflies may have similar responses to spatial heterogeneity at multiple spatial extents.

2.5.5 Important caveats and applicability of the models to other landscapes/regions

It may not be possible to directly use the predictive models presented in this study for other landscapes because they may have varying degree of spatial heterogeneity in topography, vegetation and landscape; for example, low topographic variability than Rocky Mountain National Park or varying degree of patchiness in landscape (e.g., grasslands mixed with shrubland versus grasslands mixed with forested areas) or different disturbance regimes (natural versus anthropogenic). However, similar modeling approach could be used for other smaller or larger landscapes. The unexplained variation in butterfly species richness suggests that additional variables may need to be considered in other predictive models. For example, including data on larval and host plants, or irradiance may have improved the models. Also, the smaller resource patches (< 900 m^2) were not considered in this study because of the limitation of the spatial resolution (30 x 30 m) of the vegetation map used in landscape analyses. Therefore, consideration of small resource patches by including vegetation maps generated using higher resolution remotely sensed data in landscape analyses may improve the predictive power of the models. Average vegetation height in this study was measured at sample plot level (20 x 50 m), however, landscape level vegetation height maps that can be created using the Shuttle Radar Topography Mission (SRTM) data and lidar (light detection and ranging) remote sensing technique (e.g., Simard et al. 2006), have the potential to improve butterfly species richness predictive models.

In this study, I developed butterfly species richness predictive models at varying spatial extents and fixed the grain size to 30 m; however, measures of landscape heterogeneity (i.e., landscape metrics) are also sensitive to spatial (grain size) and thematic (number of categories) resolution of the input land use map (Benson and MacKenzie 1995, O'Neill et al. 1996, Baldwin et al. 2004). The scale at which butterfly species richness data were collected can also affect the predicative models. For example, the models would vary if the data were collected using a transect method than the 20 x 50 plots I used. Therefore, further research is required to investigate how these models change with changing grain size and thematic resolution of the input map, and the sampling methods.

2.6 Conclusions

The results from this study suggest that spatial heterogeneity greatly influences patterns in butterfly species richness across the landscape and highlights the need for multi-scale and multi-level approaches for understanding the effects of spatial heterogeneity on biodiversity. The study also illustrates that management activities should consider not only the spatial heterogeneity in the management unit but also wider landscape context - what is happening around the area of interest is also important (Collinge et al. 2003, Krauss et al. 2003, Thies et al. 2003, Chapter 1). It becomes even more important when the area is prone to frequent disturbances. For example, reduction in spatial heterogeneity due to management practices or disturbances such as fire, grazing, or logging may result in a decline in butterfly species richness. Therefore, knowledge about the dominant spatial scale of the responses of different species to spatial heterogeneity may make biodiversity management more effective because a mismatch in the spatial scale of management (Cumming et al. 2006) and the spatial scale of an organism's perception may result in failure of a management strategy. However, how much area beyond the boundary of a management unit of interest should the land managers consider is not known for many species and communities? My results suggest that managers in my study area might benefit by evaluating habitat 2100 m (i.e., within 1386 ha, the dominant scale of the responses of the butterfly community to spatial heterogeneity) beyond the boundary of the study area. This study, including several others (e.g., Mazerolle and Villard 1999, Fleishman et al. 2002, Collinge et al. 2003, Chapter 1), suggest that including measures of landscape heterogeneity with traditionally used environmental covariates to predict butterfly species distributions across the landscape can provide ecologists with an additional explanatory power. Therefore, I suggest that in addition to spatial heterogeneity in vegetation and topography, climate, soil, ecologists should explicitly consider measures of landscape heterogeneity (if possible all five components; Li and Reynolds 1994) in biodiversity studies.

2.7 Acknowledgements

The data used in this study were collected by a number of field technicians assisted by many excellent taxonomists from the Natural Resource Ecology Laboratory at Colorado State University, and the U. S. Geological Survey Fort Collins Science Center. I thank staff at Rocky Mountain National Park for providing administrative and logistical support during the study. I also thank Sara Simonson, Paul Opler, Geneva Chong, Greg Newman, Richard Bray and Catherine Jarnevich for their help during the study. T.S. acknowledges funding for data analysis from NASA grant (NRA-03-OES-03). I also acknowledge the support of the Ford Foundation International Fellowships Program for Ph.D. studies at Colorado State University (Aug. 2002-Aug. 2005). To all I am grateful.

2.8 Literature cited

Allen, R. B., R. K. Peet, and W. L. Baker. 1991. Gradient analysis of latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography **18**:123-139.

Baldwin, D. J. B., K. Weaver, F. Schnekenburger, and A. H. Perera. 2004. Sensitivity of landscape pattern indices to input data characteristics on real landscapes: implications for their use in natural disturbance emulation. Landscape Ecology **19**: 255-271.

Benson, B. J., and M. D. MacKenzie. 1995. Effects of sensor spatial resolution on landscape structure parameters. Landscape Ecology **10**:113-120.

Bergman, K. O., J. Askling, O. Ekberg, H. Ignell, H. Wahlman, and P. Milberg. 2004. Landscape effects on butterfly assemblages in an agricultural region. Ecography **27**:619-628.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretical approach. Second edition. Springer, New York, New York, USA.

Clench, H. K. 1966. Behavioral Thermoregulation in Butterflies. Ecology **47**:1021-1034.

Collinge, S. K., K. L. Prudic, and J. C. Oliver. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. Conservation Biology **17**:178-187.

Cumming, G. S., D. H. M. Cumming, and C. L. Redman. 2006. Scale mismatches in social-ecological systems: causes, consequences, and solutions. Ecology and Society **11**:14 [online] URL: http:www.ecologyandsociety.org/vol11/iss1/art14/.

Dennis, R. L. H. 2004. Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. Ecological Entomology **29**:744-752.

Dennis, R. L. H., T. G. Shreeve, and H. Van Dyck. 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodiversity and Conservation **15**:1943-1966.

Dyck, H. A., and E. Matthysen.1999. Habitat fragmentation and insect flight: a changing 'design' in a changing landscape? Trends in Ecology and Evolution **14**: 172-174.

Ehlrich, P. R. 1961. Intrinsic barriers to dispersal in Checkerspot butterfly. Science **134**: 108-109.

ESRI. 2004. Environmental Systems Research Institute, Inc., 380 New York St., Redlands, CA 97373, USA.

Fleishman, E., D. D. Murphy, and P. Sjogren-Gulve. 2002. Modeling species richness and habitat suitability for taxa of conservation interest. Pages 507-517 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of scale and accuracy. Island Press, Covelo, California, USA.

Fleishman, E., G. T. Austin, and A. D. Weiss. 1998. An empirical test of Rapoport's rule: Elevational gradients in montane butterfly communities. Ecology **79**:2482-2493.

Fleishman, E., R. Mac Nally, and D. D. Murphy. 2005. Relationships among non-native plants, diversity of plants and butterflies, and adequacy of spatial sampling. Biological Journal of the Linnean Society **85**:157-166.

Forman, R. T. T., and Godron, M. 1986. Landscape ecology. John Wiley and Sons, New York, New York, USA.

Fortin, M.-J. 1999. Spatial statistics in landscape ecology. Pages 253-279 *in* R. H. Gardner, and J. M. Klopatek, editors. Landscape ecological analysis: issues and applications. Springer-Verlag, New York.

Fortin, M.-J., and A. A. Agrawal. 2005. Landscape ecology comes of age. Ecology **86**: 1965-1967.

Fortin, M.-J., and M. R. T. Dale. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, UK.

Gilbert, L. E., and M. C. Singer. 1975. Butterfly Ecology. Annual Review of Ecology and Systematics **6**:365-397.

Golden, D. M., and T. O. Crist. 1999. Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. Oecologia **118**:371-380.

Greatorex-Davies, J. N., T. H. Sparks, M. L. Hall, and R. H. Marrs. 1993. The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. Biological Conservation **63**:31-41.

Guisan, A., S. B. Weiss, and A.D. Weiss. 1999. GLM versus CCA spatial modeling of plant species distribution. Plant Ecology **143**:107-122.

Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems **1**: 143-156.

Gutierrez, D., P. Fernandez, A. S. Seymour, and D. Jordano. 2005. Habitat distribution models: are mutualist distributions good predictors of their associates? Ecological Applications **15**:3-18.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University press, Cambridge, UK.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews **80**:489-513.

Hogsden, K. L., and T. C. Hutchinson. 2004. Butterfly assemblages along a human disturbance gradient in Ontario, Canada. Canadian Journal of Zoology **82**:739-748.

Huston, M. A. 1994. Biological Diversity: the coexistence of species in changing landscapes. Cambridge University Press, UK.

Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. Pages 259-289 *in* R. F. Denno, and M. S.

McClure, editors. Variable plants and herbivore in natural and managed systems. Academic Press, New York, New York, USA.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology **83**:530-544.

Kingsolver, J. G. 1983a. Ecological significance of flight activity in Colias butterflies - implications for reproductive strategy and population structure. Ecology **64**:546-551.

Kingsolver, J. G. 1983b. Thermoregulation and flight in Colias butterflies - elevational patterns and mechanistic limitations. Ecology **64**:534-545.

Kolasa, J., and C. D. Rollo. 1991. The heterogeneity of heterogeneity: a glossary. Pages 1-23 *in* J. Kolasa, and S. T. A. Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography **30**:889-900.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications **2**:203-217.

Legendre, P. 1993. Spatial Autocorrelation - trouble or new paradigm. Ecology **74**:1659-1673.

Legendre, P., and L. Legendre.1998. Numerical ecology. Second English edition. Elsevier Science, Amsterdam, The Netherlands.

Legendre, P., and M. J. Fortin. 1989. Spatial Pattern and Ecological Analysis. Vegetatio **80**:107-138.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton.

Li, B. L., and S. Archer. 1997. Weighted mean patch size: a robust index for quantifying landscape structure. Ecological Modelling **102**:353-361.

Li, H., and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology **75**:2446-2455.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs **72**:445-463.

Luoto, M., R. K., Heikkinen, J. Poyry, and K. Saarinen 2006. Determinants of the biogeographical distribution of butterflies in boreal regions. Journal of Biogeography **33**:1764-1778.

Maier, J. A. K., J. M. V. Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research **35**:2233-2243.

Mazerolle, M. J., and M. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience **6**:117-124.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS. Spatial analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNWGTR- 351. Pacific Northwest Research Station, Portland, Oregon, USA.

Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscape. Pages 69-84 *in* J. Kolasa, and S. T. A Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Moody, A., and D. M. Johnson. 2001. Land-surface phenologies from AVHRR using the discrete Fourier transform. Remote Sensing of Environment **75**: 305-323.

Morisette, J. T., C. S. Jarnevich, A. Ullah, W. J. Cai, J. A. Pedelty, J. E. Gentle, T. J. Stohlgren, and J. L. Schnase. 2006. A tamarisk habitat suitability map for the continental United States. Frontiers in Ecology and the Environment **4**:11-17.

Murphy, D. D., and S. B. Weiss. 1992. Effects of climate change on biological diversity in Western North America: Species losses and mechanisms. Pages 355-368 *in* R. L. Peters and T. E. Lovejoy, editors. Global Warming and biological diversity. Yale University Press, London, UK.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models: regression, analysis of variance, and experimental designs. Fourth edition. Irwin, Chicago, Illinois, USA.

Nieminen, M., M. Siljander, and I. Hanski. 2004. Structure and dynamics of *Melitaea cinxia* populations. Pages 63-91 *in* P. R. Ehrlich, and Hanski, I., editors. On the wings of Checkersopts. A model system for population biology. Oxford University press, Oxford.

O'Neill, R. V., C. T. Hunsaker, S. P. Timmins, B. L. Jackson, K. B. Jones, K. H. Riitters, and J. D. Wickham. 1996. Scale problems in reporting landscape pattern at the regional scale. Landscape Ecology **11**:169-180.

O'Neill, R.V. and A.W. King.1998. Homage to St. Michael; or why are there so many books on scale? Pages 3-15 *in* D. L. Peterson and V. T Parker, editors. Ecological scale: Theory and applications. Columbia University Press, New York, USA.

Opler, P. A. 1999. A field guide to Western Butterflies. Houghton Mifflin, New York.

Parmesan, C. 1996. Climate and species' range. Nature **382**:765-766.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology **8**:3-18.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio **45**: 3-75.

Peet, R. K. 1988. Forests of the Rocky Mountains. Pages 64-101 *in* M. G. Barbour, and W. D. Billings, editors. North American Terrestrial Vegetation, Cambridge University Press, New York.

Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science **269**: 331-334.

Pollard, E. and T. J. Yates. 1993. Monitoring butterflies for ecology and conservation. Chapman and Hall, London.

Rabasa, S. G., D. Gutierrez, and A. Escudero. 2005. Egg laying by a butterfly on a fragmented host plant: a multi-level approach. Ecography **28**:629-639.

Reich, R. M., and R. A. Davis. 2006. Online spatial library for the S-PLUS 7.0 statistical software package. Colorado State University, Fort Collins, CO, USA. [online]: URL: http://www.warnercnr.colostate.edu/~robin/

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist **158**:87-99.

Risser, P. G., J. P. Karr, and R. T. T. Forman.1984. Landscape ecology: directions and approaches. Illinois Natural History Survey Special Publication Number 2, Champaign, Illinois, USA.

Risser, P.G. 1987. Landscape ecology: state-of-the-art. Pages 3-14 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

SAS Institute. 2004. SAS for Windows, version 9.1. SAS Institute, Cary, NC.

Schneider, C. 2003. The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. Ecological Entomology **28**:252-256.

Scott, J. A. 1975. Movement of Precis-Coenia, a pseudoterritorial submigrant (Lepidoptera-Nymphalidae). Journal of Animal Ecology **44**:843-850.

Simard, M., K. Q. Zhang, V. H. Rivera-Monroy, M. S. Ross, P. L. Ruiz, E. Castaneda-Moya, R. R. Twilley, and E. Rodriguez. 2006. Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. Photogrammetric Engineering and Remote Sensing **72**:299-311.

Simonson, S. E., P.A. Opler, T. J. Stohlgren, and G. W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation **10**:1369-1386.

Smallidge, P. J., and D. J. Leopold. 1997. Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. Landscape and Urban Planning **38**:259-280.

Stefanescu, C., S. Herrando, and F. Paramo. 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. Journal of Biogeography **31**:905-915.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83**:1421-1432.

Stohlgren, T. J. 2006. Measuring plant diversity: Lessons from the field. Oxford University Press, New York, NY, USA.

Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998. Comparison of rangeland vegetation sampling techniques in the central grasslands. Journal of Range Management **51**:164-172.

Stohlgren, T. J., T. T. Veblen, K. C. Kendall, W. L. Baker, C. D. Allen, J. A. Logan, and K. C. Ryan. 2002. The heart of the Rockies: montane and subalpine ecosystems. Pages 203-218 *in* J. S. Baron, editor. Rocky Mountain futures: an ecological perspective. Island Press, Washington, D.C., USA.

Strathmann, K. S. 2005. Local and landscape influences on meadow butterfly communities in northeastern Sierra Nevada. MS Thesis. San Francisco State University, San Francisco, CA, USA. [online] URL: http://sagehen.ucnrs.org/Documents/Theses/Strathmann.pdf

Summerville, K. S., J. A. Veech, and T. O. Crist. 2002. Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? Oikos **97**:195-204.

Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos **101**:18-25.

Thomas, C. D., and H. C. Mallorie. 1985. Rarity, Species Richness and Conservation - Butterflies of the Atlas Mountains in Morocco. Biological Conservation **33**:95-117.

Thomas, C. D., and I. Hanski.1997. Butterfly metapopulations. Pages 359-384 *in* I. Hanski, and M. Gilpin, editors. Metapopulation biology. Academic Press, London, UK.

Thomas, C. D., M. Baguette, and O. T. Lewis. 2000. Butterfly movement and conservation in patchy landscapes. Pages 85-104 *in* L. M. Gosling, W. J. Sutherland, editors. Behavior and conservation. Cambridge University Press, Cambridge, UK.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B-Biological Sciences **360**:339-357.

Turner, M. G. 2005. Landscape ecology: What is the state of the science. Annual Review of Ecology Evolution and Systematics **36**:319-344.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice- pattern and process. Springer-Verlag, New York, USA.

Turner, M. G., R. H. Gardner, V. H. Dale, and R. V. O'Neill. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos **55**: 121-129.

Vogelmann, J. E., T. L. Sohl, P. V. Campbell, and D. M. Shaw. 1998. Regional land cover characterization using Landsat thematic mapper data and ancillary data sources. Environmental Monitoring and Assessment **51**:415-428.

Wagner, H. H., and M. -J. Fortin 2005. Spatial analysis of landscapes: Concepts and statistics. Ecology **86**: 1975-1987.

Wahlberg, N., T. Klemetti, V. Selonen, and I. Hanski. 2002. Metapopulation structure and movements in five species of checkerspot butterflies. Oecologia **130**:33-43.

Warren, M. S. 1984. The biology and status of the wood white butterfly Leptidea sinapis. (Lepidoptera: Pieridae) in the British Isles. Entomologist's Gazette **35**:207-223.

Warren, M. S. 1985. The influence of shade on butterfly numbers in woodland rides, with special reference to the Wood White Leptidea-Sinapis. Biological Conservation **33**:147-164.

Warren, T. L., M. G. Betts, A. W. Diamond, and G. J. Forbes. 2005. The influence of local habitat and landscape composition on cavity-nesting birds in a forested mosaic. Forest Ecology and Management **214**:331-343.

Wettstein, W., and B. Schmid. 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. Journal of Applied Ecology **36**:363-373.

Wood, P. A., and M. J. Samways. 1991. Landscape element pattern and continuity of butterfly flight paths in an ecologically landscaped botanical garden, Natal, South-Africa. Biological Conservation **58**:149-166.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

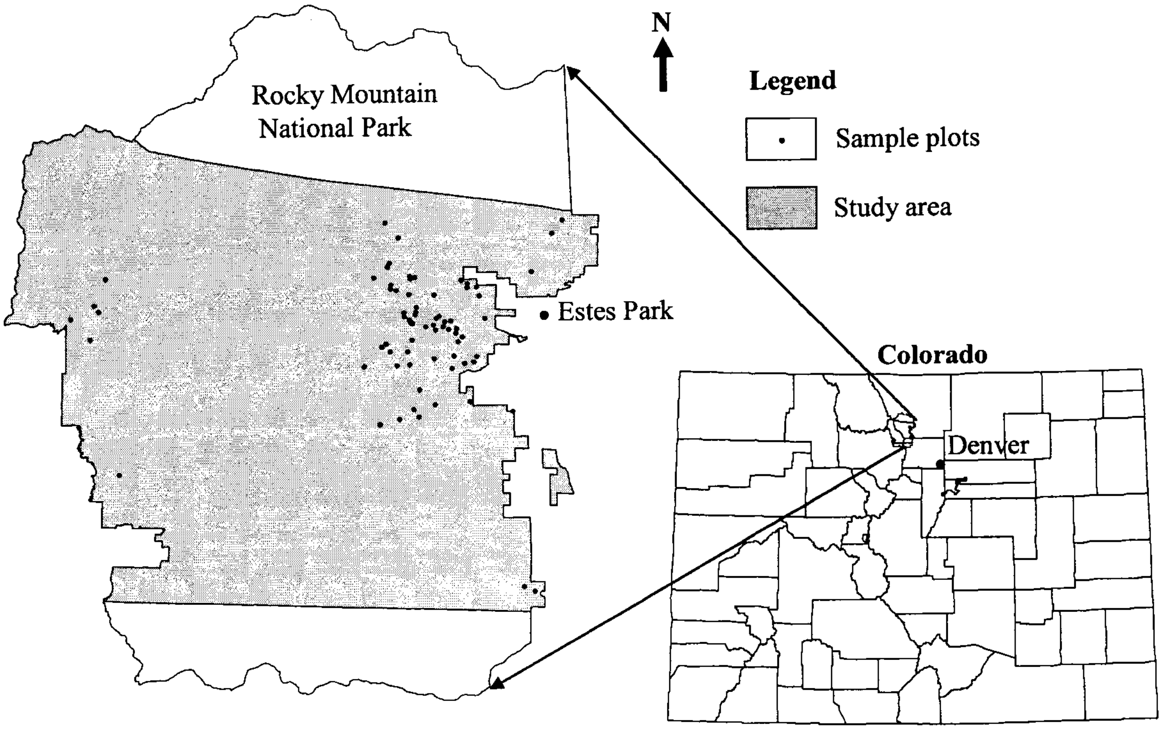

Figure 2.1: Map of study area.

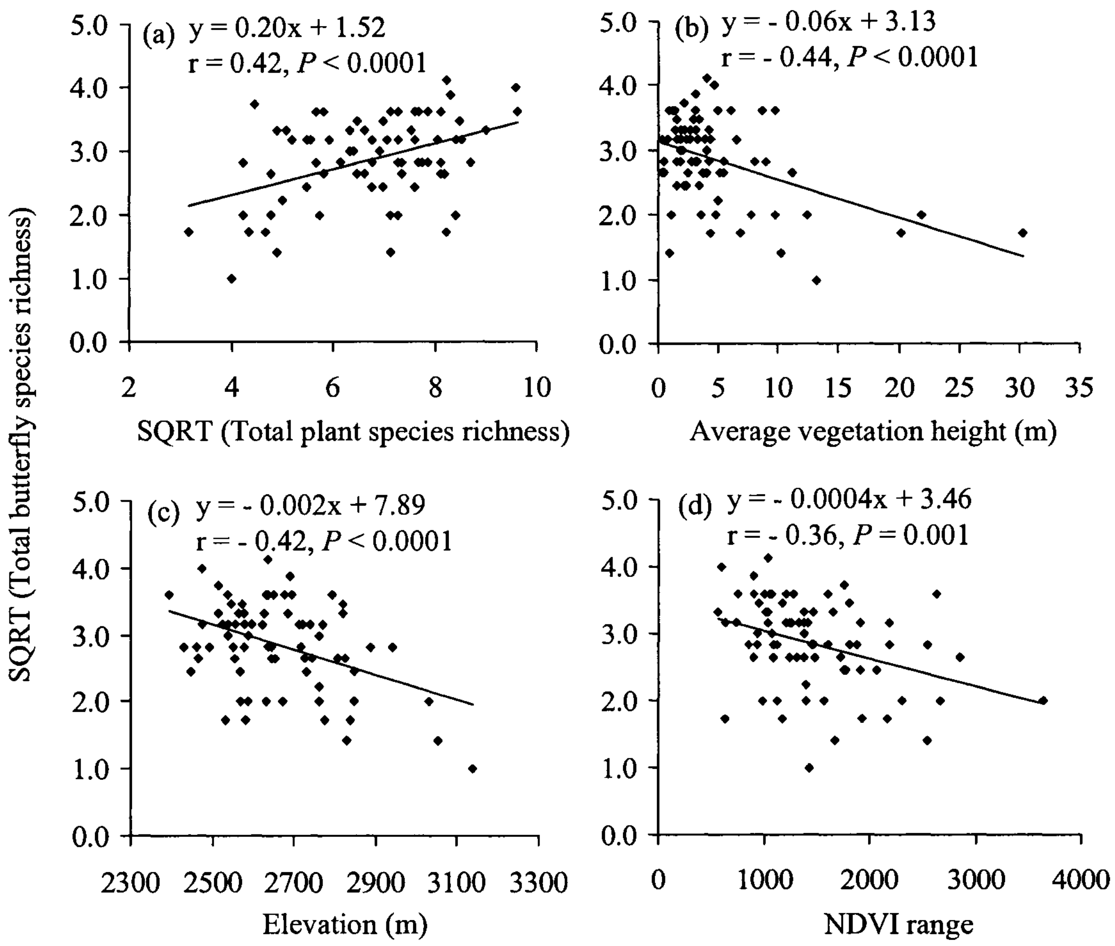

Figure 2.2: Relationship between total butterfly species richness (SQRT, square root transformed) and plot level (0.1 ha) (a) total plant species richness (SQRT); (b) average vegetation height (m); (c) elevation (m), and (d) range in NDVI (250 x 250 m).

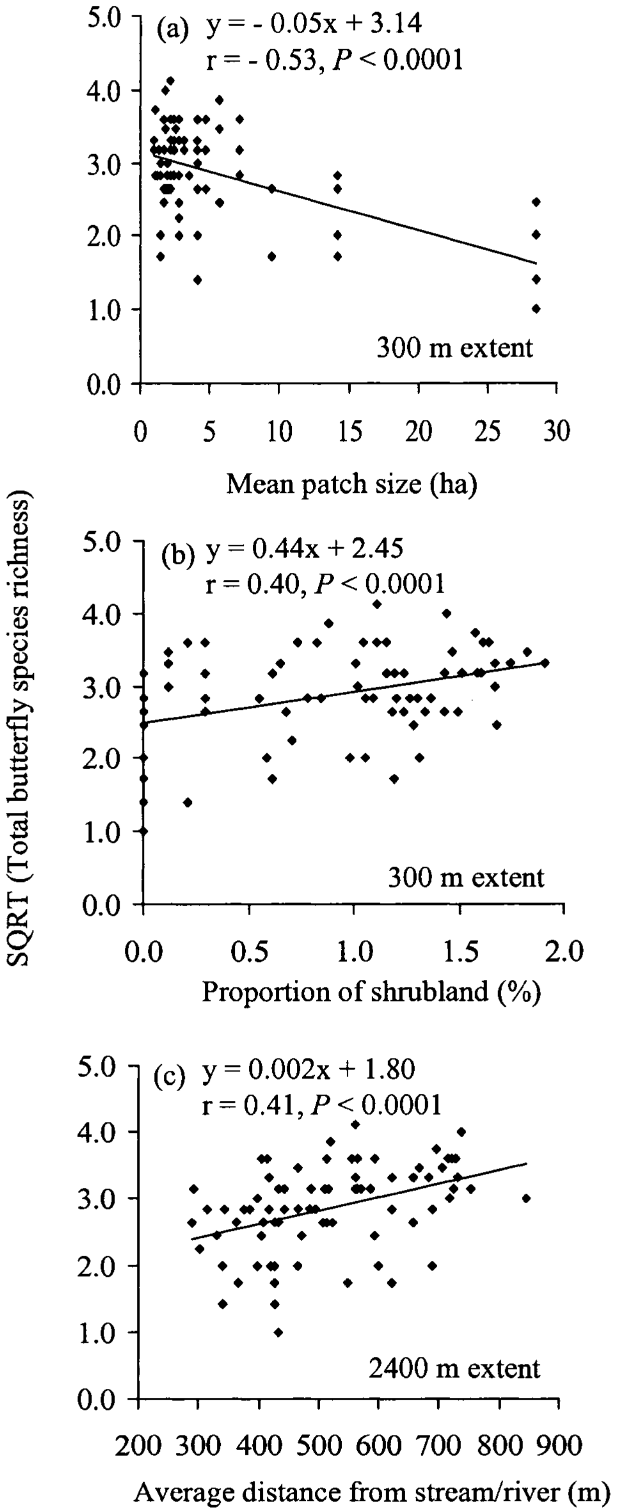

Figure 2.3: Relationship between total butterfly species richness (SQRT, square root transformed) and (a) mean patch size (ha); (b) proportion of shrubland ($\log_{10}$ transformed); and (c) average distance from stream/river (m).

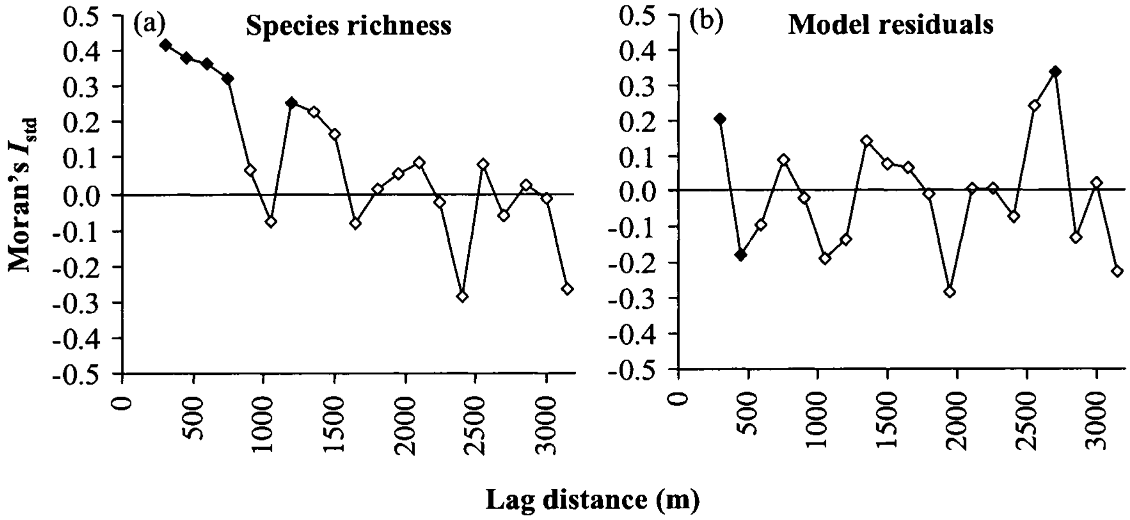

Figure 2.4: Correlograms of (a) total butterfly species richness (square root transformed), and (b) residuals from the best model at 2100 m spatial extent. Open diamonds represent nonsignificance, and closed diamonds indicate significance (one-tailed test ($\alpha = 0.05$) for positive spatial autocorrelation adjusted using progressive Bonferroni correction [Legendre and Legendre 1998, Lichstein et al. 2002]). Lag distance 150 m, except first lag distance that was extended to 300 m to accommodate an adequate number of site pairs.

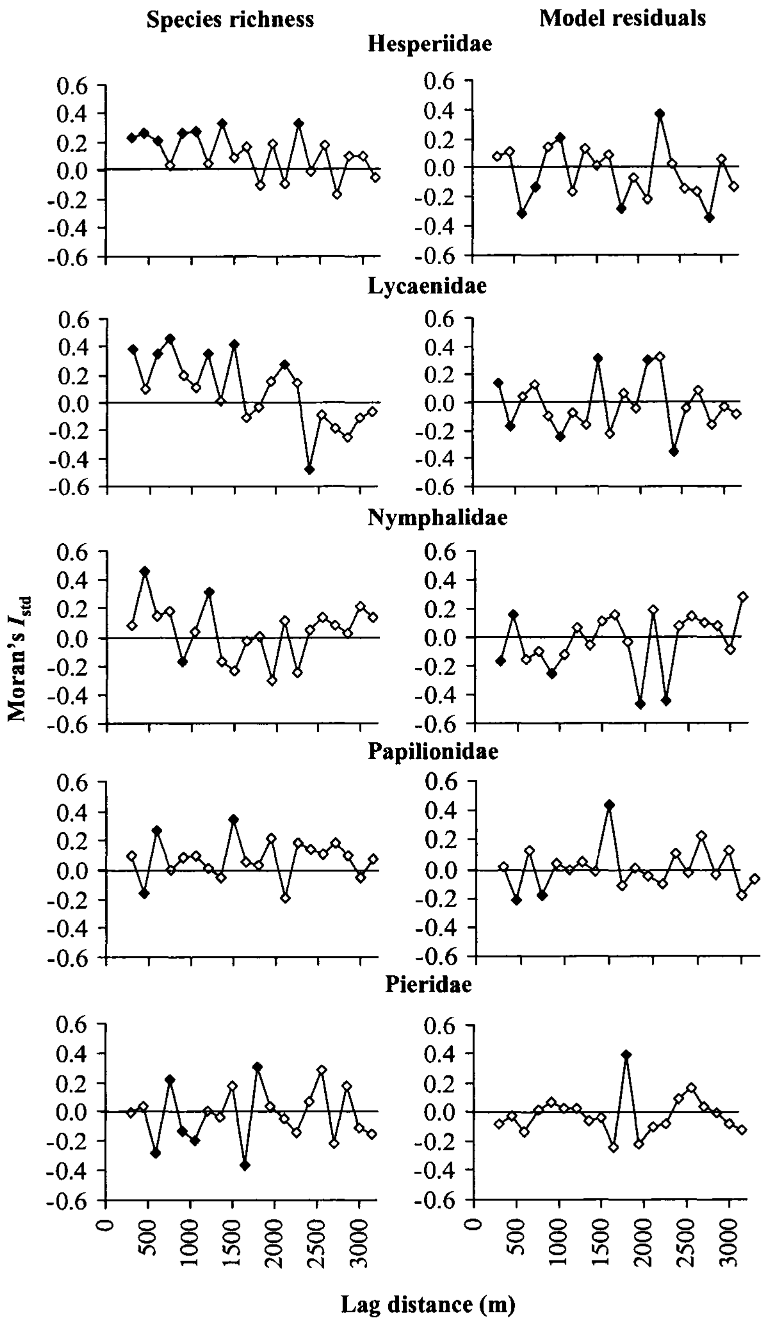

Figure 2.5: Moran's I_{std} correlograms of five butterfly families' species richness (square root transformed) and residuals from their best models at different spatial extents. Open diamonds represent nonsignificance, and closed diamonds indicate significance (one-tailed test ($\alpha = 0.05$) for positive spatial autocorrelation adjusted using progressive Bonferroni correction [Legendre and Legendre 1998, Lichstein et al. 2002]). Lag distance 150 m, except first lag distance that was extended to 300 m to accommodate an adequate number of site pairs.

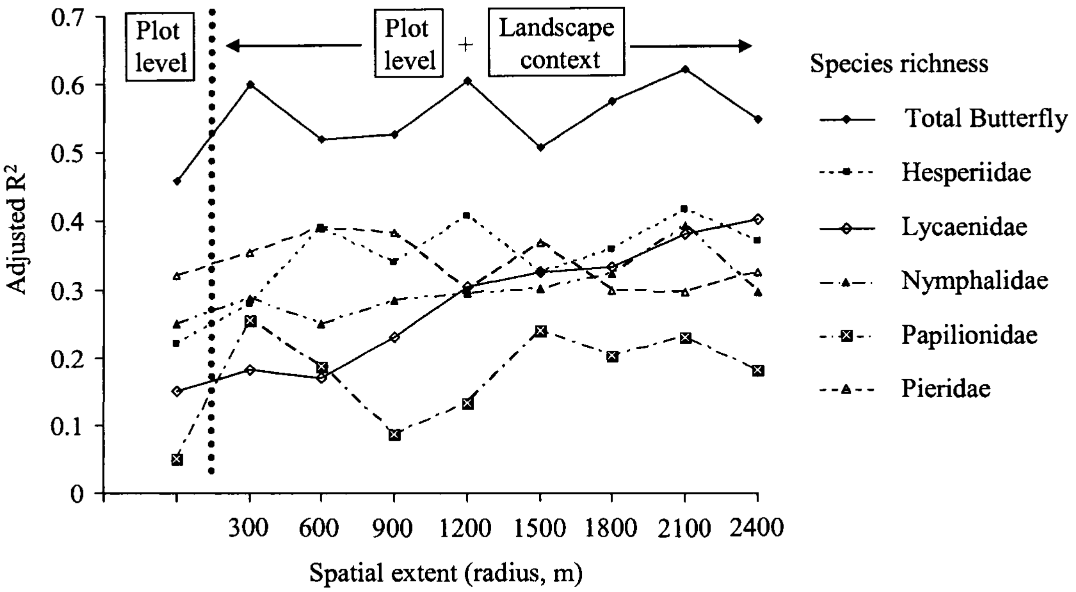

Figure 2.6: Variation explained in total butterfly species richness and five families' species richness by plot level variables (total plant species richness and average vegetation height (m), quantified at 0.1 ha, and range in NDVI (250 x 250 m)); and by plot level variables plus landscape context variables (topographic and landscape heterogeneity, quantified at different spatial extents).

Table 2.1: Edge contrast weights between land cover types (values vary from 0.0 to 1.0, where 1.0 is the maximum contrast and 0.0 no contrast), based on information in Peet (1981) and Stohlgren et al. (2002).

Land cover type	Conifer	Deciduous	Grasslands	Shrubland
Deciduous	0.2			
Grasslands	0.9	0.8		
Shrubland	0.8	0.7	0.4	
Non-vegetated	1.0	1.0	0.2	0.3

Table 2.2: Cross-correlations (Pearson correlation coefficients) among predictor variables that were a part of the best model of total butterfly species richness at 2100 m spatial extent (n = 76, 0.1 ha plots).

	Total butterfly SR	Total plant SR	Average vegetation height	Mean patch size	Patch richness density	IJI	Elevation (SD)
Total butterfly SR	1.0						
Total plant SR	0.42	1.0					
Average vegetation height	- 0.44	- 0.25	1.0				
Mean patch size	- 0.35	0.12^{ns}	- 0.06^{ns}	1.0			
Patch richness density	- 0.11^{ns}	- 0.17^{ns}	0.07^{ns}	- 0.37	1.0		
IJI	- 0.06^{ns}	- 0.18^{ns}	0.05^{ns}	- 0.41	- 0.10^{ns}	1.0	
Elevation (SD)	- 0.01^{ns}	0.02^{ns}	- 0.06^{ns}	0.50	- 0.16^{ns}	- 0.09^{ns}	1.0

Notes: SR is species richness; IJI is interspersion and juxtaposition index; SD is standard deviation. Transformed data were used where it was appropriate. Correlations are significant at alpha = 0.05, except where noted; "ns" is the nonsignificance at alpha > 0.05.

Table 2.3: Pearson correlation coefficients (r) between total butterfly species richness (square root transformed) and selected predictor variables at eight spatial extents (within radii of 300, 600, 900, 1200, 1500, 1800, 2100, and 2400 m from the center of the sample plot).

Type	Predictor variable (units)	300 m	600 m	900 m	1200 m	1500 m	1800 m	2100 m	2400 m
Landscape configuration									
	Mean patch size (ha)	- 0.53	- 0.34	- 0.35	- 0.31	- 0.32	- 0.35	- 0.35	- 0.37
	Area weighted mean patch size (ha)	- 0.43	- 0.34	- 0.28	- 0.23	- 0.23	- 0.20^{ns}	- 0.15^{ns}	- 0.13^{ns}
	Mean patch size of shrubland (ha)	0.34	0.27	0.27	0.27	0.28	0.28	0.23	0.14
	Area weighted mean patch size of shrubland (ha)	0.35	0.29	0.29	0.28	0.29	0.21^{ns}	0.14^{ns}	0.09^{ns}
	Mean patch size of grasslands (ha)	0.26	0.15^{ns}	0.13^{ns}	0.10^{ns}	0.06^{ns}	0.02^{ns}	0.09^{ns}	0.07^{ns}
	Area weighted mean patch size of grasslands (ha)	0.26	0.21^{ns}	0.18^{ns}	0.14^{ns}	0.15^{ns}	0.21^{ns}	0.18^{ns}	0.16^{ns}
	Mean patch size of conifer (ha)	- 0.45	- 0.29	- 0.27	- 0.17^{ns}	- 0.18^{ns}	- 0.24	- 0.22^{ns}	- 0.21^{ns}
	Mean patch size of deciduous (ha)	0.10^{ns}	- 0.04^{ns}	- 0.24	- 0.26	- 0.28	- 0.36	- 0.30	- 0.29
	Mean patch size of non-vegetated (ha)	0.06^{ns}	0.07^{ns}	- 0.01^{ns}	- 0.05^{ns}	- 0.08^{ns}	- 0.12^{ns}	- 0.13^{ns}	0.11^{ns}
	Patch richness density (no. /100 ha)	0.37	- 0.01^{ns}	- 0.11^{ns}	- 0.07^{ns}	- 0.10^{ns}	- 0.08^{ns}	- 0.11^{ns}	0.11^{ns}
	Interspersion/juxtaposition index (%)	0.42	0.33	0.18^{ns}	0.01^{ns}	- 0.05^{ns}	- 0.05^{ns}	- 0.06^{ns}	- 0.15^{ns}
	Mean edge contrast index (%)	0.40	0.33	0.31	0.26	0.06^{ns}	- 0.06^{ns}	- 0.06^{ns}	- 0.02^{ns}
	Edge density (m/ha)	0.40	0.33	0.35	0.33	0.31	0.31	0.32	0.31
	Mean nearest neighbor distance (m)	0.53	- 0.24	- 0.36	- 0.33	- 0.18^{ns}	- 0.24	- 0.24	- 0.17^{ns}
	Shannon-diversity index	0.40	0.30	0.25	0.22^{ns}	0.20^{ns}	0.16^{ns}	0.15^{ns}	0.17^{ns}
	Mean fractal dimension	0.26	0.27	0.24	0.30	0.22^{ns}	0.29	0.12^{ns}	0.04^{ns}
Landscape composition									
	Proportion of shrubland (%)	0.40	0.38	0.30	0.33	0.34	0.33	0.31	0.29
	Proportion of grasslands (%)	0.26	0.23	0.19^{ns}	0.17^{ns}	0.17^{ns}	0.24	0.18^{ns}	0.25
	Proportion of conifer (%)	- 0.34	- 0.26	- 0.24	- 0.22^{ns}	- 0.22^{ns}	- 0.20^{ns}	- 0.19^{ns}	- 0.20^{ns}
	Proportion of deciduous (%)	0.33	0.23	0.08^{ns}	- 0.06^{ns}	- 0.05^{ns}	0.01^{ns}	0.07^{ns}	0.12^{ns}
	Proportion of non-vegetated (%)	0.02^{ns}	- 0.02^{ns}	- 0.06^{ns}	- 0.08^{ns}	- 0.15^{ns}	- 0.20^{ns}	- 0.21^{ns}	- 0.19^{ns}
Topography									
	Mean elevation (m)	- 0.39	- 0.36	- 0.34	- 0.32	- 0.30	- 0.28	- 0.28	- 0.28
	Mean exposure (m)	- 0.24	- 0.29	- 0.30	- 0.30	- 0.30	- 0.30	- 0.25	- 0.28
	Distance from stream/river	- 0.15^{ns}	- 0.03^{ns}	0.09^{ns}	0.18^{ns}	0.29	0.37	0.40	0.41

Note: Correlations were significant at $P \leq 0.05$, except where noted; "ns" indicates nonsignificance at $P > 0.05$. Transformed data were used where it was appropriate.

Table 2.4: Best regression models linking patterns of butterfly species richness (n = 76, 0.1 ha) with measures of spatial heterogeneity in vegetation, topographic and landscape.

Dependent variable (spatial extent)	Independent variable	Parameter estimate	Factor P	Partial R^2	Model Adj. R^2, F, P
$(\text{Total butterfly SR})^{0.5}$	Average vegetation height	- 0.047	< 0.0001	0.197	$R^2 = 0.62$,
	Mean patch size	- 0.243	< 0.0001	0.169	$F_{6, 69} = 21.57$,
(2100 m)	Total plant species richness	0.161	< 0.0001	0.147	$P < 0.0001$
	Patch richness density	- 10.873	< 0.0001	0.055	
	Interspersion and juxtaposition index	- 0.019	0.0020	0.047	
	Elevation (standard deviation)	0.004	0.0085	0.037	
$(\text{Hesperiidae SR})^{0.5}$	Distance from stream or river	0.002	0.0009	0.256	$R^2 = 0.42$,
	Average vegetation height	- 0.045	0.0008	0.064	$F_{5, 70} = 11.83$,
(2100 m)	Mean patch size	- 0.165	< 0.0001	0.054	$P < 0.0001$
	Mean patch size of shrubland	- 0.825	0.0210	0.052	
	Patch richness density	- 6.397	0.0468	0.032	
$(\text{Lycaenidae SR})^{0.5}$	Area weighted mean patch size of grasslands	0.661	< 0.0001	0.227	$R^2 = 0.40$,
	Minimum elevation	- 0.005	< 0.0001	0.133	$F_{3, 72} = 17.93$,
(2400 m)	Edge density	- 0.011	0.0046	0.068	$P < 0.0001$
$(\text{Nymphalidae SR})^{0.5}$	Total plant species richness	0.182	< 0.0001	0.261	$R^2 = 0.39$,
	Maximum exposure	- 0.002	0.0023	0.090	$F_{4, 71} = 13.16$,
(2100 m)	Cohesion	28.991	0.0333	0.038	$P < 0.0001$
	Mean patch size	- 0.095	0.0040	0.037	
$(\text{Paplionidae SR})^{0.5}$	Mean nearest neighbor distance	0.364	< 0.0001	0.254	$R^2 = 0.25$,
					$F_{1, 74} = 25.18$,
(300 m)					$P < 0.0001$
$(\text{Pieridae SR})^{0.5}$	Average vegetation height	- 0.043	< 0.0001	0.267	$R^2 = 0.39$,
	Area weighted mean patch size of grasslands	0.141	0.0005	0.061	$F_{4, 71} = 13.10$,
(600 m)	Maximum exposure	- 0.002	0.0158	0.050	$P < 0.0001$
	Total plant species richness	0.096	0.0083	0.047	

Note: Average vegetation height (m) and total plant species richness data were collected at plot level (0.1 ha). Other predictors in the models were quantified at eight spatial extents. Note the varying spatial extent for the best models. The variables were transformed where it was appropriate. SR is species richness.

Table 2.5: Regression models evaluated for total butterfly species richness (n = 76, 2100 m extent).

Model No.	Category of heterogeneity	Predictors of total butterfly species richness (sign of regression coefficient)	Adj. R^2	K	AIC_C	ΔAIC_C
1	Landscape + topographic + vegetation	MPS (-), AvgHt (-), PRD (-), Total plant SR (+), IJI (-), ElevSD (+)	0.62	7	-128.97	0.00
2	Landscape + vegetation	MPS (-), AvgHt (-), PRD (-), Total plant SR (+), IJI (-),	0.59	6	-123.93	5.25
3	Topographic + vegetation	AvgHt (-), Total plant SR (+), RngNDVI (-), ExpSD (-), StrmDist (+)	0.54	6	-115.88	13.09
4	Vegetation	RngNDVI (-), AvgHt (-), Total plant SR (+)	0.46	4	-105.33	23.64
5	Landscape + topographic	ExpSD (-), ElevMax (+), EdgeCont (-), StrmDist (+), ENN (-)	0.38	6	-92.81	36.15
6	Topographic	ExpMax (-), ElevMax (-), StrmDist (+)	0.30	4	-85.76	43.21
7	Landscape	MPS (-), PRD (-), IJI (-)	0.29	4	-85.12	43.85

Notes: MPS = mean patch size; AvgHt = average vegetation height; PRD = patch richness density; SR = species richness; IJI = interspersion/ juxtaposition index; ElevSD = elevation standard deviation; RngNDVI = range in Normalized Difference Vegetation Index; ExpSD = exposure standard deviation; StrmDist = average distance from the stream or river; ElevMax = maximum elevation; EdgeCont = mean edge contrast index; ENN = nearest neighbor distance (m); ExpMax = maximum exposure; AIC_c = Akaike's Information criterion adjusted for small sample size; K is the number of estimable parameters in the model. The variables were transformed where it was appropriate. The predictor variables are arranged in order of their decreasing importance (based on standardized coefficient).

Table 2.6: Results from spatial autocorrelation analyses of butterfly species richness (raw data, total and family levels) and residuals from the best models presented in Table 2.4.

	Moran's I_{std} (P value)	
	Species richness (raw data)	Model residuals
Total butterflies	0.121 (< 0.0001)	- 0.016 (0.997)
Hesperiidae	0.117 (< 0.0001)	- 0.010 (0.879)
Lycaenidae	0.140 (< 0.0001)	0.014 (0.328)
Nymphalidae	0.026 (0.174)	- 0.043 (0.308)
Papilionidae	0.068 (0.024)	- 0.008 (0.673)
Pieridae	- 0.022 (0.827)	- 0.023 (0.813)

Appendix A: List of butterfly species recorded on two visits to 20m X 50m plots in Rocky Mountain National Park, Colorado. This field survey list includes 68 of the 134 butterfly species that are known to occur in the park http://www.npwrc.usgs.gov/resource/insects/insect/rmnp.htm, and follows the order of the list of the Peterson Field Guide to Western Butterflies by Opler (1999).

1. Hesperiidae: Skipper family

(Spreadwing Skippers, Skipperlings, Grass Skippers)

- Common Checkered-Skipper *Pyrgus communis* (Grote)
- Common Roadside-Skipper *Amblyscirtes vialis* (W.H. Edwards)
- Draco Skipper *Polites draco* (W.H. Edwards)
- Dreamy Duskywing *Erynnis icelus* (Scudder and Burgess)
- Garita Skipperling *Oarisma garita* (Reakirt)
- Nevada Skipper *Hesperia nevada* (Scudder)
- Persius Duskywing *Erynnis persius* (Scudder)
- Russet Skipperling *Piruna pirus* (W.H. Edwards)
- Snow's Skipper *Paratrytone snowi* (W.H. Edwards)
- Western Branded Skipper *Hesperia colorado* (Scudder)
- Woodland Skipper *Ochlodes sylvanoides* (Boisduval)

2. Lycaenidae: Gossamer wing family

(Coppers, Hairstreaks and Blues)

- Arctic Blue *Agriades glandon* (de Prunner)
- Blue Copper *Lycaena heteronea* Boisduval
- Boisduval's Mountain Blue *Icaricia icarioides* (Boisduval)
- Greenish Blue *Plebejus saepiolus* (Boisduval)
- Lupine Blue *Icaricia lupini* (Boisduval)
- Melissa Blue *Lycaeides melissa* (W.H. Edwards)
- Purplish Copper *Lycaena helloides* (Boisduval)
- Reakirt's Blue *Hemiargus isola* (Reakirt)

Rocky Mountain Dotted-Blue *Euphilotes ancilla* (Barnes and McDunnough)

Ruddy Copper *Lycaena rubidus* (Behr)

Silvery Blue *Glaucopsyche lygdamus* (Doubleday)

Spring Azure *Celastrina ladon* (Cramer)

Thicket Hairstreak *Callophrys spinetorum* (Hewitson)

Western Pine Elfin *Callophrys eryphon* (Boisduval)

Western Tailed-Blue *Everes amyntula* (Boisduval)

3. Nymphalidae: Brushfoot family

(Fritillaries, Checkerspots, Anglewings, Admirals, Wood Nymphs, and Arctics)

Aphrodite Fritillary *Speyeria aphrodite* (Fabricius)

Arctic Fritillary *Boloria chariclea* (Schneider)

Atlantis Fritillary *Speyeria atlantis* (W.H. Edwards)

Chryxus Arctic *Oeneis chryxus* (Doubleday and Hewitson)

Common Ringlet *Coenonympha tullia* (Muller)

Dotted Checkerspot *Poladryas minuta* (W.H. Edwards)

Edwards' Fritillary *Speyeria edwardsii* (Reakirt)

Field Crescent *Phyciodes pratensis* (Behr)

Gorgone Checkerspot *Chlosyne gorgone* (Hubner)

Gray Comma *Polygonia progne* (Cramer)

Green Comma *Polygonia faunus* (W.H. Edwards)

Hoary Comma *Polygonia gracilis* (Grote and Robinson)

Milbert's Tortoiseshell *Nymphalis milberti* (Godart)

Mormon Fritillary *Speyeria mormonia* (Boisduval)

Mourning Cloak *Nymphalis antiopa* (Linnaeus)

Northern Checkerspot *Chlosyne palla* (Boisduval)

Northern Crescent *Phyciodes cocyta* (Cramer)

Northwestern Fritillary *Speyeria hesperis* (W.H. Edwards)

Painted Lady *Vanessa cardui* (Linnaeus)

Red Admiral *Vanessa atalanta* (Linnaeus)

Silver-bordered Fritillary *Boloria selene* (Holland)

Silvery Checkerspot *Chlosyne nycteis* (Doubleday and Hewitson)

Small Wood-Nymph *Cercyonis oetus* (Boisduval)

Variegated Fritillary *Euptoieta claudia* (Cramer)

Weidemeyer's Admiral *Limenitis weidemeyerii* (W.H. Edwards)

4. Papilionidae: Swallowtail family

(Parnassians and Swallowtails)

Anise Swallowtail *Papilio zelicaon* (Lucas)

Black Swallowtail *Papilio polyxenes* (Fabricus)

Pale Swallowtail *Papilio eurymedon* (Lucas)

Rocky Mountain Parnassian *Parnassius smintheus* (Doubleday)

Two-tailed Swallowtail *Papilio multicaudatus* (W.F. Kirby)

Western Tiger Swallowtail *Papilio rutulus* (Lucas)

5. Pieridae: White and Sulfur family

(Whites, Marbles, and Sulfurs)

Cabbage White *Pieris rapae* (Linnaeus)

Checkered White *Pontia protodice* (Boisduval and Leconte)

Clouded Sulphur *Colias philodice* (Godart)

Large Marble *Euchloe ausonides* (Lucas)

Margined White *Pieris marginalis* (Scudder)

Orange Sulphur *Colias eurytheme* (Boisduval)

Pine White *Neophasia menapia* (C. and R. Felder)

Queen Alexandra's Sulphur *Colias alexandra* (W.H. Edwards)

Scudder's Sulphur *Colias scudderi* (Reakirt)

Spring White *Pontia sisymbrii* (Boisduval)

Western White *Pontia occidentalis* (Reakirt)

Literature cited:

Opler, P. A. 1999. A field guide to Western Butterflies. Houghton Mifflin, New York.

Appendix B: Environmental covariates considered for developing predictive models of total butterfly species richness and family butterfly species richness. Variables representing landscape composition and configuration were calculated with FRAGSTATS 3.3 according to McGarigal and Marks (1995).

Category of heterogeneity	Variable (units) (spatial extent)
Vegetation	
	Total plant species richness (plot level - 0.1 ha)
	Average vegetation height (m) (plot level - 0.1 ha)
	Range in NDVI (MODIS; 250 x 250 m - 6.25 ha; see Morisette et al. 2006)
Topographic	
All variables were calculated at eight spatial extents: 300, 600, 900, 1200, 1500, 1800, 2100, and 2400 m radius around the center of the sample plot.	
	Mean elevation (m)
	Minimum elevation (m)
	Maximum elevation (m)
	Standard deviation of elevation (m)
	Mean slope (degrees)
	Maximum slope (degrees)
	Minimum slope (degrees)
	Standard elevation of slope (degrees)
	Mean Eastness (calculated as: 100*sine (aspect in degrees); see Fleishman et al. 2002)
	Minimum Eastness
	Maximum Eastness
	Standard deviation of Eastness
	Mean Northness (calculated as: 100*cosine (aspect in degrees); see Fleishman et al. 2002)
	Minimum Northness
	Maximum Northness
	Standard deviation of Northness
	Mean topographic exposure (calculated as: (elevation of the centroid cell – mean elevation of all cell with in a specified radius); see Fleishman et al. (2002)
	Minimum topographic exposure (m)
	Maximum topographic exposure (m)
	Standard deviation of topographic exposure (m)
	Mean distance from stream/river (m)

Landscape Metrics

All metrics were calculated at eight spatial extents: 300, 600, 900, 1200, 1500, 1800, 2100, and 2400 m radius around the center of the sample plot; see McGarigal and Marks (1995) for definitions and formulas.

Composition

- Proportion of conifer (%)
- Proportion of deciduous (%)
- Proportion of grasslands (%)
- Proportion of shrubland (%)
- Proportion of non-vegetated (%)

Configuration

- Mean patch size (ha)
- Mean patch size of each of the five land cover types (ha)
- Area weighted mean patch size (ha)
- Area weighted mean patch size of each of the five land cover types (ha)
- Patch richness density (no. /100 ha)
- Interspersion and juxtaposition index (%)
- Cohesion
- Mean edge contrast index (%)
- Edge density (m/ha)
- Mean nearest neighbor distance (m)
- Shannon-diversity index
- Simpson's diversity index
- Mean fractal dimension
- Mean shape index

Literature cited

Fleishman, E., D. D. Murphy, and P. Sjogren-Gulve. 2002. Modeling species richness and habitat suitability for taxa of conservation interest. Pages 507-517 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editor. Predicting species occurrences: issues of scale and accuracy. Island Press, Covelo, California, USA.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS. Spatial analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNWGTR- 351. Pacific Northwest Research Station, Portland, Oregon, USA.

Morisette, J. T., C. S. Jarnevich, A. Ullah, W. J. Cai, J. A. Pedelty, J. E. Gentle, T. J. Stohlgren, and J. L. Schnase. 2006. A tamarisk habitat suitability map for the continental United States. Frontiers in Ecology and the Environment **4**:11-17.

CHAPTER 3 THE ROLE OF SPATIAL AUTOCORRELATION IN NATIVE-EXOTIC PLANT SPECIES RICHNESS RELATIONSHIPS

3.0 Abstract

Spatial autocorrelation in many ecological variables can significantly affect any ecological relationship. Several experimental and observational studies have shown positive or negative relationships between native and exotic plant species richness at different spatial scales. However, how spatial autocorrelation affects these relationships is not yet known. I used native and nonnative plant species richness data collected from 180 (0.1 ha) modified-Whittaker plots from Rocky Mountain National Park, Colorado, USA. I used principal coordinates of neighbor matrices (PCNM) approach to quantify broad-scale spatial dependence, and conditional autoregressive regression (CAR) for modeling fine-scale spatial autocorrelation. I used a variation partitioning approach to quantify how much of the variation in exotic plant species richness was explained by: (i) native plant species richness; (ii) space (i.e., spatial dependence and fine-scale spatial autocorrelation); and (iii) spatially structured environmental processes. After variation partitioning, I found that native plant species richness accounted only for 9% of the variation in exotic plant species richness; however, pure space, and spatially structured environmental processes explained 34% and 17% of the variation in exotic plant species richness, respectively (n = 180, 0.1-ha plots). My results suggest that spatial autocorrelation and spatially structured environmental processes are relatively more important than native plant species richness alone in shaping the native-exotic plant species richness relationships.

Keywords: Exotic species, native species, principal coordinates of neighbor matrices (PCNM), plant invasion, spatial autocorrelation, spatial dependence, spatial scale, species richness, SpaceMaker, variation partitioning.

3.1 Introduction

Invasion of habitats by exotic (nonnative, alien, or non-indigenous) species is a global phenomenon and is one of the major threats to native biodiversity (Mack *et al.* 2000). The ecological and economic cost of invasions to society is alarmingly high (Pimentel *et al.* 2005), which necessitates the early detection and rapid response to new invasions. Managing species invasions in space and time requires an understanding of the factors that influence the spatial and temporal distributions of native and exotic species across the landscape (Stohlgren & Schnase 2006a).

Spatial structures in ecological variables may result due to biotic (e.g., dispersal, growth, reproduction, and mortality) and abiotic (e.g., light, climate, topography, and disturbance) factors and their interactions (Legendre & Legendre 1998; Borcard & Legendre 2002). Such factors may not only affect species distributions, but they also influence the ecological interactions among species and control the spatial and temporal organization of these interactions. The ecological processes, which may themselves be spatially and temporally structured, affect native and exotic plant species at multiple spatial and temporal scales. For example, processes such as competition, facilitation, mutualism, and allelopathy may influence native-exotic plant species relations at small spatial scales whereas other processes such as climate, productivity, disturbance and topography may effect at larger spatial or temporal scales.

Disturbances such as fire, flood, grazing, insect outbreaks, and logging can alter the existing spatial structure or create new ones. Successional changes in vegetation communities can also change spatial structure. Changing climates may also influence the spatial structure by affecting the migration patterns of native and exotic plant species or by altering their phenology. For example, early flowering of some species in certain areas and late flowering of other species in other areas may eventually change their spatial distributions and interactions with other organisms and thus may influence the spread of invasive species. Thus, it is important to understand the linkages between spatial structure and native and exotic plant species.

Spatial autocorrelation in a variable can be defined as the lack of independence among sampling locations (Legendre & Legendre 1998). It can be caused by spatial dependence (or broad-scale spatial trend) of the community on environmental factors or due to ecological processes (e.g., dispersal, growth, mortality, and competition; Legendre & Legendre 1998, Wagner & Fortin 2005). In any case, the presence of spatial autocorrelation in the response or predictor variables can pose a problem in applying parametric statistical methods because of the violation of the assumption of independence of observations (Legendre 1993, Wagner & Fortin 2005). To evaluate the magnitude of this problem, one can either remove the spatial dependency, or alternatively modify the statistical methods to take spatial autocorrelation into account (Legendre 1993), or acknowledge that in ecological variables spatial autocorrelation is the "fact of life" (Fortin & Dale 2005) and include it by incorporating spatial variables (a polynomial trend surface as a function of geographic coordinates of observations) to account for broad-scale spatial trend (Legendre 1993) and a spatial autoregressive term to model fine-scale spatial autocorrelation (Lichstein *et al.* 2002).

Spatial autocorrelation can affect the spread of exotic plant species across the landscape. For example, spatially autocorrelated populations of an exotic plant species in a landscape might have a higher probability of spreading more quickly, spatially and temporally, than spatially isolated ones. In addition, spatial autocorrelation in abiotic variables such as elevation or soil characteristics may further increase the rate of spread of exotic plant species (Bergelson *et al.* 1993). Spatial autocorrelation among vegetation communities can also influence the processes of immigration and local extinction of exotic species among metapopulations including their establishment and persistence. Therefore, understanding how spatial autocorrelation affect native-exotic plant species richness relationship is vital and can help in predicting currently invaded habitats and habitats susceptible to future invasions. It may also aid restoration efforts in already invaded habitats by suggesting sites for creating dispersal barriers among spatially autocorrelated locales.

Several experimental, observational, and theoretical studies have shown positive or negative relationships between native and exotic plant species richness at different spatial scales (Stohlgren *et al.* 1999, 2003, 2006b, Tilman 1999, Shea & Chesson 2002, Keeley *et al.* 2003,). Many mechanisms behind these relationships have been suggested (see reviews by Stohlgren 2002, and Fridley *et al.* 2007). However, how spatial autocorrelation affects these relationships has rarely been discussed. For example, recent reviews (e.g., Richardson & Pysek, 2006, Fridley *et al.* 2007, Melbourne *et al.* 2007) on species invasions did not include any discussion on the role of spatial autocorrelation in the invasion process. I used a variation partitioning approach to partialling the total variation in exotic plant species richness into: (i) nonspatial environmental variation (or variation explained by native plant species richness alone); (ii) spatially structured environmental variation; (iii) pure spatial (i.e., spatial dependence and fine-scale spatial autocorrelation) variation unrelated to environmental variables; and (iv) unexplained variation (Borcard *et al.* 1992, Legendre & Legendre 1998).

I tested the null hypothesis of no effect of spatial autocorrelation on native-exotic plant species richness relationships. My specific objectives were to:

(i) Quantify the spatial autocorrelation in native and exotic plant species richness, and its effect on the native-exotic plant species richness relationships;

(ii) Partition the variation in exotic plant species richness into the variation explained by native plant species richness, spatial structure (i.e., spatial dependence and fine-scale spatial autocorrelation) and spatially structured environmental processes; and

(iii) Compare two different methods, trend surface analysis and principal coordinates of neighbor matrices (PCNM), of incorporating space in ecological models.

3.2 Study area

The data were collected from the central portion of Rocky Mountain National Park, Colorado, USA, which is located between 40^0 10' - 40^0 34' N latitude and 105^0 30' - 105^0 55' W longitude and covers approximately 107, 500 ha. The park has a rugged terrain where elevation varies from 2,300 m to over 4,300 m above mean sea level and is a part of the Front Range of the southern Rocky Mountains in Colorado (Fig. 3.1). The mean annual precipitation is 36 cm, and the average annual temperatures varies from –1.5 ^{0}C to 14.0 ^{0}C. Species distribution in the park is influenced by temperature and precipitation gradients, which vary with elevation and topographic position (Peet 1981, 1988, Allen *et al.* 1991).

Several vegetation communities in the area include many native and exotic plant species and vary from prairie to tundra. Dominant vegetation types and their native plant species include: prairie vegetation dominated by short grasses (*Bouteloua gracilis* Vasey in Rothr., *Buchloe dactyloides* Engelm.) and sage brush (*Artemisia tridentate* Nutt.); ponderosa pine (*Pinus ponderosa* Douglas ex. C. Lawson; 2320-3170 m); douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; 2370-3213 m); lodgepole pine (*Pinus contorta* Doug. ex. Loud; 2380-3480 m); aspen (*Populus tremuloides* Mich.; 2350-3500 m); limber pine (*Pinus flexilis* James; 2620-3560 m); and spruce (*Picea Engelmannnii* Perry ex. Engel.; 2530-3710 m) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.; 2530-3710 m; Peet 1988). Most of these vegetation communities are invaded by many exotic plant species such as Cheatgrass (*Bromus tectorum* L.), Canada thistle (*Cirsium arvense* (L.) Scop.), Dalmation toadflax (*Linaria genistifolia* (L.) Miller ssp. *dalmatica* (L.) Maire & Petitm.), Kentucky bluegrass (*Poa pratensis* L.), and Russian thistle (*Salsola australis* R. Br.).

3.3 Methods

3.3.1 Data collection

I used native and exotic plant species richness data collected from one hundred and eighty 20 X 50 m (0.1-ha) modified-Whittaker, multi-scale plots with the long axis parallel to the environmental gradient (Fig. 3.1; Stohlgren *et al.* 1998) between 1995 and 1999. Within each plot there were 10 0.5 X 2 m (1-m^2) nested subplots that were systematically spaced along the inside border, two 2 X 5 m (10-m^2) subplots in alternate corners, and a 5 X 20 m (100-m^2) subplot in the center of the plot (Fig. 3.1). Remotely sensed color aerial photographs (1:15840 scale) were used to locate sample points in different vegetation types using stratified random sampling. Each site was sampled as close to peak biomass as possible. Plant species that could not be identified in the field were collected and identified in the herbarium at Colorado State University (Department of Biology, Fort Collins, Colorado). Less than five percent of the specimens encountered could not be identified to species due to phenological stage or missing flower parts. In these cases, plants were identified to genus and treated as individual species. Local and regional floras were used to classify native and exotic plant species. I used a global positioning system (GPS; Trimble Navigation Limited) to record plot locations. The coordinates were taken using the universal transverse mercator (UTM) system (Zone 13 N), which provides x, y coordinates in meters from a regional reference point.

3.3.2 Generation of spatial variables

Several methods have been suggested to incorporate 'space' as an explicit explanatory variable in ecological studies such as trend surface analysis, principal coordinates of neighbor matrices (PCNM), spatial generalized least-squared or spatial autoregressive models (Legendre & Legendre 1998; Borcard & Legendre 2002; Lichstein *et al.* 2002; Borcard *et al.* 2004). In this study, I used and compared two different methods- trend surface analysis approach and PCNM approach to modeling spatial dependence. In addition, conditional autoregressive regression (CAR) models were used to model fine-scale spatial autocorrelation (Cressie 1993, Lichstein et al. 2002).

3.3.2.1 Trend surface analysis approach

The trend surface analysis approach (Borcard *et al.* 1992, Legendre 1993) is one of the most widely used methods in ecological studies in which polynomials of x and y coordinates are used as predictor variables. Using this approach, the spatial component is modeled as a third-order polynomial of geographic coordinates of the sampling locations in the form

$$z = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \qquad (1)$$

where z is the response variable, and x and y represent latitude and longitude (UTM coordinates), respectively, of the sampling locations. The first-order terms in the equation (1) capture linear trend while quadratic and cubic terms model non-linear trend of the spatial pattern in the study area. Prior to regressing exotic plant species richness ($\log_{10}$ transformed) on all third-degree polynomial terms, x and y coordinates were standardized to mean zero and unit variance. Insignificant terms ($P > 0.05$) were removed using stepwise forward regression.

3.3.2.2 Principal coordinates of neighbor matrices (PCNM) approach

The principal coordinates of neighbor matrices (PCNM) approach to including space in ecological models is a fairly new approach introduced by Borcard & Legendre (2002) and Borcard *et al.* (2004). This method generates a suite of spatial variables (called PCNMs) based on geographic coordinates of sampling locations that can be used as predictor variables in multiple regression or canonical analysis. The main advantages of this approach over trend surface are: (i) the PCNMs are orthogonal and uncorrelated, and (ii) spatial dependence can be detected over a wide range of spatial scales (Borcard & Legendre 2002; Borcard *et al.* 2004). I used the *SpaceMaker2* (Borcard & Legendre

2002) program to calculate PCNM spatial variables by computing principal coordinates of a truncated matrix of Euclidean distance among sampling locations (for details see Borcard & Legendre 2002, and Borcard *et al.* 2004; and Gonzalez-Megias *et al.* 2005, and Crist *et al.* 2006 for recent ecological applications). Based on the maximum distance among sampling locations (Borcard & Legendre 2002, and Borcard *et al.* 2004) the PCNMs were generated using 600, 700 and 800 m truncation distances. The most parsimonious models were obtained by selecting significant ($P < 0.05$) PCNM variables from eigenvectors corresponding to the positive eigenvalues in each case using forward stepwise regression. The set of PCNMs that produced the best model (with lowest Akaike's Information Criterion adjusted for small sample size (AIC_c); Burnham & Anderson 2002) and explained the highest amount of total variation in the response variable was used for further analyses. Prior to developing PCNM-based regression models, the linear spatial trend from the response variable was removed by fitting a submodel by conducting a regression with x and y coordinates of the sampling locations.

3.3.3 Statistical analyses

All statistical analyses were conducted with S-PLUS (MathSoft Inc. Seattle, Washington, USA) with an alpha = 0.05 significance level. The stepwise forward selection method was used to eliminate insignificant predictors from the models ($P > 0.05$). Variables were transformed where it was appropriate to improve normality. For example, exotic plant species richness was $\log_{10}$ transformed. Since I was interested in only looking at how spatial autocorrelation affect the native-exotic plant species richness relationships, I did not consider any other environmental variable in my exotic plant species richness models except native species richness. In addition, spatial variables generated by trend surface or PCNM approach were used to represent spatial structure. An example where a suite of environmental variables were considered in native and exotic plant species richness models can be found in Chapter 1. Three types of ordinary least square (OLS) regression models were developed:

(i) OLS_N – this model contained only native plant species richness as a predictor of exotic plant species richness;

(ii) OLS_S – this model included only spatial variables (trend surface variables or PCNMs); and

(iii) OLS_{N+S} – this model included both native plant species richness and spatial variables as predictors of exotic plant species richness.

Since trend surface variables and PCNMs account only for broad-scale spatial dependence (or 'trend'), spatially explicit models of exotic plant species richness were also developed using conditional autoregressive regressions (CAR; Cressie 1993, Lichstein *et al.* 2002, Bahn *et al.* 2006) using the S+ SpatialStats module (Kaluzny *et al.* 1998). CAR models capture the fine-scale spatial autocorrelation in the data and include information on the residuals of neighboring locations and are solved iteratively (Bahn *et al.* 2006). Neighborhood size for the CAR models was determined by visually examining the variograms from the OLS_S and OLS_{N+S} model residuals (Cressie 1993); it was 300 m for trend surface based CAR models and 600 m for PCNM approach based CAR models. The spatial weight matrix was calculated by defining the neighbor weights as $w_{ij} = 1/\text{distance}_{ij}$. The following two types of CAR models were developed:

(i) $CAR_{S+\rho}$ – this model included spatial autoregressive parameter (ρ) and spatial variables (trend surface or PCNMs);

(ii) $CAR_{N+S+\rho}$ – this model included native plant species richness, ρ and spatial variables.

The percent of variation explained (R^2) by each model was calculated using Nagelkerke's (1991) formula that uses log-likelihood of the model of interest and the log-likelihood of the null model with only an intercept. Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham & Anderson 2002) was used to select the best model from a set of candidate models developed using PCNM variables generated at different truncation distances by the *SpaceMaker2* program. Spatial autocorrelation in native and exotic plant species richness raw data and the residuals from spatial and non-spatial models of exotic plant species richness was measured by calculating Moran's *I* (Moran 1948) coefficient of spatial autocorrelation.

I used a slightly modified version of the variation partitioning approach (Bahn *et al.* 2006) than the original approach of Borcard *et al.* (1992). In the modified approach, the spatial component (or 'space') included both spatial dependence (broad-scale spatial autocorrelation or 'trend') and fine-scale spatial autocorrelation (autocorr; Bahn *et al.* 2006). The total variation explained in exotic plant species richness (R^2) was partialled out into (a) nonspatial environmental variation (or variation explained by native plant species richness alone); (b) spatially structured environmental variation; (c) pure spatial (i.e. spatial dependence and fine-scale spatial autocorrelation) variation unrelated to environmental variable; and (d) unexplained variation (Borcard *et al.* 1992, Legendre & Legendre 1998; Bahn *et al.* 2006), as follows:

(a) = R^2 ($CAR_{N+S+\rho}$) – R^2 ($CAR_{S+\rho}$);

(c) = R^2 ($CAR_{N+S+\rho}$) – R^2 (OLS_N);

(b) = R^2 ($CAR_{N+S+\rho}$) – (a + c); and

(d) = 1 – R^2 ($CAR_{N+S+\rho}$).

3.4 Results

The PCNM approach to incorporating spatial dependence performed better (R^2 = 0.61; log-likelihood = -151.7) than trend surface approach (R^2 = 0.54; log-likelihood = -181.3; Table 3.1), which may be because it accounts for spatial structure over a wider range of spatial scales than trend surface (Borcard & Legendre 2002; Borcard *et al.* 2004). Therefore, hereafter I discuss the results from the exotic plant species richness models that included spatial variables generated using the PCNM approach.

A significant amount of linear trend was detected in exotic plant species richness ($R^2 = 0.15$, $P < 0.0001$). Therefore, I used detrended exotic plant species richness (log transformed) as the response variable in all PCNM based models (Borcard & Legendre 2002). Principal coordinate decomposition of the truncated distance matrices produced 150, 145, and 141 PCNM variables with positive eigenvalues at truncation distances of 600, 700, and 800 m, respectively. Forward stepwise selection retained 15 PCNM variables in each case. The best model, with the lowest AIC_c, and with the highest amount of variation explained in exotic plant species richness, was obtained by the set of PCNMs generated by the 700 m truncation distance ($R^2 = 0.471$; $P < 0.0001$; $AIC_c = -219.48$; Table 3.1) whereas the other two truncation distances, 600 m and 800 m, produced poorer models and explained relatively less variation in exotic plant species richness ($R^2 = 0.461$; $AIC_c = -218.26$, and $R^2 = 0.427$; $AIC_c = -209.68$; respectively). Therefore, PCNM variables based on the 700 m truncation threshold were used in developing spatially explicit models and in variation partitioning. The predictor variables were checked for multicollinearity by examining cross-correlations among them. No significant correlations were found among PCNM variables and the highest significant correlation was found between native and PCNM27 (correlation coefficient, r = - 0.21, P = 0.006).

3.4.1 Ordinary least square (OLS) models

The OLS native model (OLS_N) explained 26% of the variation in exotic plant species richness (log transformed, detrended; Table 3.1). The OLS model that included only PCNM spatial variables (OLS_S) explained 47% of the variation in exotic plant species richness (Table 3.1). However, a model with a combination of both native and PCNM spatial variables as predictors (OLS_{N+S}) accounted for 55% of the variation in exotic plant species richness (Table 3.1). There was a significant change in parameter values for native species richness after including spatial variables in the OLS model (0.0116 in non-spatial, and 0.0071 in spatial model; Table 3.2). Initially, there was a significant positive spatial autocorrelation in exotic plant species richness (log transformed, detrended; Moran's I = 0.134, $P < 0.0001$; Table 3.3), a part of which was explained by broad-scale spatial dependence (trend) that can be seen in a decrease in Moran's I for the OLS_S model residuals (Moran's I = 0.094; $P < 0.0001$; Table 3.3). However, including native plant species with spatial variables in the model (OLS_{N+S}) did not help in accounting for the remaining spatial autocorrelation in model residuals; in contrast, it increased the spatial autocorrelation (Moran's I = 0.137; $P < 0.0001$; Table 3.3). This could be because native plant species richness itself exhibited significant positive spatial autocorrelation (Moran's I = 0.076; $P < 0.0001$; Table 3.3). These results showed that OLS models were not able to account for all the spatial autocorrelation observed in the response variable which may be because PCNM (or trend surface) spatial variables accounted for only broad-scale spatial dependence and missed the fine-scale spatial autocorrelation. Therefore, CAR models were used to quantify fine-scale spatial autocorrelation.

3.4.2 Conditional autoregressive (CAR) models

CAR models showed considerable improvement over the OLS models (Tables 3.1 & 3). The total amount of variation explained in exotic plant species richness by the spatially explicit CAR model that included native plant species richness, spatial variables and a spatial autoregressive term ($\text{CAR}_{\text{N+S+}\rho}$; $R^2 = 0.61$) was higher than the total variation explained by the OLS model ($\text{OLS}_{\text{N+S}}$; $R^2 = 0.55$; Table 3.1). The CAR model based on spatial variables and a spatial autoregressive term ($\text{CAR}_{\text{S+}\rho}$) explained more variation in exotic plant species richness ($R^2 = 0.51$) than the OLS model with only spatial variables (OLS_{S}; $R^2 = 0.47$; Table 3.1). The spatial autoregressive term (ρ) which accounted for fine-scale spatial autocorrelation explained 9% of the total variation in exotic plant species richness (Table 3.1). In most cases, parameter estimates decreased in magnitude in $\text{OLS}_{\text{N+S}}$ and $\text{CAR}_{\text{N+S+}\rho}$ models than in OLS_{N} and OLS_{S} models (Table 3.2). For example, parameter estimate for native species richness decreased to 0.0071 in the $\text{OLS}_{\text{N+S}}$ model from 0.0116 in the OLS_{N} model; however, it increased slightly more (0.0078) in the $\text{CAR}_{\text{N+S+}\rho}$ model than in the $\text{OLS}_{\text{N+S}}$ model (Table 3.2). The CAR models were successful in removing all the spatial autocorrelation observed in the response variable (Table 3.3). There was no significant spatial autocorrelation left in the $\text{CAR}_{\text{N+S+}\rho}$ model residuals (Moran's $I = 0.019$; $P = 0.24$) whereas the $\text{OLS}_{\text{N+S}}$ model residuals had shown significant positive autocorrelation ($I = 0.137$; $P < 0.0001$).

3.4.3 Variation partitioning

Native plant species richness explained 26% of the variation in exotic plant species richness (Table 3.1). However, all of this explained variation should not be attributed to native plant species richness alone, because some of it could be due to shared common spatial structure by native and exotic species. To find out how spatial structure influenced native-exotic plant species richness relationship, I used modified version of variation partitioning method (Borcard *et al.* 1992, Bahn *et al.* 2006). After controlling for the effects of spatial structure, native plant species richness explained only 9.2 % of the variation in exotic plant species richness (Fig. 3.2; Table 3.4), whereas the pure spatial component which included both broad-scale spatial dependence and fine-scale spatial autocorrelation explained 34.2% of the variation in exotic plant species richness (Fig. 3.2; Table 3.4). Spatially structured environmental processes explained 17.2% of the total variation in exotic plant species richness (Fig. 3.2; Table 3.4), which showed that native and exotic plant species shared a common spatial structure or spatial gradient (Borcard *et al.* 1992) such as elevation or precipitation. About 39.4% of the variation in exotic plant species richness could not be explained which may be due to "unknown factors and stochastic variations" (Borcard *et al.* 1992).

3.4.4 Trend surface versus PCNM approach

In most of the cases, PCNM approach seemed to perform better than trend surface approach (Tables 3.1 – 3.4). For example, the full model from the PCNM approach explained more variation ($R^2 = 0.61$) in exotic plant species richness than the full model from the trend surface approach ($R^2 = 0.54$; Table 3.1). Variation partitioning results showed that the trend surface approach over emphasized the role of native plant species richness in the native-exotic plant species richness relationship and was not able to separate out the spatially structured environmental variation (Table 3.4). However, the trend surface approach was equally good in modeling broad-scale spatial dependence in exotic plant species richness data. This was apparent from the pure spatial variation explained by the trend surface approach (0.331; Table 3.4) and the PCNM approach (0.342; Table 3.4) and the measures of spatial autocorrelation from the OLS_S model residuals (Moran's $I = 0.093$; $P < 0.0001$ for trend surface, and $I = 0.094$; $P < 0.0001$ for PCNM based model; Table 3.3).

3.5 Discussion

In this study, I showed that spatial autocorrelation significantly affects the native-exotic plant species richness relationship, and that space and spatially structured environmental processes are relatively more important in shaping this relationship than native plant species richness alone. My results also suggested that spatial models of exotic species richness were an improvement over non-spatial models, and that both broad-scale and fine-scale spatial autocorrelation influenced the native-exotic plant species richness relationship. With this evidence, I suggest that proper attention should be paid to considering spatial autocorrelation when investigating the native-exotic plant species richness relationships and predicting plant species invasions; wherever possible spatially explicit models should be developed. Furthermore, the presence of spatial autocorrelation in the OLS model residuals might result in a change in parameter estimates, associated standard errors and the explained variation and model selection (e.g., Lichstein *et al.* 2002).

3.5.1 OLS versus CAR models

In my study, spatially explicit CAR models explained more variation in exotic plant species richness than the OLS or non-spatial models (Table 3.1). This may be due to the additional variation explained by spatial variables and the spatial autoregressive term. The magnitude of the parameter estimates also varied in two types of models (Table 3.2). For example, parameter estimates for native plant species richness significantly decreased in spatially explicit models (Table 3.2). This was expected because the statistical models and tests that do not account for spatial variation may overestimate the effects of environmental variables (Legendre & Legendre 1998, Fortin & Dale 2002). This is also consistent with previous studies that explicitly included spatial variables in ecological models (e.g., Lichstein *et al.* 2002). The CAR models were also very effective in removing all of the spatial autocorrelation from the model residuals (Table 3.3), because the OLS spatial models accounted only for broad-scale spatial dependence and did not model fine-scale spatial autocorrelation.

3.5.2 Spatial autocorrelation and native-exotic plant species richness relationships

The observed positive relationship between native and exotic species richness does not mean that native species are driving the spread of exotic species (Stohlgren *et al.* 1999); however, the relationship may be because both native and exotic species are responding to similar resources or level of heterogeneity (Stohlgren *et al.* 1999). For example, native and exotic plant species richness may be spatially autocorrelated with soil characteristics such as clay and nitrogen (Stohlgren *et al.* 1999). The presence of higher spatial autocorrelation in exotic plant species richness than native plant species richness (Table 3.3) suggests that spatial structure has greater influence on exotic plant species distribution than native plant species. It may be due to the higher propagule pressure in the close proximity of the invaded areas (or source populations) than in isolated habitats. Among spatial variables broad-scale spatial dependence accounted for higher variation in exotic plant species richness than fine-scale spatial autocorrelation (Table 3.1). This suggests that broad-scale ecological processes play a vital role in the spread of exotic species.

3.5.3 Methods of incorporating space in ecological models- trend surface versus PCNM approach

Considering the two methods of incorporating space as an explicit explanatory variable in exotic species richness models, the PCNM approach performed better than the trend surface analysis approach. This could be because the PCNM approach can detect spatial structure over a wider range of spatial scales than the trend surface analysis approach (Borcard & Legendre 2002). Trend surface analysis mainly captures broad-scale spatial structure with relatively simpler shapes such as planes, saddles, or parabolas representing bumps and troughs and misses the finer-level spatial structures (Borcard & Legendre 2002). Moreover, the individual polynomial terms in trend surface analysis are highly correlated, which prevent the modeling of independent structures at different spatial scales (Borcard & Legendre 2002), whereas the PCNM spatial variables generated by the PCNM approach are orthogonal and uncorrelated. Therefore, I suggest using the PCNM approach over trend surface for incorporating spatial variation in ecological studies in heterogeneous areas; trend surface analysis might be adequate for fairly homogeneous areas (Dray *et al.* 2006).

Regarding the effects of spatial structure on the positive relationship between native-exotic plant species richness, however, it would be interesting to see how these effects vary in the case of a negative relationship between native-exotic plant species richness (Stohlgren *et al.* 2006b). The results obtained in this study are sensitive to sample plot area (0.1 ha), the extent of the study area, and the level of heterogeneity. Therefore, more research is needed on how these results would change with varying plot area, extent of the study area and homogeneous versus heterogeneous landscapes. Finally, I draw attention to the need of incorporating both broad-scale and fine-scale spatial autocorrelation in the studies on biological invasions.

3.6 Acknowledgements

I am grateful to several field technicians who collected data and many excellent taxonomists from the Natural Resource Ecology Laboratory at Colorado State University, and the U. S. Geological Survey Fort Collins Science Center, Fort Collins. I thank Catherine Jarnevich for providing helpful comments on a draft of this Chapter and the staff at Rocky Mountain National Park for providing housing and logistical support. I also acknowledge the support of the Ford Foundation International Fellowships Program for Ph.D. studies at Colorado State University (Aug. 2002 – Aug. 2005).

3.7 Literature cited

Allen, R.B., Peet, R.K. & Baker, W.L. (1991). Gradient analysis of latitudinal variation in southern Rocky Mountain forests. *J. Biogeo.* 18:123-139.

Bahn, V., O'Connor, R. J. & Krohn,W. B. (2006). Importance of spatial autocorrelation in modeling bird distributions at a continental scale. *Ecography*, 29, 835-844.

Bergelson, J., Newman, J.A. & Floresroux, E.M. (1993). Rate of Weed Spread in Spatially Heterogeneous Environments. *Ecology*, 74, 999-1011.

Burnham, K.P. & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach.* Second edition edn. Springer, New York, New York, USA.

Borcard, D., Legendre, P. & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73, 1045-1055.

Borcard, D. & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.*, 153, 51-68.

Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, 85, 1826-1832.

Cressie, N.A.C. (1993). *Statistics for spatial data. Revised edition.* John Wiley and Sons, New York, New York, USA.

Crist, T.O., Pradhan-Devare, S.V. & Summerville, K.S. (2006). Spatial variation in insect community and species responses to habitat loss and plant community composition. *Oecologia*, 147, 510-521.

Dray, S., Legendre, P. & Peres-Neto, P.R. (2006). Spatial modeling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). *Ecol. Model.*, 196, 483-493.

Fortin M.-J., and M. R. T. Dale (2005) *Spatial analysis: a guide for ecologists.* Cambridge University Press, Cambridge, UK.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. (In Press). The invasion paradox: reconciling pattern and process in species invasion. *Ecology*.

Gonzalez-Megias, A., Gomez, J.M. & Sanchez-Pinero, F. (2005). Consequences of spatial autocorrelation for the analysis of metapopulation dynamics. *Ecology*, 86, 3264-3271.

Kaluzny, S.P., Vega, S.C., Cardoso, T. P. & Shelly, A.A. (1998). S+ SpatialStats: user's manual for Windows and UNIX. Insightful Corporation, Seattle. p. 344.

Keeley, J.E., Lubin, D. & Fotheringham, C.J. (2003). Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol. Appl.*, 13, 1355-1374.

Legendre, P. (1993). Spatial autocorrelation - trouble or new paradigm. *Ecology*, 74, 1659-1673.

Legendre, P. & Legendre, L. (1998). *Numerical ecology.* Second English edn. Elsevier Science, Amsterdam, The Netherlands.

Lichstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002). Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.*, 72, 445-463.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans H., Clout, M. & Bazzaz, F.A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.*, 10, 689-710.

Melbourne, B.A., Cornell, H.V., Davies, K. F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K. & Yokomizo, H. (2007). Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol. Lett.*, 10, 77-94.

Moran, P.A.P. (1948). The interpretation of statistical maps. *J. Royal Stat Soc.* Series B, 10, 243-251.

Nagelkerke, N.J.D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78, 691-692.

Peet, R.K. (1981). Forest vegetation of the Colorado Front Range. *Vegetatio* 45: 3-75.

Peet, R.K. (1988). Forests of the Rocky Mountains. In: *North American terrestrial vegetation.*(eds. Barbour MG. & W.D. Billings.), Cambridge University Press, New York, USA, pp.
64-101.

Pimentel, D., Zuniga, R. & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econo.*, 52, 273-288.

Richardson, D.M. & Pysek, P. (2006). Plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog. Physic. Geog.*, 30, 409-431.

Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170-176.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999). Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.*, 69, 25-46.

Stohlgren, T.J., Bull, K.A. & Otsuki, Y. (1998). Comparison of rangeland vegetation sampling techniques in the central grasslands. *J. Range Manage.*, 51, 164-172.

Stohlgren, T.J. (2002). Beyond theories of plant invasions: lessons from natural landscapes. *Comments Theo. Biology*, 7, 355-379.

Stohlgren, T.J., Barnett, D.T. & Kartesz, J. (2003). The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Env.*, 1, 11-14.

Stohlgren, T.J. & Schnase J. (2006a). Biological Hazards: What we need to know about invasive species. *Risk Assess. Journal*, 26, 163-173.

Stohlgren, T.J., Jarnevich C.S., Chong, G. & Evangelista, P. (2006b). Scale and plant invasions: A theory of biotic acceptance. *Preslia,* 78, 405-426.

Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*, 80, 1455-1474.

Wagner, H.H. & Fortin, M.J. (2005). Spatial analysis of landscapes: Concepts and statistics. *Ecology*, 86, 1975-1987.

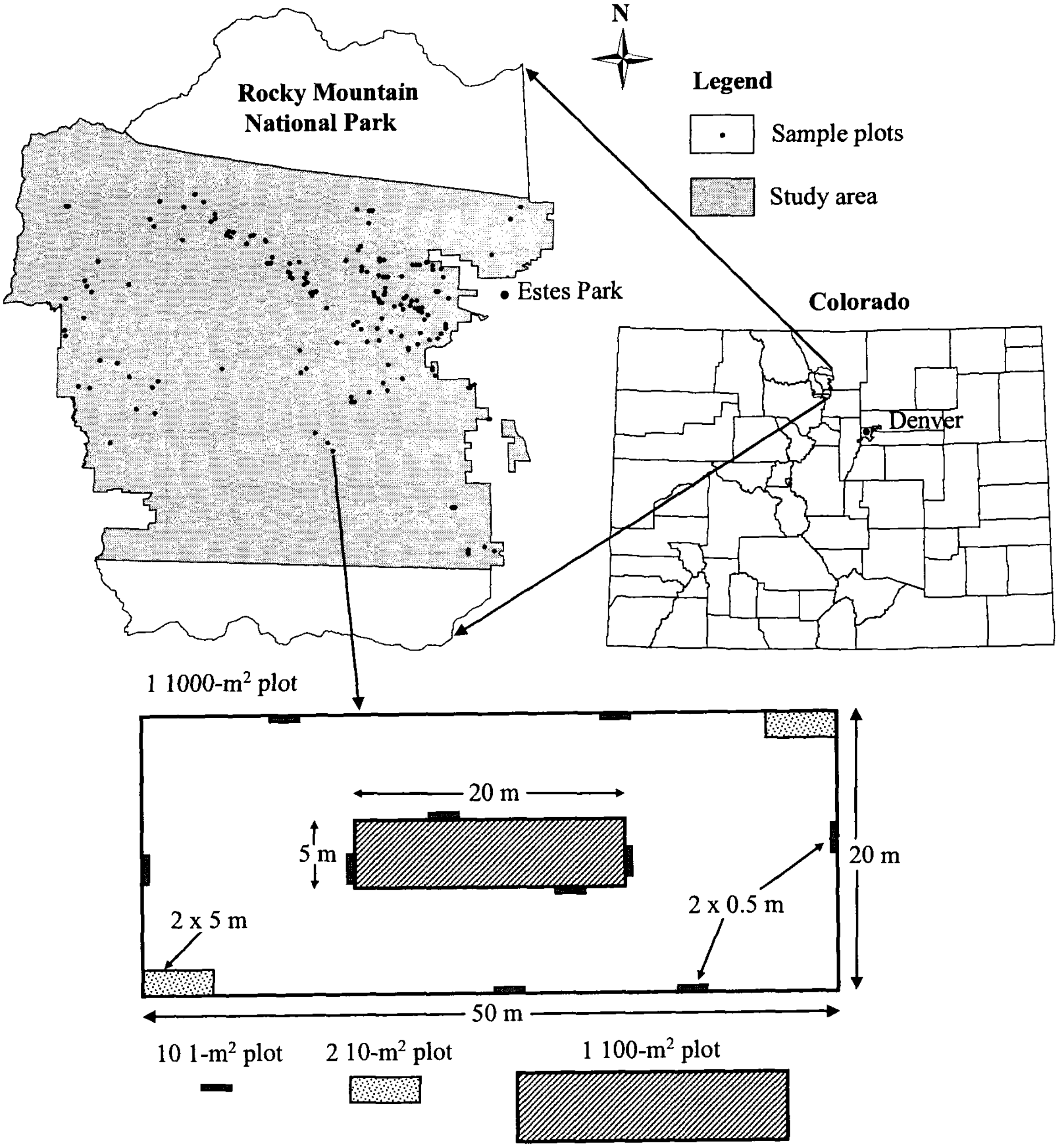

Figure 3.1: Study area map with modified-Whittaker (Stohlgren et al. 1998) plot design.

Total variation explained in exotic plant species richness = 60.6%

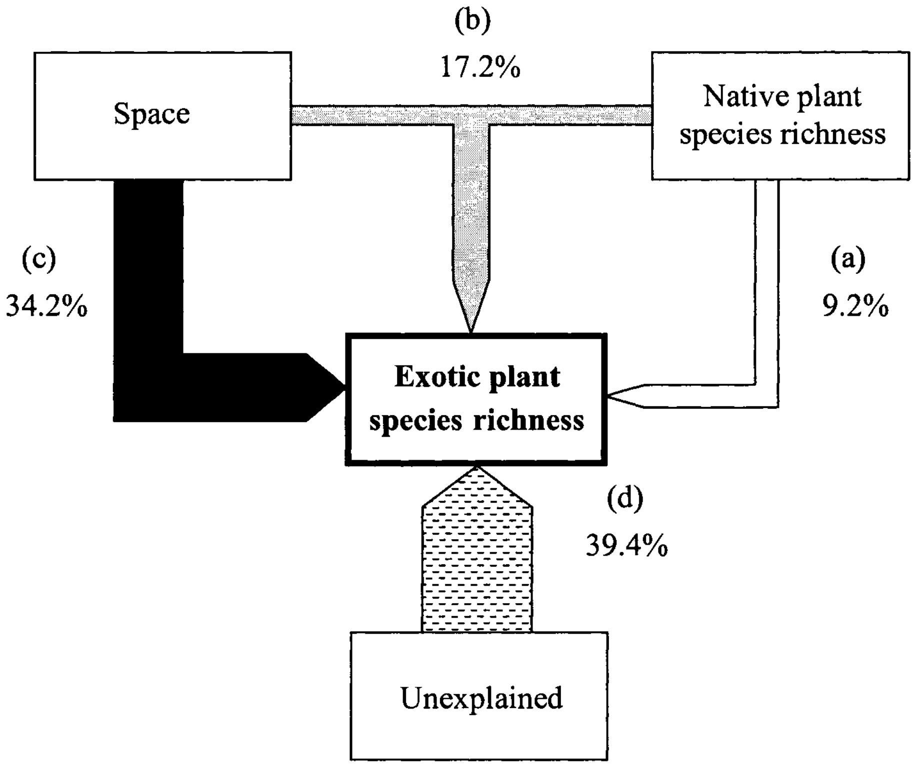

Fig. 3.2: Model representation of the effects of spatial autocorrelation on native-exotic plant species richness relationship in Rocky Mountain National Park, Colorado, USA. Space included both broad-scale spatial autocorrelation (modeled by ordinary least square (OLS) regression) and fine-scale spatial autocorrelation (modeled by conditional autoregressive (CAR) regression) (n = 180, 0.1 ha plots). a = nonspatial environmental variation; b = spatially structured environmental variation; c = pure spatial dependence that is not shared by environmental variables; and d = unexplained variation or the fraction of the species variation explained by neither spatial coordinates nor by environmental data (Borcard et al. 1992).

Table 3.1: Ordinary least squares (OLS) and conditional autoregressive (CAR) regression models of exotic plant species richness (n = 180, 0.1 ha plots).

	R^2					
Response variable	OLS native	OLS trend	OLS trend/ native	autocorr	CAR trend	CAR trend/ native
Trend surface approach						
Log_{10} (exotic)	0.21	0.28	0.50	0.05	0.34	0.54
PCNM approach						
Log_{10} $(\text{exotic})_{\text{detrended}}$	0.26	0.47	0.55	0.09	0.51	0.61

Note: PCNM is principal coordinates of neighbor matrices. Exotic plant species ($\log_{10}$ transformed) was detrended for PCNM approach. Environment was represented by native plant species richness alone. "autocorr" is the fine-scale spatial autocorrelation represented by the CAR model with only intercept and rho (ρ).

Table 3.2: Parameter estimates for predictors in exotic plant species richness non-spatial and spatial regression models.

Predictor variable	OLS native model	OLS trend model	OLS trend/native model	CAR trend model	CAR trend/native model
Trend surface analysis approach (response = $\log_{10}$(exotic))					
Native	0.0112	-	0.0116	-	0.0113
X		0.296	0.305	0.332	0.321
XY		0.034	0.022 ^{NS}	0.017 ^{NS}	0.013 ^{NS}
X3		- 0.064	- 0.065	- 0.073	- 0.067
ρ		-	-	27.73	27.33
PCNM approach (response = $\log_{10}(\text{exotic})_{\text{detrended}}$)					
Native	0.0116	-	0.0071	-	0.0078
PCNM12		0.541	0.496	0.455	0.396
PCNM15		0.489	0.425	0.288	0.181 ^{NS}
PCNM17		0.551	0.454	0.607	0.535
PCNM27		- 0.748	- 0.525	- 0.671	- 0.449
PCNM30		- 0.526	- 0.472	- 0.516	- 0.463
PCNM41		0.765	0.561	0.766	0.545
PCNM42		- 0.810	- 0.587	- 0.830	- 0.590
PCNM51		1.052	0.940	1.051	0.929
PCNM54		- 1.174	- 1.035	- 1.175	- 1.022
PCNM58		1.065	0.941	1.065	0.929
PCNM67		0.909	0.842	0.912	0.837
PCNM77		0.829	0.605	0.828	0.584
PCNM87		- 0.792	- 0.536 ^{NS}	- 0.794	- 0.513 ^{NS}
PCNM100		- 3.757	- 2.648	- 3.762	- 2.551
PCNM121		7.438	8.042	7.599	8.210
ρ		-	-	26.13	27.53

Note: PCNM is principal coordinates of neighbor metrics. All predictors were significant at alpha = 0.05, unless otherwise mentioned. NS = not significant (alpha = 0.05). OLS is ordinary least square, and CAR is conditional autoregressive, and ρ is spatial autoregressive term.

Table 3.3: Spatial autocorrelation (Moran's *I*) observed in raw data (native and exotic plant species richness) and residuals from spatial and non-spatial models' of exotic plant species richness.

Raw data	Moran's *I* (*P*-value)
Native	0.076 (< 0.0001)
Log_{10} (exotic)	0.193 (< 0.0001)
Log_{10} (exotic) $_{\mathrm{detr}}$	0.134 (< 0.0001)
Model residuals	
Trend surface analysis approach	
Model	Moran's *I* (*P*-value)
Log_{10} (exotic) ~ Native	0.251 (< 0.0001)
Log_{10} (exotic) ~ X, XY, X3	0.093 (< 0.0001)
Log_{10} (exotic) ~ Native, X, XY, X3	0.104 (< 0.0001)
Log_{10} (exotic) ~ X, XY, X3, ρ	0.007 (0.571)
Log_{10} (exotic) ~ Native, X, XY, X3, ρ	0.013 (0.348)
PCNM approach	
Log_{10} (exotic)$_{\mathrm{detr}}$ ~ Native	0.171 (< 0.0001)
Log_{10} (exotic)$_{\mathrm{detr}}$ ~ PCNMs	0.094 (< 0.0001)
Log_{10} (exotic)$_{\mathrm{detr}}$ ~ Native, PCNMs	0.137 (< 0.0001)
Log_{10} (exotic)$_{\mathrm{detr}}$ ~ PCNMs, ρ	0.001 (0.723)
Log_{10} (exotic)$_{\mathrm{detr}}$ ~ Native, PCNMs, ρ	0.019 (0.236)

Note: PCNM is principal coordinates of neighbor metrics. CAR is conditional autoregressive. Log_{10} (exotic)$_{\mathrm{detr}}$ is log transformed and detrended exotic plant species richness, and ρ is spatial autoregressive term.

Table 3.4: Variation partitioning of exotic plant species richness data (log transformed for trend surface, and log transformed (detrended) for PCNM approach) using two different approaches to include space in ecological models: Trend surface and PCNM approaches (n = 180, 0.1-ha plots).

Approach (predictor variables)	a (Native)	b (Native + space)	c (space)	d (undetermined)
Trend Surface approach				
Native, X, XY, X^3, ρ	0.201	- 0.070	0.331	0.462
PCNM approach				
Native, PCNM12, PCNM15, PCNM17, PCNM27, PCNM30, PCNM41, PCNM42, PCNM51, PCNM54, PCNM58, PCNM67, PCNM77, PCNM87, PCNM100, PCNM121, ρ	0.092	0.172	0.342	0.394

Note: Where ρ is spatial autoregressive term. X and Y are the standardized UTM coordinates of sample locations. PCNM is principal coordinates of neighbor matrices, a = nonspatial environmental variation; b = spatially structured environmental variation; c = pure spatial dependence that is not shared by environmental variables; and d = unexplained variation or the fraction of the species variation explained by neither spatial coordinates nor by environmental data (Borcard et al. 1992). Environment was represented by native plant species richness alone.

CONCLUSION

Most of the studies on species diversity in the past included only plot-level information for understanding species distributions across the landscape and developed species diversity predictive models. However, recently with the advent of new techniques such as remote sensing and geographical information system (GIS), ecologists have started considering spatial heterogeneity around the sample plots. This research project offered an approach to quantify spatial heterogeneity around the sample plots and related it to native and nonnative plant and butterfly species richness to develop multi-level and multi-scale predictive.

Chapter 1 of this dissertation showed that spatial heterogeneity greatly influences native and nonnative plant species richness in Rocky Mountain National Park, Colorado, and that this effect is highly scale dependent. Native and nonnative plant species richness both strongly responded to spatial heterogeneity within 240-m radius (~ 18 ha) around the sample plots. Nonnative plant species were found to be more sensitive to spatial heterogeneity than native plant species. Including measures of landscape heterogeneity (i.e., landscape metrics) in addition to variables representing soil, and environmental/topographic heterogeneity significantly improved native and nonnative plant species richness models. This suggests that landscape composition and configuration also affect plant species richness, in addition to other environmental variables, and that the future studies on plant species diversity should consider landscape metrics as potential predictors of plant species diversity. The results demonstrate that land managers should explicitly consider spatial heterogeneity in managing native and nonnative plant species.

Chapter 2 provided an empirical evidence for the strong effects of spatial heterogeneity on butterfly community in Rocky Mountain National Park. Butterflies strongly responded to spatial heterogeneity within 2100-m radius (~ 1386 ha) around sample plots, and that different butterfly families had differential responses to spatial heterogeneity. The total butterfly species richness was strongly positively correlated with plant species richness, proportion of shrubland, mean patch size of shrubland, and negatively correlated with mean patch size (landscape level), average vegetation height, elevation, and range in normalized difference vegetation index (NDVI). Butterfly species richness models were also significantly improved by considering landscape metrics in addition to other environmental predictors. This study showed that butterflies are influenced by the composition and configuration of the landscape including other environmental variables.

Chapter 3 addressed the question of how spatial autocorrelation affect native-exotic plant species richness relationships. Geographical space was quantified by incorporating broad-scale spatial dependence and fine-scale spatial autocorrelation in the exotic species richness models. Two different approaches, trend surface analysis and principal coordinates of neighbor matrices (PCNM), of incorporating spatial dependence were used in addition to conditional autoregressive regressions (CAR) for modeling fine-scale spatial autocorrelation. Variation partitioning showed that the spatial autocorrelation and spatially structured environmental processes are relatively more important than native plant species richness alone in shaping the native-exotic plant species richness relationships. The results suggested that spatial autocorrelation should be explicitly considered in the studies on plant species invasions.

The models presented in Chapter 1 and 2 developed insights about the factors that influence native and nonnative plant and butterfly species richness in Rocky Mountain National Park, Colorado, USA. These models can be used to prepare predictive maps to inform land managers about the spatial distribution of native and nonnative plant and butterfly species in the area. The question remains: How applicable these models are to other areas? These models are only applicable to Rocky Mountain National Park because the predictor variables were dependent of the level of spatial heterogeneity present in the study area. Therefore, these models can not be directly applied or transferred to other areas. However, the approach presented here could be used for developing models for other areas. Insights gained about the effects of spatial autocorrelation on native-exotic plant species richness relationships in Chapter 3 could be generally applied to any studies on biological invasions because spatial autocorrelation in ecological variables is a general phenomenon.

The dominant scale of the response of native and nonnative plant and butterfly species to spatial heterogeneity identified in this study may not be the same for other areas and would vary with the species present in those areas and the level of heterogeneity. Therefore, multi-scale landscape analyses, as presented in this study, should be conducted to find out the dominant scale of response of the communities in other areas. Single scale studies may not capture the right scale at which species in the area might be responding to spatial heterogeneity. The spatial extent of the dominant scale may be larger in relatively homogeneous areas whereas smaller in more heterogeneous areas than what I found for plant and butterfly species for Rocky Mountain National Park.

The use of landscape metrics in species richness models provided an additional explanatory power. This could be because landscape metrics might integrate complex environmental conditions that influence an organism which may not by accounted by other environmental variables. However, care must be taken while choosing the landscape metrics because most of them are highly correlated and represent similar aspect of landscape configuration. Selection of landscape metrics for any study should be backed by the biological reasoning and not at random. One should also be aware of the uncertainties associated with the calculation of landscape metrics. For example, landscape metrics are sensitive to thematic resolution of the input land use land cover map and grain size of the map and extent of the study area. Therefore, future research might include addressing the questions of: (1) How these models change with a change in thematic resolution of the input map? (2) What are the effects of changing grain size of the spatial layers used? (3) What are the effects of using different size sample plots (e.g., 1-m^2, 10-m^2 or 100-m^2) for recording species richness?

How can the models presented here be improved? Adding information about vertical heterogeneity and multi-scale estimates of soil variables might improve native and nonnative plant species richness models. Butterfly models could be improved by considering information on habitat quality (e.g., number of host plants), and landscape level estimates of vegetation height. Including information on the dispersal abilities of different native and nonnative plant and butterfly species could further improve the models; however, it is very difficult to get information about the dispersal distances for so many species in the area. In any case, habitat heterogeneity must be explored, quantified, and understood.