DISSERTATION

SPATIAL STRUCTURE AND SCALING OF BEETLE, BIRD AND PLANT COMMUNITIES IN NORTH AMERICAN GRASSLANDS.

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JONATHAN BOSSENBROEK ENTITLED SPATIAL STRUCTURE AND SCALING OF BEETLE, BIRD AND PLANT COMMUNITIES IN NORTH AMERICAN GRASSLANDS BE ACCEPTED FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

SPATIAL STRUCTURE AND SCALING OF BEETLE, BIRD AND PLANT COMMUNITIES IN NORTH AMERICAN GRASSLANDS.

The spatial structure and scale of biotic communities are functions of the natural history of the organisms and the heterogeneity of the landscape in which these organisms exist. The relationships between these organisms, the environment and geographic space differ at different locations. The primary goal of this dissertation was to present new methods by which to understand these relationships. To examine these relationships, ground-dwelling beetles, breeding birds, and vascular plant communities were studied at four sites along the transition from short-grass steppe in Colorado to tallgrass prairie in Kansas. At these four sites, two 2-km transects were established along which taxonomic surveys were conducted and environmental data, including soil texture, shrub density and landsat imagery, were collected in the late spring of 2000 and 2001. Environmental data were collected at three scales: trap scale (1 m^2), local scale (75 – 300 m^2) and landscape scale (900 m^2). Using these geographically referenced environmental and community data, three questions were addressed: 1) How are different biotic communities structured with respect to their mobility and response to environmental heterogeneity? 2) What environmental and spatial factors explain the variance in this spatial structure? and 3) Are the patterns of species richness within these communities predictable based on area and heterogeneity. To answer these questions I employed three different methods. Multi-scale ordination with canonical correspondence analysis was used to determine the spatial structure of these communities. Using hierarchical variance partitioning, the variance in community structure was apportioned by scale to assess the ability of environmental variables measured at different scales to explain community structure. Species-area-habitat relationships were quantified using a scale-dependent measure of heterogeneity, which enabled the predictions of species accumulation curves across the study region. Based on these analyses, it was shown that there are systematic differences in community structure across a regional gradient, there are differences between taxonomic groups at specific sites and across the region that are not consistent and underscore the limitations of using "indicator" taxa to predict overall biodiversity, and the three methods used in this dissertation highlight current progress in understanding scale-dependent species-environment relationships.

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CHAPTER 1: INTRODUCTION

The spatial structure and scale of biotic communities are functions of the natural history of the organisms and the heterogeneity of the landscape in which these organisms exist. The objectives of this research were to determine the spatial structure of biotic communities and how these patterns of community composition change across a major environmental gradient. The primary questions addressed within this dissertation are: 1) How are different biotic communities structured with respect to their mobility and response to environmental heterogeneity? 2) What environmental and spatial factors explain the variance in this spatial structure? and 3) Are the patterns of species richness within these communities predictable based on area and heterogeneity. To examine these issues, ground-dwelling beetle, breeding bird, and vascular plant communities were studied across the North American Great Plains from central Colorado to Central Kansas, which spans the transition from short-grass steppe to tallgrass prairie.

The following chapters are the culmination of research conducted in part of a larger project funded by the U.S. Environmental Protection Agency (EPA) titled *Methodologies for Extrapolating from Local to Regional Ecosystem Scales: Scaling Functions and Thresholds in Animal Responses to Landscape Pattern and Land Use.* The objective of this EPA project was to "develop and test new concepts and methodologies for evaluating how changes in scale and scale-dependent thresholds in system processes are expressed in ecological landscapes." The three primary chapters within this dissertation are aimed at testing new methods, developed through this project, that enable an understanding of scale-dependent community-environment relationships.

Data collection for this project was conducted at five sites (from east to west): the Konza Prairie Long-Term Ecological Research site (LTER), Kansas; the Saline Experimental Range of Kansas State University; the Smoky Valley Ranch, Kansas and Fox Ranch, Colorado (Arikaree), both Nature Conservancy properties; and the Short-grass Steppe LTER located within the Pawnee National Grasslands, Colorado. Depending on the site, two to four 2km transects were established at each site and sampled every 50m during the late spring of 2000. In the year 2001, two "main" transects were selected from each site to resample (see Appendix I for descriptions of these transects). Two additional intensive transects were also established parallel to the "main" transects in 2001 that were 250m in length and sampled every 10m. Along each transect, surveys were conducted of ground-dwelling beetles, breeding birds and vascular plants (Species lists for these groups can be found in Appendices II-IV). Environmental data ranging from soil texture to shrub density to satellite imagery were also collected for these transects. The analyses within this dissertation are focused on the data from the "main" transects from both 2000 and 2001. Due to inclement weather, which negatively impacted beetle sampling and prevented a bird survey, and the lack of soil hardness data, the data from the Saline Experimental Range was not included in this dissertation.

The initial focus of the EPA project was to develop methods that elucidate the scale-dependent relationships of communities and the environment based on other existing data sets. The results presented in the forth coming chapters focus on testing these methods with the data collected at our study sites. The three methods used in this dissertation are: 1) multi-scale ordination using canonical correspondence analysis (MSO, Wagner 2003), 2) hierarchical canonical variance partitioning (Cushman and McGarigal 2002), and 3) predicting species richness based on area and scale-dependent heterogeneity quantified using spectral variance (Palmer 2000, Palmer et al. 2002).

The spatial structure of the ground-dwelling beetle, breeding bird, and vascular plant communities surveyed were analyzed using MSO in Chapter III. The spatial structure of a community can be produced by two forces, spatial dependence or spatial autocorrelation (Legendre 1993). Spatial dependence is the response of organisms to environmental variables that are spatially structured (Legendre 1993). Spatial autocorrelation is the result of interactions between organisms, through such behavior as competition or mutualism (Tilman and Kareiva 1997). The spatial structure of these communities will also depend on their mobility (Addicott et al. 1987, Wiens 1989) and the heterogeneity of the underlying environment upon which these organisms respond (Kotliar and Wiens 1990, Milne 1991). I predicted that there would be systematic difference in community structure between the taxonomic groups corresponding to their differing mobilities as well as systematic differences across the sites in response to changes in the environmental heterogeneity.

Hierarchical canonical variance partitioning was used in Chapter II to determine the scale-dependent relationships between the beetle, bird and plant communities and environmental variables measured at three different scales. Environmental data was measured at three scales along each of our transects; at the trap-scale ($1m^2$) data collecting included soil texture, soil hardness and vegetation height; at the local-scale ($75-500m^2$) shrub and cactus density was assessed; and at the landscape-scale ($>900m^2$)

satellite imagery and digital elevation models were acquired. The inertia or variance in community composition explained by these environmental variables was partitioned by scale for each community sampled. The three taxonomic groups studied perceive and respond to the environmental at different scales. I expected these different taxonomic groups to respond to the different scales of environmental variables in proportion to their ability to respond to the environment.

The ability to predict the number of species within a particular region based on area and the heterogeneity of that site would be a valuable tool for the conservation of biodiversity. I used spectral variance (Palmer et al. 2000, Palmer et al. 2002) to quantify environmental heterogeneity in a scale dependent manner. In Chapter IV, I use this measure of heterogeneity and area to explain the variance in species accumulation curves. I also use these factors to predict species accumulation curves within transects based on models developed using data from across the region. I expected that the incorporation of a scale-dependent measure of heterogeneity would increase our ability to predict the species accumulation curves of specific locations.

The mission of many conservation organizations (e.g. Nature Conservancy 2001) and governmental agencies (e.g. U.S. Fish & Wildlife Service 1999) is to preserve biodiversity on a regional scale. Few studies have been conducted on a regional basis that include several taxonomic groups such as this project. This dissertation provides examples of three methodologies, which can assist in understanding the scale-dependent relationships of species and the environment on a regional basis. Understanding these relationships and how they change across taxonomic groups and a regional gradient will add to the success of regional conservation planning.

Literature Cited

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods - scaling environmental patterns. Oikos **49**:340-346.

Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology **17**:637-646.

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

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

Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscapes. Pages 69-84 *in* T. F. H. Allen, editor. Ecological Heterogeneity. Springer-Verlag, New York.

Nature Conservancy. 2001. Conservation by design. The Nature Conservancy, Arlington, Virginia.

Palmer, M. W., P. G. Earls, B. W. Hoagland, P. S. White, and T. Wohlgemuth. 2002. Quantitative tools for perfecting species lists. Environmetrics **13**:121-137.

Palmer, M. W., T. Wohlgemuth, P. G. Earls, J. R. Arévalo, and S. D. Thompson. 2000. Opportunities for long-term ecological research at the Tallgrass Prairie Preserve, Okalahoma. Pages 123-128 *in* K. Vanderbilt, editor. Cooperation in Long Term Ecological Research in Central and Eastern Europe: Proceedings of the ILTER Regional Workshop. Oregon State University, Corvallis, OR.

Tilman, D., and P. M. Kareiva. 1997. Spatial ecology : the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.

U.S. Fish & Wildlife Service. 1999. Conserving the nature of America. Department of the Interior, Washington, D.C.

Wagner, H. H. 2003. Direct multiscale ordination with canonical correspondence analysis. Ecology.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

CHAPTER 2: TAXON-DEPENDENT SCALING: BEETLES, BIRDS AND VEGETATION AT FOUR NORTH AMERICAN GRASSLAND SITES.

Abstract

Because organisms respond to the environment at different scales, it is important to develop ways of determining the appropriate scales for a specific ecological process and organism. I consider whether the relative importance of different scales can be predicted from organism mobility, and whether this relationship is independent of landscape characteristics, or are the differences between landscapes at least predictable. I observed species abundance for vascular plants, ground-dwelling beetles and breeding birds along eight 2-km transects of 40 sampling stations each, distributed over four sites along the regional gradient from shortgrass steppe in Eastern Colorado to tallgrass prairie in Eastern Kansas. For each transect and taxonomic group, the relative importance of factors measured at the trap-scale (1 m; soil texture and hardness, vegetation height, bare ground), at the local scale (10 m; density of shrubs and cacti) and at the landscape scale (30 m; Landsat 7 TM spectral bands, slope and elevation) was assessed using hierarchical canonical variance partitioning with forward selection of explanatory variables. Plants, beetles and birds all responded to factors measured at all three scales, and factor influence was more consistent between transects and between plants and beetles for the more homogeneous landscapes of the shortgrass steppe than for the more heterogeneous landscapes of the tallgrass prairie. I conclude that independent of the mobility of a taxonomic group, factors at several scales are

important, their importance may shift along regional gradients, and the variability between sites is high even for nearby sites.

Introduction

The influences of scale and spatial patterns on species distributions and community structure have become dominant issues in ecology, particularly landscape ecology (Allen and Starr 1982, Addicott et al. 1987, O'Neill et al. 1989, Wiens 1989, Legendre 1993, Schneider 1994). Both local and regional processes influence the distribution of species and the structure of communities (Brown 1984, Ricklefs 1987, Ohmann and Spies 1998). For example, McIntyre (1997) demonstrated that the tenebrionid beetle, *Eleodes hispilabris*, responds to different environmental factors at different scales in the grasslands of north-central Colorado: at local scales, *E. hispilabris* prefers areas of vegetative detritus, while at broader scales *E. hispilabris* is associated with shrub-dominated lowlands.

One common method for determining the environmental factors that are related to community structure is Canonical Correspondence Analysis (Terbraak 1986). Canonical Correspondence Analysis is a direct ordination technique using environmental and biological data to examine species-environment relationships (Palmer 1993). Most studies using this method focused on either single taxonomic groups or were conducted at single sites, limiting the generalizations that can be made and the usefulness of such studies for understanding general mechanisms that structure communities across regions or taxonomic groups.

To enhance the applicability of Canonical Correspondence Analysis, Borcard et al. (1992) introduced variance partitioning using Canonical Correspondence Analysis, a method that decomposes the variance (inertia) explained by different factors. In Borcard et al.'s initial example, the variance in an orbatid mite community was partitioned into the effects of environmental factors, geographic space, and the overlap between these two groups of variables. Others have used this method to examine the canopy and abiotic factors that influence sapling communities in an old growth forest (Arii and Lechowicz 2002) and to determine which landscape and habitat factors influence plants, insects and birds in pastures of southern Sweden (Soderstrom et al. 2001). More recently, Cushman and McGarigal (2002) extended this model by introducing hierarchical canonical variance partitioning to show the influence of scale in bird community composition in the Oregon Coast Range. In their study, environmental variables were measured at three scales, thus allowing the explained variance to be partitioned among different hierarchical levels. Using this framework, hypotheses can be generated concerning the scale of response of different organisms or taxonomic groups. This could enable ecologists to differentiate between variance in community structure explained by local interactions between resources and species and the influence of broader scale variables such as productivity and climate.

A primary goal of community ecology is to understand the causal mechanisms underlying ecological patterns, therefore it should be expected that defining these driving forces at one location would provide insights into the mechanisms that operate at a location just down the road, as well as across a region. If regional planning is to be effective for managing and conserving different taxonomic groups, developing predictions across sites and taxonomic groups is essential

I studied three taxonomic groups at four sites that span a major environmental gradient to determine if and how environmental variables measured at different scales are related to different taxonomic groups. I focus on three primary questions: (1) What scale of environmental variables explains the most variance in community structure for beetles, birds and plants at four sites across a regional gradient?, (2) Do these relationships change in a systematic way across a regional gradient? and (3) Beyond the scale of each variable, are there particular variables that are important in potentially structuring the different communities across these sites?

Methods

Study Sites

This research was conducted at the Konza Prairie Long-Term Ecological Research site (LTER), Kansas; the Smoky Valley Ranch, Kansas and Fox Ranch, Colorado (Arikaree), both Nature Conservancy properties; and the Shortgrass Steppe LTER located within the Pawnee National Grasslands, Colorado (Fig. 2.1). At each of these sites, two 2-km transects were established based on digitally available environmental data, including soil, topographic and vegetation maps. Rather than locating the transects randomly, I positioned them to encapsulate a wide range of the variation that exists within a site in order to assess the influence of gradients upon biological communities. At several sites, transects encompassed uplands, valleys, and floodplains and on some occasions crossed streams or rivers. Along each transect, sampling stations were established every 50 m for a total of 40 sampling stations per transect. Table 2.1 lists the location, dominant vegetation and precipitation information for these five sites. (More detailed descriptions of the transects can be found in Appendix I).

Biological data

Biotic data, including bird surveys, pitfall trapping for ground-dwelling beetles, and quadrat sampling of vegetation, were collected along each transect. At each sampling station, plant composition was surveyed in a 1-m^2 quadrat during May and early June of 2000, to asses early season vegetation, and August 2000, to incorporate late season grasses and forbs. Within each quadrat, the abundance of each vascular plant species was recorded using 7 cover classes (1 = <2%, 2 = 2 - 5%, 3 = 5 - 25%, 4 = 25 - 50%, 5 = 50 - 75%, 6 = 75 - 95%, 7 = 95 - 100%). These ordinal rankings were square-root transformed for analysis.

Beetles were sampled at each sampling location using pitfall traps during late May and early June 2000 and 2001. The pitfall traps (~8 cm diameter) were dug flush with the ground and allowed to settle at least 10 days before sampling. The pitfall traps were then opened for 72 ± 2 h. Ethylene glycol was used as a killing and preserving agent in each pitfall trap (Weeks and McIntyre 1997, Koivula et al. 2003). After 3 days, the traps were collected and taken into the laboratory for analysis. Beetles were counted and identified to morpho-species. Reference specimens for all the species from each site were pinned and labeled for consistency in identification. After all individuals had been examined at least twice, sample specimens of the most abundant families (Carabidae, Scarabaeidae, and Tenebrionidae) were sent to specialists to confirm identifications. Professors and students of the C.P. Gillette Museum of Arthropod Diversity of Colorado

State University identified all other beetle specimens to the lowest taxonomic level possible, typically to the level of genus.

Bird surveys were conducted along each transect in May or early June in 2000 and 2001 to assess bird community composition. The surveys began at dawn and lasted approximately 3 h. The surveyor slowly walked each transect until a bird was located and identified, visually or aurally. The bird's location was determined by measuring the distance and angle from the surveyor to the bird, as well as the distance to the next sampling station. Using this method, birds were assigned to the nearest location that environmental variables were sampled, instead of being assigned to the location of the observer.

For mobile organisms such as beetles or birds, the effective area sampled by a pitfall trap or survey is difficult to assess due to the different dispersal potentials or home ranges of different species. Also, for mobile organisms a complete census of the species present is rarely feasible. To more accurately portray the bird and beetle communities through time the results from the 2 yr of sampling were combined. I considered joining the two years of data justified due to similarities in community structure across the two years based on canonical analysis. Both beetle and bird abundance data were transformed using the Napierian logarithm [$y' = \ln(y + 1)$] for analysis.

Environmental Variables

At each sampling location along each transect, environmental data were collected at three scales. At the trap scale (1 m^2), I sampled soil, vegetation height, percent bare ground, and soil hardness (see Table 2.1 for descriptions). Soil samples were returned to the laboratory to measure soil pH and percent sand, silt and clay for each location. For the western three sites, soil texture was measured using a hydrometer method, while a private laboratory analyzed the soil samples from Konza due to the high organic fraction in some of the samples. Percent bare ground was estimated by visual assessment. I also measured soil hardness four times at each location using a soil penetrometer.

At the local scale, I measured several aspects of shrubs and cacti to assess their density and cover using a point-centered quarter method (Cottam and Curtis 1956). Within each quadrant in a 5-m radius of each sampling location, I estimated the percent cover of each shrub and cactus species. Within a 30-m radius I measured the distance to the nearest cactus, shrub (<1 m in height), and large shrub / tree (1-3 m in height) in each quadrat.

At a regional scale, I acquired satellite (Landsat 7 TM) imagery and digital elevation models (USGS 1998). The Landsat images for each of the sites were taken from either May or June of 2000. The imagery and digital elevation models had 30 m resolution. Based on the digital elevation models, I calculated elevation, slope and aspect. Considering the inappropriateness of using a single number to define aspect within a regression (i.e. 5 degrees and 355 degrees are only 10 degrees apart and not 250 degrees) two values for aspect were calculated: degrees from north and degrees from west. Using a geographic information system (ESRI 2002) I associated each sampling location with the Landsat band values (1-5, 6a, 6b, 7-8), elevation, aspect values, and slope. The geographic location of each sampling station was also included in the analysis.

Considering different process act at different scales, comparisons conducted across scales is necessarily conducted across different variables. For instance, a variable such as percent cover of a shrub species would be meaningless at 1 m^2 because it would not accurately portray the differences in shrub density at different sampling locations. Rather, comparing the explanatory power of different scales of variables is a comparison of variables that are measurable at a particular resolution.

Statistical Analysis

To reduce the number of environmental variables incorporated in these analyses a forward selection process was used, which was based on the amount of variance in community composition the variables explained. A selection process was necessary because more environmental variables were measured than there were observations, which would violate rules of a canonical correspondence analysis (see McCune 1997). The following process was conducted for each taxonomic group for each transect; thus, each community-by-transect group had a unique set of explanatory variables. First, each variable was independently included in a canonical correspondence analysis. The variable that explained the most variance was then tested for significance using an ANOVA-like permutation test (anova.cca in the vegan library of the statistical language R, version 1.6.1), which tests for the joint effect of constraints in canonical correspondence analysis (Legendre and Legendre 1998). The variable was selected if the p-value was less than 0.15 based on a pseudo F statistic. The remaining variables were then each combined with the initial variable and tested for the amount of variance explained. Again, the variable that increased the explained variance by the largest amount was retained and tested for significance; this process was repeated until no more variables could be added that were significant.

To examine the influence of the scale of environmental variables and geographic space on their ability to explain patterns of community structure in plant, beetle and bird communities, I used hierarchical canonical variance partitioning (Cushman and McGarigal 2002) with the addition of geographic space as an explanatory variable. Hierarchical canonical variance partitioning is a method that partitions the explained variance (constrained inertia) of a CCA by the different scales at which the environmental variables were measured. For three scales of measurement, hierarchical canonical variance partitioning results in seven components of variance:

- Pure trap-scale effects
- Pure local-scale effects
- Pure landscape-scale effects
- Joint effects of trap- and local-scale variables
- Joint effects of trap- and landscape-scale variables
- Joint effects of local- and landscape-scale variables
- Joint effects of trap-, local- and landscape-scale variables.

In this analysis, I also included geographic space, so for each of the seven components there are seven more partitions corresponding to the variance explained by both the component listed above and by geographic space. A 15th component is the variance explained by pure geographic space. Combing hierarchical canonical variance partitioning with geographic space thus results in 15 components of variance (see Fig. 2.2). These 15 components were used to compare the variance explained in community composition by different scales of environmental variables and geographic space. The canonical correspondence analyses conducted and the method to calculate each of these 15 components are detailed in Tables 2.3 and 2.4.

Based on the results of these analyses, I made two primary comparisons. First, I compared the amount of variance of each community along each transect explained by the environmental variables, by environmental variables plus geographic space, and by geographic space alone. Second, I compared the amount of variance of each community along each transect explained by each scale of environmental variable: trap, local, and landscape.

In addition to attempting to explain variance within a particular transect, I also assessed the ability of the variables chosen at one location to predict community structure along another transect at the same site. Using canonical correspondence analysis to define the variables that explain most of the variance in community composition assumes that these variables may represent causal mechanisms or driving forces within these systems. If this is so, then it might be expected that these variables would also explain a similar proportion of variance along replicate transects.

To test the hypothesis that a common set of variables will explain a similar amount of variance in community structure along transects in nearby locations, I analyzed the amount of variance explained along transects at Pawnee and Konza by using the variables selected from one transect to explain the variance explained along the other transect at that site. I conducted this analysis for beetle, bird, and vegetation data.

Results

At least 33% of the variance in community composition was explained for each community analyzed using CCA hierarchical variance partitioning (Fig. 2.3). The maximum variance explained for any community was 72% for the vascular plants along transect K2. On average across all sites, more variance was explained for plant communities than for either the beetle or bird communities. Along all eight transects at least 49% of the variance in community composition was explained for the vascular plants. For birds and the beetles, the minimum and maximum variance explained for all transects was 33% and 42%, and 54% and 61%, respectively.

The inclusion of geographic space in these analyses only slightly increased the explained variance in community composition (Fig. 2.3). In only two instances was the explained variance increased by more than 5%. These instances occurred for birds and plants along transect 1 of Pawnee (P1). For the beetle communities, incorporating geographic space only increased the explained variance by an average of 2.3%.

At Pawnee, the partitioning of explained variance among scales was very similar for the two transects for both the vascular plants and beetles (Fig. 2.4). Comparing the three taxonomic groups along transect P1, the local-scale variables explain the most variance within these groups. In all taxonomic groups of transect P1, the local variables explained at least 40% of the total explained variance. Along transect P2 the most influential scale was the landscape scale, although the explained variance along this transect was more evenly distributed among the three scales.

None of the transects at the Arikaree site showed a clear pattern or dominance of one scale of variables in explaining variance in community composition. Compared to Pawnee, however, the trap-level variables at Arikaree contributed more to the amount of variance explained for all taxonomic groups. Along transect A2 the trap-level variables explained at least 40%, and as much as 57%, of the total explained variance.

For all taxonomic groups and transects at Smoky Valley, the landscape-scale variables explained more variance than either the trap- or local-scale variables. Along transect S2, landscape-scale variables accounted for 72 % of the explained variance in beetle community composition. Local-scale variables dominated the explained variance for the transects at Konza Prairie, while the trap-scale variables typically explained the least amount of variance. The one exception to this was beetles at transect K1, for which trap-scale variables explained twice as much variance as did the landscape-scale variables.

In view of the strong environmental gradient from Pawnee to Konza, I expected that there would be systematic shifts in the response of different taxonomic groups to the scale of environmental variables. The variance explained in plant-community composition across this gradient was evenly distributed among the three scales at all the sites, except for the dominance of local-scale variables at Konza prairie. Along many of these transects, but particularly at Arikaree and Smoky Valley there was also considerable overlap in the variance explained by different scales of variables. For example, along transect S1, 4% of the variance in the plant community composition was explained by all three sets of variables, 6% of the variance was explained by trap- and landscape-scale variables combined, and 9% of the variance was explained by local- and landscape-scale variables combined. Examining the community composition of beetles along this gradient showed no systematic shift in the scale of explanatory variables.

For bird-community composition across this gradient, the analysis showed that local- and landscape-scale variables typically explained the most variance. In one instance (K2), no trap-scale variables were selected in the forward selection process.

Beyond examining the scale at which birds, beetles and plants respond to environmental heterogeneity, I also examined the specific variables that were included in the analysis (Table 2.5). In general, more variables were selected to explain the variance in plant communities than for either beetles or birds. On average, the number of variables selected for the analyses were 14.4, 12.1, and 7.8 variables for plants, beetles, and birds, respectively.

Along the two transects at Pawnee, over 50% of the variables selected for the plants were also selected for beetles. For transect P1, of the 11 variables selected for analysis of beetle community composition, 7 were also selected for analysis of the plant community. There was similar concordance of variables between beetles and plants for transect P2, although, these similarities did not hold across transects. For the analysis of beetles from the two transects at Pawnee, only three of the same variables were used in the analyses of these two transects. Interestingly, these three variables were all associated with the presence of cactus. There was very little overlap between the variables used to analyze bird-community composition and beetles and plants, except that the bird analysis also contained a variable associated with cactus.

Transect A2 had five of the same variables selected for all three taxonomic groups; these were: mean vegetation height, percent silt, proportion of quarters containing shrubs <1m in height, the distance to cactus and Landsat band 7. This suggests that all three of these communities may be influenced or structured by a similar suite of variables.

Even though all the results at Smoky Valley were dominated the landscape-scale variables, there was very little similarity between the groups in terms of specific variables. Along transect S1 there were only two variables, elevation and slope, that were selected for the analysis of all three taxonomic groups. Elevation was the only consistently selected variable for the analyses of transect S2.

At Konza there was almost no overlap in the variables selected for analysis for the three taxonomic groups. Comparing just the beetle and plant communities, however, there was similarity in the variables selected for analysis. Five of the same variables were selected for analysis of beetles and plants along transect K1; four of these variables were local-scale variables. Seven variables were selected for both beetles and plants for transect K2, of which three were each trap- and local-scale variables. The only common variable between these two groups at the landscape-scale was elevation.

To test the value of this approach in predicting the variance explained in community composition along different transects, I examined the results for a transect based on the variables selected from the other transect within the same site, using the two transects at Pawnee and at Konza. I used transects P1 and K1 to define the predictor variables for the communities of transect P2 and K2, respectively. I compared the variance explained for each scale as well as with all variables combined, excluding geographic space. For transect P2, the variables from the P1 analysis explained at least 75% as much variance in community composition as was explained by the P2 variables

(Table 2.6). For the vascular plants, the variables selected for transect P1 explained 90% as much variance as was explained by the variables selected for transect P2. The P1 analysis for plants, however, selected two more variables than did the P2 analysis. The ability of the P1 variables to explain almost as much variance in community composition as the initial analysis was contingent on this increased number of variables.

The influence of an increased number of variables is most notable when the individual scales are examined. For plants at Pawnee, the P1 variables explained more variance in community composition at the local scale than the P2 variables; however, the P1 analysis selected three more variables than did the P2 analysis. Except for the amount of variance in plant community composition explained by local-scale variables at Pawnee, the variables selected by the P2 analysis always explained more variance than the P1 variables.

Comparing the variance explained along the K2 transect using either the K2 or the K1 variables clearly showed the influence of the number of variables included in the analysis (Table 2.6). The analysis of plants of transect K2 included seven more variables than the K1 analysis. Thus, the variables selected by the K1 analysis only explained 52% of the variance explained by the K2 analysis. The opposite occurred for the birds, for which the analysis for transect K1 selected six more variables than the K2 analysis. Thus the K1 variables explained more variance in bird-community composition than did the original analysis. The number of variables included in the analyses of beetles along the two Konza transects only differed by one, thus giving a better indication of the ability of the variables of one transect to explain variance in community composition along another transect. The variables selected by the K1 analysis for beetles explained 71% of the variance that was explained by the K2 variables.

Discussion

This research highlights two primary issues that confront research and conservation efforts aimed at a regional scale. In particular, I have shown that: (1) certain taxonomic groups are influenced more by certain scales of environmental variables; and (2) the transition along the moisture gradient from the shortgrass steppe to the tallgrass prairie is associated with a shift in the relationship in patterns of community –environment relationships between different taxonomic groups.

As I expected, some taxonomic groups in the study were more strongly associated with environmental variables at some scales than at others. Such patterns may indicate the scales at which these organisms respond to the environment. For birds, the local or landscape-level variables explained more variance in bird community structure along all of the transects than did the trap-scale variables. This result is consistent with the expectations for two reasons. First, birds perceive the landscape at a much larger scale and are more mobile than either plants or ground-dwelling beetles. Bird community structure has been shown to be correlated with the coverage of shrub species (Wiens and Rotenberry 1981) and patterns of bird abundance have also been correlated with heterogeneity measured using landsat imagery (Valiulis 2003). Second, the trap-level variables were measured at the sampling locations of the beetles and plants, so there was less spatial concordance in the measures being compared. Nonetheless, at all the sites except Konza, the trap-scale variables accounted for at least 30% of the total explained variance.

In contrast to the birds, I expected the variance in the beetle and plant communities to be explained mostly by trap-scale variables, as both beetles (Stapp 1997) and plants (Kinraide 1984, Dodd et al. 2002)are known to respond to localized soil texture in shortgrass steppe. The results showed that all three scales were important in explaining variance in the community structure of beetles and plant communities.

The influence of local-scale variables at Konza for all taxonomic groups is an obvious departure from the more equal distribution of the effects of explanatory variables across scales, which was exhibited at the other sites. The Konza Prairie is at the western edge of the tallgrass prairie. Along with the dominance of tallgrass species such as big bluestem (*Andropogon gerardii*), Konza prairie is much more diverse in shrubs and woody plants. Most of the variables associated with the local scale are those describing the density and proximity to shrubs and cactus. At the other sites, only 2-3 shrub species were usually recorded along a transect, while at least three times that many at Konza. The greater number of shrubs at Konza increased in the number of shrub species consequently increased the number of possible variables to be selected for the suite of local-variables.

Across the moisture gradient encompassed by the study sites, there was a shift in the coherence of patterns between plant and beetle communities. At Pawnee and Arikaree there was considerable consistency in the specific variables selected. These two sites were also the most homogeneous in terms of elevation changes and shrub cover. The community structure of both beetles and plants at these two sites was consistently related to parameters associated with soil texture and soil hardness. As heterogeneity increased from west to east, this coherence dissipated, suggesting that the mechanisms related to community structure are similar at Pawnee and Arikaree, the more homogenous sites. In more heterogeneous landscapes, such as Konza, it appears that the factors structuring vascular-plant and ground-dwelling beetle communities are related to vegetation structure than soil properties.

The concordance between different taxonomic groups has significant implications for management of grassland systems. Beetles (Dufrene and Legendre 1997, Rykken et al. 1997, Larsen et al. 2003) and plants (Panzer and Schwartz 1998) have been used as indicator species for other taxonomic groups as well as for overall diversity. Understanding where scaling relationships are similar between different taxonomic groups, such as beetles and vegetation at Pawnee and Arikaree, may justify managing these groups in the same manner. However, translating the same management scheme to a different location, such as Smoky Valley or Konza, may not be justified due to the differences in scale relationships of different taxonomic groups.

To manage biodiversity on a regional basis, it would be advantageous to be able to identify key factors at certain scales that might act as driving forces in structuring communities throughout that region. However, the results show that finding these key factors acting upon several taxonomic groups across a broad region is not an easy goal to achieve. Nonetheless, a regional approach to conservation is the goal of many federal agencies and non-governmental agencies. For example the U. S. Fish and Wildlife Service has adopted an "ecosystem approach" to "achieve landscape-level conservation of fish, wildlife, plants and their habitats" (U.S. Fish & Wildlife Service 1999), and The Nature Conservancy focuses on ecoregions, which "provide a framework for capturing ecological and genetic variation in biodiversity across a full range of environmental gradients" (Nature Conservancy 2001). Both of these statements not only highlight a regional focus, but also focus on several taxonomic groups rather than focal species or species of interest.

Regional approaches come at a cost. Sampling designs such as the long transect used in this study are apt to miss detailed relationships and aspects of communities that are important for preservation. The 2-km transect design, used to collect the data presented here, was initially developed to assess changes in community composition across a gradient. Statistical sampling designs such as unstratified systematic or random sampling tend to miss rare habitats and thus rare and endemic species, while defining patterns of dominant vegetation. Despite the shortcomings of transect designs, particularly with respect to sampling patterns of vegetation diversity (Stohlgren et al. 1995), this design seemed the most advantageous for sampling a multitude of taxonomic groups and a large suite of environmental variables that could all be analyzed using the same techniques.

Conclusions

The study of several taxonomic groups across a major environmental gradient shows the importance of including variables from multiple scales to explain variance in community composition (Brown 1984, Ricklefs 1987, Ohmann and Spies 1998). Assuming that small organisms, such as beetles, only respond to environmental variables measured at fine-scales or that larger and more mobile species, such as birds, only respond to broad-scale variables may limit the ability of researchers to explain patterns in community structure. Many organizations concerned with the conservation of biodiversity call for regional approaches. For this goal to be achieved, a concerted effort needs to be made to understand the influence of processes acting at multiple scales. Regional studies sacrifice detailed information at particular sites for increased breadth and generalization in hopes of finding regional patterns consistent with the goal of conserving regional biodiversity. The study has shown that finding specific factors that explain variance in communities across taxonomic groups and throughout a region is not an easy goal to achieve given typical cost and logistical constraints. In the study area, however, I did show that across a regional gradient there is often a systematic shift in the effect of certain types of explanatory variables, such as the shift from the importance of soil texture in arid sites to the importance of vegetation structure in the tallgrass prairie.

Literature Cited

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods - scaling environmental patterns. Oikos **49**:340-346.

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

Arii, K., and M. J. Lechowicz. 2002. The influence of overstory trees and abiotic factors on the sapling community in an old-growth *Fagus-Acer* forest. Ecoscience **9**:386-396.

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

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist **124**:255-279.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytological sampling. Ecology **37**:451-460.

Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology **17**:637-646.

Dodd, M. B., W. K. Lauenroth, I. C. Burke, and P. L. Chapman. 2002. Associations between vegetation patterns and soil texture in the shortgrass steppe. Plant Ecology **158**:127-137.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

ESRI. 2002. ArcGIS Version 7.1. ESRI, Redlands, CA.

Kinraide, T. B. 1984. The influence of soil texture on the vegetation of a grazed, short-grass prairie in Colorado. Southwestern Naturalist **29**:277-287.

Koivula, M., D. J. Kotze, L. Hiisivuori, and H. Rita. 2003. Pitfall trap efficiency: do trap size, collecting fluid and vegetation structure matter? Entomologica Fennica **14**:1-14.

Larsen, K. I., T. T. Work, and F. F. Purrington. 2003. Habitat use patterns by ground beetles (Coleoptera : Carabidae) of northeastern Iowa. Pedobiologia **47**:288-299.

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

Legendre, P., and L. Legendre. 1998. Numerical ecology, 2nd English edition. Elsevier Science B.V., Amsterdam.

McCune, B. 1997. Influence of noisy environmental data on canonical correspondence analysis. Ecology **78**:2617-2623.

McIntyre, N. E. 1997. Scale-dependent habitat selection by the darkling beetle *Eleodes hispilabris* (Coleoptera: Tenebrionidae). American Midland Naturalist **138**:230-235.

Nature Conservancy. 2001. Conservation by design. The Nature Conservancy, Arlington, Virginia.

Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs **68**:151-182.

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.

Palmer, M. W. 1993. Putting Things in Even Better Order - the Advantages of Canonical Correspondence-Analysis. Ecology **74**:2215-2230.

Panzer, R., and M. W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. Conservation Biology **12**:693-702.

Ricklefs, R. E. 1987. Community Diversity - Relative Roles of Local and Regional Processes. Science **235**:167-171.

Rykken, J. J., D. E. Capen, and S. P. Mahabir. 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. Conservation Biology **11**:522-530.

Schneider, D. C. 1994. Quantitative ecology : spatial and temporal scaling. Academic Press, San Diego, California.

Soderstrom, B., B. Svensson, K. Vessby, and A. Glimskar. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiversity and Conservation **10**:1839-1863.

Stapp, P. 1997. Microhabitat use and community structure of darkling beetles (Coleoptera:Tenebrionidae) in shortgrass prairie: Effects of season, shrub cover and soil type. American Midland Naturalist **137**:298-311.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117**:113-121.

ter Braak, C. J. F. 1986. Canonical correspondence analysis - a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

U.S. Fish & Wildlife Service. 1999. Conserving the nature of America. Department of the Interior, Washington, D.C.

USGS. 1998. U.S. Geological Survey DEM 7.5 Quadrangle. U.S. Geological Survey, Reston, VA, USA.

Valiulis, J. 2003. The use of continuous and categorical measures of landscape structure in predicting biotic response: An example using grassland birds. Thesis. Colorado State Universiy, Fort Collins, Colorado.

Weeks, R. D., and N. E. McIntyre. 1997. A comparison of live versus kill pitfall trapping techniques using various killing agents. Entomologia Experimentalis et Applicata **82**:267-273.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs **51**:21-41.

Table 2.1: Site descriptions, including location, average precipitation and dominant vegetation.

Site	State	County	Latitude	Longitude	Average Precipitation	Dominant Vegetation
Pawnee National Grasslands Long Term Ecological Research Station	Colorado	Weld	40°47′N	104°42′W	320 mm	*Bouteloua gracilis* *Buchloe dactyloides*
Fox Ranch (Arikaree) The Nature Conservancy	Colorado	Yuma	39°44′N	102°28′W	448 mm	*Bouteloua gracilis* *Stipa comata*
Smoky Valley The Nature Conservancy	Kansas	Logan	38°50′N	100°58′W	533 mm	*Artemesia filifolia* *Bouteloua gracilis*
Konza Prairie Long Term Ecological Research Station	Kansas	Riley	39°04′N	96°34′W	835 mm	*Andropogon gerardi* *Sorghastrum nutans*

Table 2.2: Environmental variables measured at one of three scales, which were used to explain the variance in community composition of beetles, birds and vegetation. The scales at which environmental variables were measured were: trap (1 m^2), local (75 – 300 m^2) and landscape (900 m^2). Trap and local scale variables were measured at the locations at which beetles and vegetation were sampled. The landscape variables were obtained via satellite imagery and digital elevation models.

Scale	Variable(s)	code(s)
Trap	Soil pH	ph
	Mean soil hardness (based on 4 measurements)	mhard
	Soil hardness - standard deviation	sdhard
	Soil texture	sand silt clay
	Percent bareground	brgd
	Mean vegetation height (based on 4 measurements)	mvght
	Maximum vegetation height	mxvght
	Vegetation height standard deviation	sdvght
Local	Distance to nearest cactus	nearcac
	Proportion of quadrants containing cacti	propcac
	Distance to nearest shrub <1 m tall	near1
	Proportion of quadrants containing shrubs <1 m tall	prop1
	Distance to nearest tall shrub (1-3 m tall)	near13
	Proportion of quadrants containing shrubs between 1 and 3 m tall	prop13
	Location containing <2% cactus in a 5 m radius – An ordinal dummy variable.	cact1
	Location containing 2-5% cactus	cact2
	Location containing 5-25% cactus	cact3
	Location containing 25-50% cactus	cact4
	The previous 4 variables were also measured for each species of shrub within a 5 m radius, including *Amorpha canescens, Artemesia ludoviciana, Atriplex canescens*, *Cornus drummondii, Rhus gluaca* (stag), *Rhus aromatica* (arom), *Rosa arkansana, Yucca glauca*	
Landscape	Elevation	elev
	Slope	slp
	Aspect measured in degrees from North	nasp
	Aspect measured in degrees from West	wasp
	Landsat bands 1-5, 6a, 6b, 7, 8	ls1, ls2 etc

Table 2.3: Explanation of the 25 canonical and partial canonical ordinations that were conducted in order to partition the explained variance in beetle, bird and plant community composition by scale and geographic space. The numbers in parentheses correspond to the 15 components identified in Figure 2.2. The * indicate the ordinations that were actually used for the analysis.

Symbol	Explanatory Set	Covariable Set	Variance Explained
[A] *	Trap	None	(1)+(4)+(5)+(7)+(8)+(11)+(12)+(14)
[B]	Local	None	(2)+(5)+(6)+(7)+(9)+(12)+(13)+(14)
[C]	Landscape	None	(3)+(4)+(6)+(7)+(10)+(11)+(12)+(14)
[D] *	Space	None	(8)+(9)+(10)+(11)+(12)+(13)+(14)+(15)
[E] *	Trap	Local	(1)+(4)+(8)+(11)
[F] *	Trap	Landscape	(1)+(5)+(8)+(12)
[G] *	Trap	Space	(1)+(4)+(5)+(7)
[H] *	Trap	Local + Landscape	(1)+(8)
[I] *	Trap	Local + Space	(1)+(4)
[J] *	Trap	Landscape + Space	(1)+(5)
[K] *	Trap	Local + Landscape + Space	(1)
[L] *	Local	Trap	(2)+(6)+(9)+(13)
[M] *	Local	Landscape	(2)+(5)+(9)+(12)
[N] *	Local	Space	(2)+(5)+(6)+(7)
[O] *	Local	Trap + Landscape	(2)+(9)
[P] *	Local	Trap+ Space	(2)+(6)
[Q] *	Local	Landscape + Space	(2)+(5)
[R] *	Local	Trap + Landscape + Space	(2)
[S]	Landscape	Trap	(3)+(6)+(10)+(13)
[T]	Landscape	Local	(3)+(4)+(10)+(11)
[U]	Landscape	Space	(3)+(4)+(6)+(7)
[V] *	Landscape	Trap + Local	(3)+(10)
[W]	Landscape	Trap + Space	(3)+(6)
[X]	Landscape	Local + Space	(3)+(4)
[Y] *	Landscape	Trap + Local + Space	(3)

Table 2.4: Description and method of calculating the components of Figure 2.2. Components used for calculation are based on the results of canonical and partial canonical ordinations described in Table 2.3. The letters correspond to the first column of Table 2.3. By adding and subtracting different calculations from Table 2.3 the variance attributed to each component of Figure 2.2, the numbers in parentheses, was determined based on the following calculations.

Number	Component Description	Component Calculation
(1)	Variation due to trap factors alone.	K
(2)	Variation due to local factors alone.	R
(3)	Variation due to landscape factors alone.	Y
(4)	Variation jointly explained by trap and landscape factors, independent of local factors and space.	I – K
(5)	Variation jointly explained by trap and local factors, independent of landscape factors and space.	J – K
(6)	Variation jointly explained by local and landscape factors, independent of trap factors and space.	P – R
(7)	Variation jointly explained by trap, local and landscape factors, independent of space.	N – P – Q – R
(8)	Variation jointly explained by trap factors and space, independent of local and landscape factors.	H – K
(9)	Variation jointly explained by local factors and space, independent of trap and landscape factors.	O – R
(10)	Variation jointly explained by landscape factors and space, independent of trap and local factors.	V – Y
(11)	Variation jointly explained by trap and landscape factors and space, independent of local factors.	E – R – I + K
(12)	Variation jointly explained by trap and local factors and space, independent of landscape factors.	M – O – Q + R
(13)	Variation jointly explained by local and landscape factors and space, independent of trap factors.	L – O – P – R
(14)	Variation jointly explained by trap, local and landscape factors and space.	A – E + H – F + P + Q – N – R
(15)	Variation due to geographic space alone.	D + G – A + P – L + Y – V

Table 2.5: Environmental parameters selected as explanatory variables for canonical correspondence analyses of three taxonomic communities along eight transects at four grassland sites. The four sites are the Pawnee National Grasslands (P), Fox Ranch (A), Smoky Valley Ranch (S), and Konza Prairie (K). The environmental variables are separated by the scale at which they were measured. The explanatory variables were determined using forward selection based on the amount of variance explained for the plant, beetle and bird communities. The variables within each scale are in order of their selection, thus indicating the relative amount of variance explained by a variable within a particular scale.

Transect	Trap Variables			Local Variables			Landscape Variables		
	Plants	Beetles	Birds	Plants	Beetles	Birds	Plants	Beetles	Birds
P1	brgd mxvght sand stvght	mxvght brgd	clay brgd	cact1 nearcac atri2 prop1 propcac near1	cact1 yucc3 prop1 propcac nearcac	nearcac atri2	ls6a ls5 slp ls3	ls6a ls8 ls2 ls1	ls6b
P2	sdhard mhard silt ph	sdhard silt	silt brgd	propcac atri2 atri1	propcac atri2 cact1 nearcac	propcac	ls7 ls2 ls6a wasp ls4	ls7 ls4 ls5 elev ls8	ls6b elev
A1	clay brgd ph silt mhard	mvght ph brgd sdhard mhard	stvght brgd	prop1 near1 yucc1	near1 nearcac atri2 cact2 yucc3	cact1	ls7 ls4 ls5 yucc2 yucc3	elev slp ls6b ls8 ls3 ls4 ls1	elev ls1 ls6a ls6b
A2	mvght silt clay sdhard mhard	mvght sdhard silt mhard	mvght silt brgd	near1 prop1 nearcac atri2	prop1 near1 nearcac propcac	prop1 atri1 nearcac atri4	ls62 nasp ls7 ls8 ls5 ls6a	ls7 slp ls1 ls2	ls7 ls1 slp
S1	silt sand sdhard	brgd silt	stvght clay brgd	nearcac near1 prop1 yucc2	near1 arte4 yucc2	nearcac arte2	slp ls5 ls6a ls1 ls7 ls3 wasp elev ls8	ls1 ls5 slp elev	elev wasp slp
S2	sand silt mxvght mvght	sdhard	stvght clay mxvght	yucc2 propcac yucc1	yucc2 cact1	near1	wasp elev ls4 ls1	slp ls4 ls7 ls6a	ls6a nasp wasp elev

							ls2	elev ls8 ls6b	ls7 ls2
K1	clay ph	mvght clay brgd mxvght	mvght	corn3 rosa2 rosa1 soft2 amor3 stag3 stag2	stag4 rosa2 near1 soft2 stag3 amor1 corn3	arom1 stag2 stag4 prop13 prop1 soft1 soft2	elev wasp ls8 ls6a	ls6b nasp	ls2 ls6b ls5 slp
K2	mvght ph silt brgd stvght	mvght stvght brgd	----	near13 rosa1 rosa2 corn2 corn4 stag3 soft2 arom1 rosa3	rosa2 corn4 stag1 amor1 soft3 soft1	arom1 amor1 near13 prop1 soft1	ls8 elev ls4 nasp ls6b ls2	elev ls6a ls4 ls7 ls8	ls8

Table 2.6: Comparison of the amount of variance explained using canonical correspondence analyses for plant, beetle and bird community composition along a transect in the Pawnee National Grassland, Colorado. For this analysis, the variance in community composition along transect P2 was analyzed using variables that were selected specifically for transect P2 and those variables that were selected to explain variance in community composition along transect P1. The numbers in parentheses represent the difference in the actual number of variables selected to explain variance by environmental variables at a particular scale. Numbers in bold indicate instances in which the variables from transect P1 explain more variance than the variables selected for transect P2. The column title "All" represents the combination of all the scales of environmental variables. Variables representing geographic space were not included in this analysis.

Taxon		Variables			
		Trap	Local	Landscape	All
Plants	P2	0.15	0.18	0.22	0.50
	P1	0.11 (0)	**0.24 (+3)**	0.16 (-1)	0.46 (+2)
Beetles	P2	0.08	0.17	0.18	0.41
	P1	0.04 (0)	0.14 (+1)	0.11 (-1)	0.30 (0)
Birds	P2	0.12	0.10	0.17	0.30
	P1	0.06 (0)	0.10 (+1)	0.09 (-1)	0.23 (0)

Table 2.7: Comparison of the amount of variance explained using canonical correspondence analyses for plant, beetle and bird community composition along a transect at Konza Prairie, Kansas. For this analysis, the variance in community composition along transect K2 was analyzed using variables that were selected specifically for transect K2 and those variables that were selected to explain variance in community composition along transect K1. The numbers in parentheses represent the difference in the actual number of variables selected to explain variance by environmental variables at a particular scale. Numbers in bold indicate instances in which the variables from transect K1 explain more variance than the variables selected for transect K2. The column title "All" represents the combination of all the scales of environmental variables. Variables representing geographic space were not included in this analysis.

		Variables			
Taxon		Trap	Local	Landscape	All
Plants	K2	0.27	0.32	0.23	0.54
	K1	0.10 (-3)	0.19 (-2)	0.17 (-2)	0.36 (-7)
Beetles	K2	0.11	0.21	0.20	0.49
	K1	**0.13 (+1)**	0.15 (+1)	0.08 (-3)	0.35 (-1)
Birds	K2	0.00	0.27	0.04	0.31
	K1	**0.02 (+1)**	0.22 (+2)	**0.11 (+3)**	**0.39 (+6)**

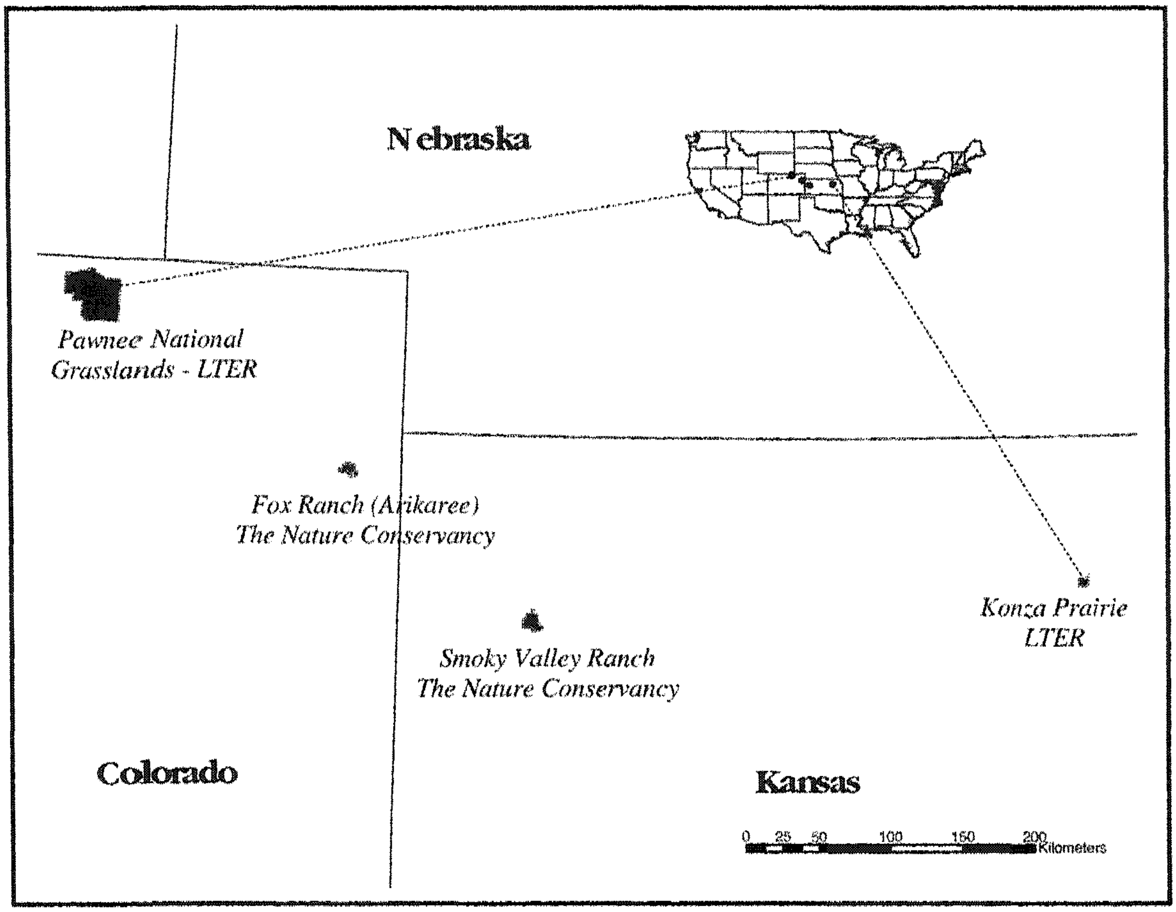


Figure 2.1: Location of study sites.

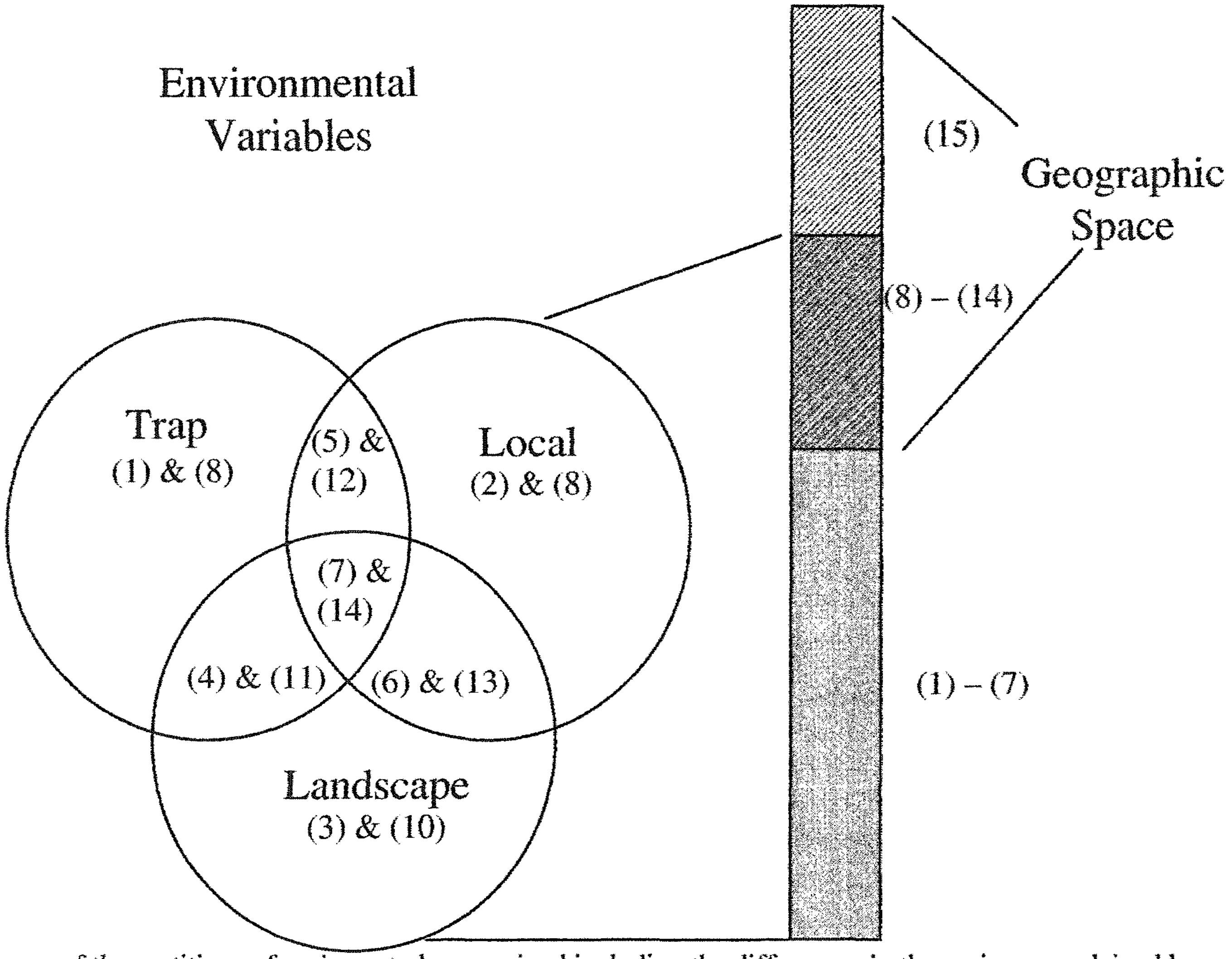


Figure 2.2: Diagram of the partitions of variance to be examined including the differences in the variance explained by geographic space or environmental variables, as well as the partitioning of environmental variables into three scales. The numbers in parentheses correspond to the proportions of variance that are explained by partial correspondence analysis as referred to in Table 2.4.

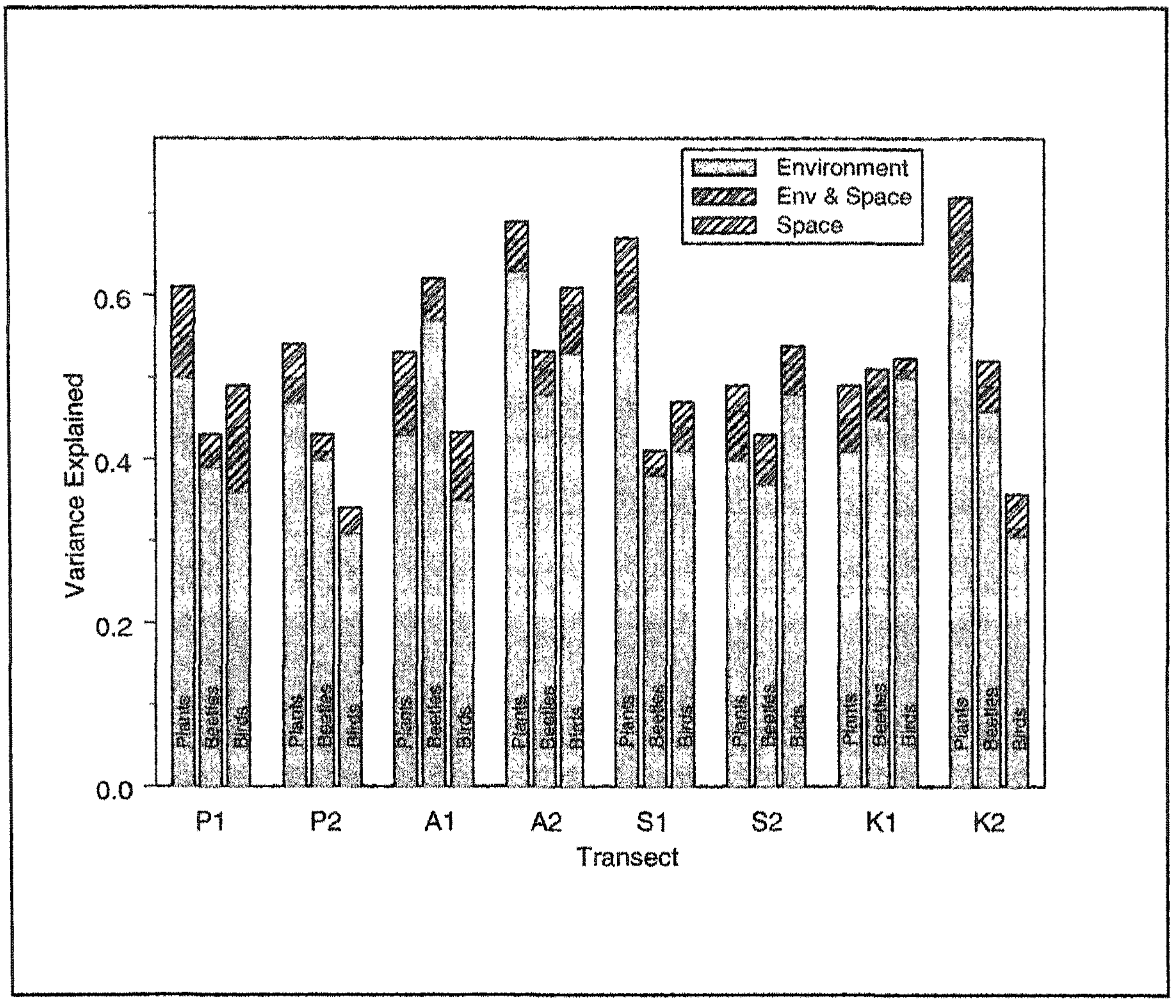
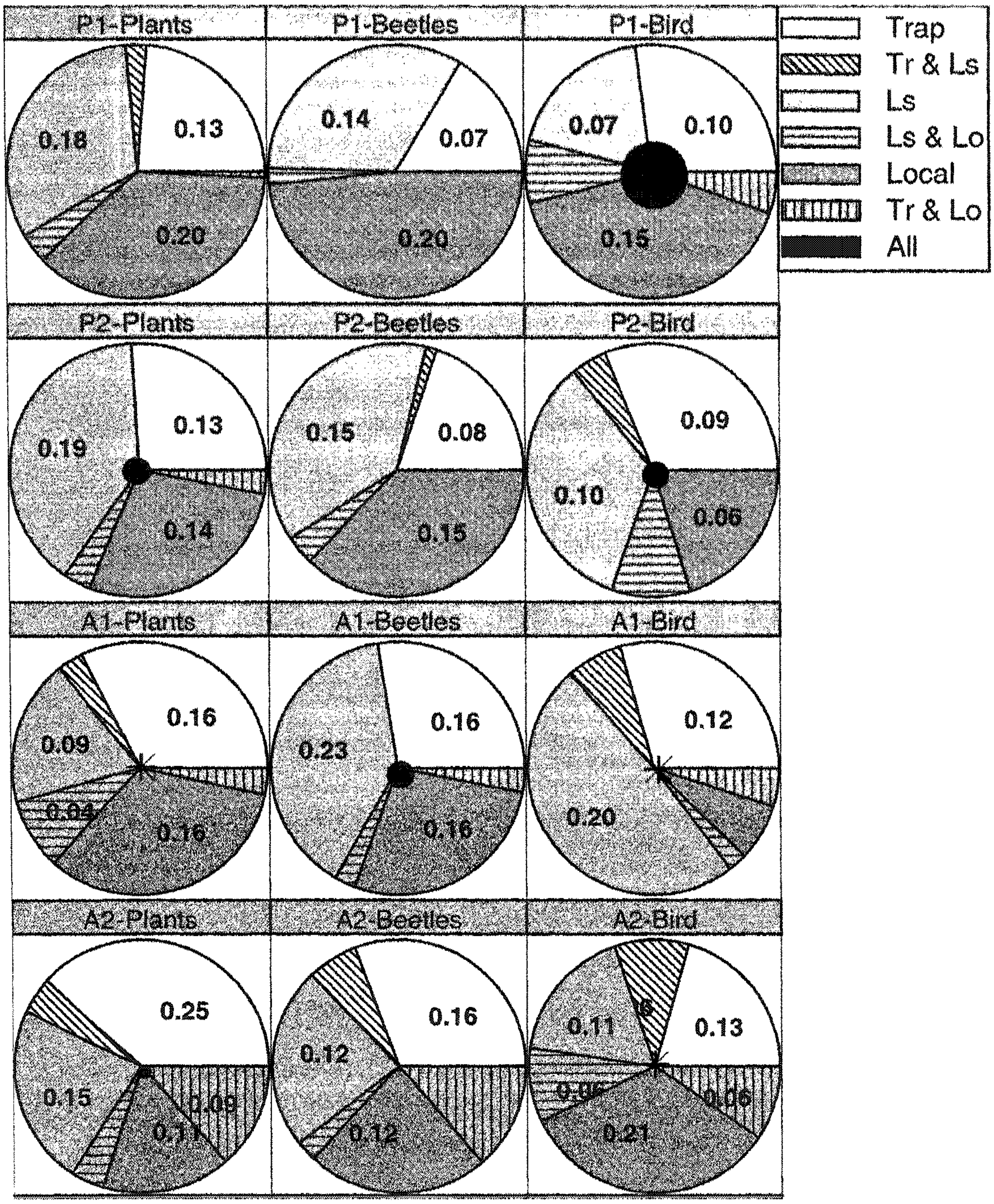


Figure 2.3: Amount of variance explained for plant, beetle, and bird communities at 8 transects using canonical correspondence analysis. The variance has been partitioned by environmental variables and geographic space. The transects are identified as P1/P2 - the Pawnee National Grasslands, Colorado, A1/A2 – the Fox Ranch, Colorado (Arikaree), S1/S2 - the Smoky Valley Ranch, Kansas, and K1/K2 – the Konza Prairie, Kansas.


P1-Plants
0.18
0.13
0.20
P1-Beetles
0.14
0.07
0.20
P1-Bird
0.07
0.10
0.15
Trap
Tr & Ls
Ls
Ls & Lo
Local
Tr & Lo
All
P2-Plants
0.13
0.19
0.14
P2-Beetles
0.15
0.08
0.15
P2-Bird
0.09
0.10
0.06
A1-Plants
0.16
0.09
0.04
0.16
A1-Beetles
0.16
0.23
0.16
A1-Bird
0.12
0.20
A2-Plants
0.25
0.15
0.09
0.11
A2-Beetles
0.16
0.12
0.12
A2-Bird
0.11
6
0.13
0.06
0.06
0.21

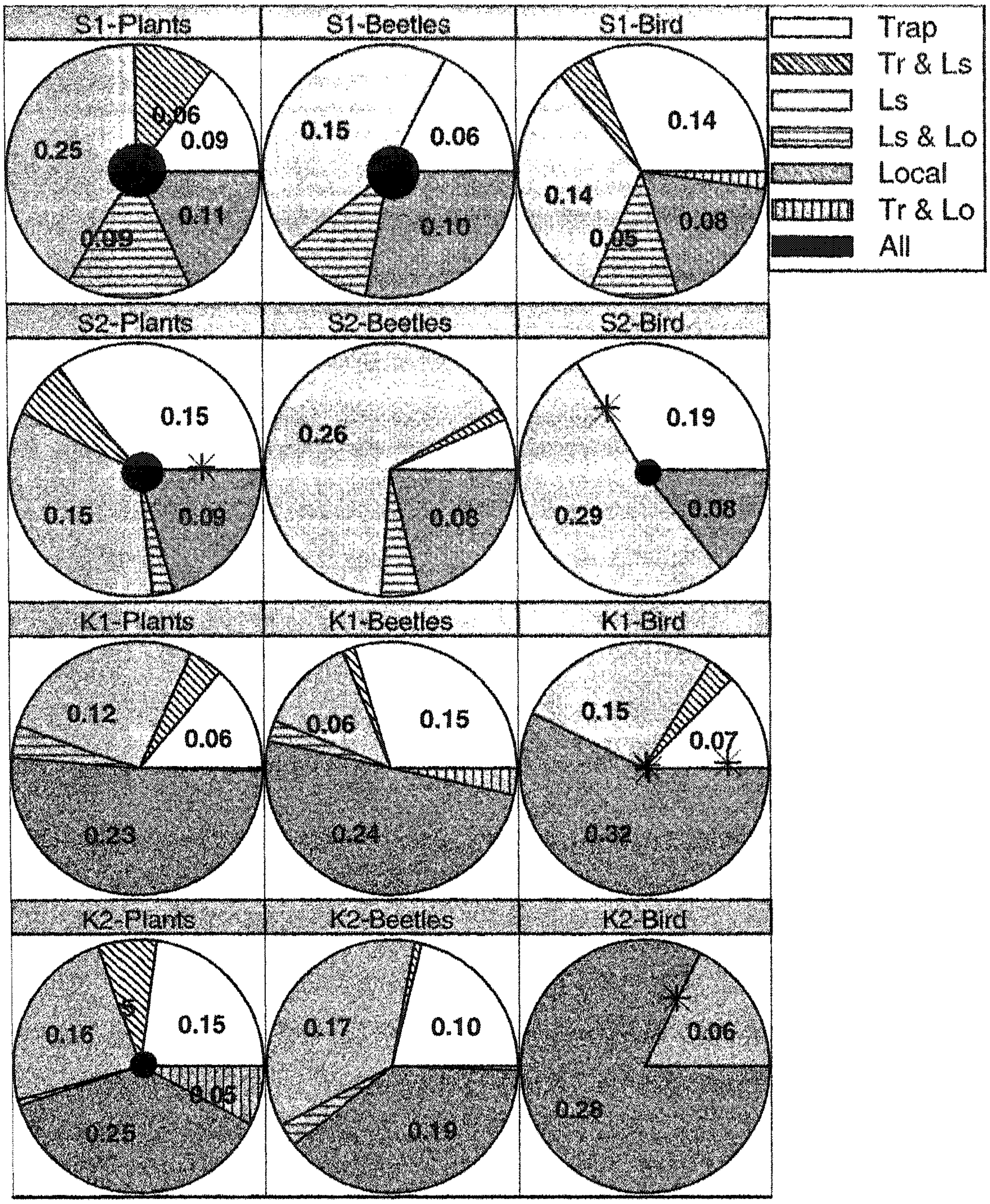


Figure 2.4: Amount of variance explained using hierarchical canonical variance partitioning for plant, beetle, and bird communities at 8 transects. The explained variance has been partitioned by the scale at which the environmental variables were measured. The scales at which environmental variables were measured were: trap (1 m^2), local (75 – 300 m^2) and landscape (900 m^2). The transects are identified as P, transects at the Pawnee National Grasslands, Colorado, A – transects at the Fox Ranch, Colorado (Arikaree), S - the transects at the Smoky Valley Ranch, Kansas, and K – transects at the Konza Prairie, Kansas. Asterisks (*) indicate locations in which there was negative variance. In all instances, the negative variance was less than 1% of the total variance explained.

CHAPTER 3: SPATIAL DEPENDENCE AND AUTOCORRELATION IN BEETLE, BIRD AND PLANT COMMUNITIES ACROSS A REGIONAL GRADIENT.

Abstract

The structure of a biotic community is inherently spatial for two reasons: spatial autocorrelation and spatial dependence. Spatial autocorrelation within communities can be produced by species interactions, such as competition, mutualism behavior or morphological factors, while spatial dependence results when a community is responding to aspects of the environment that are themselves spatially structured. For different taxonomic groups, the spatial autocorrelation and spatial dependence in community structure may also be influenced by the mobility of the organisms and the heterogeneity of the environment.

To elucidate how mobility and heterogeneity relate to the spatial structure of biotic communities, I conducted studies at four locations that span the moisture gradient defining the shift from shortgrass steppe to tallgrass prairie in the Great Plains of the United States. Along two 2-km transects at each site, I sampled ground-dwelling beetles, vascular plants, breeding birds, and environmental variables including soil texture, vegetation height, percent cover of shrubs, and values from Landsat TM 7 images. Using direct multi-scale ordination with canonical correspondence analysis, the structure of these communities was examined to determine the degree to which they were influenced by spatial autocorrelation or by spatial dependence. For the three taxonomic groups, particularly the beetles and plants, there was autocorrelation at fine scales in most transects. This fine-scale autocorrelation (< 200 m) is consistent with the potential mobility of beetles and plants. The patterns of autocorrelation also suggested that heterogeneity influenced the spatial structure of these communities in different ways across the four sites. The spatial structure in plant communities was primarily due to spatial dependence. Across all sites, 86% of the occurrences of spatial autocorrelation were accounted for by environmental variables. beetles and the birds the influence of spatial dependence decreased with increasing heterogeneity. Understanding the relationship between spatial dependence and spatial autocorrelation has direct relevance to the management of grassland communities.

Introduction

The spatial structure of a biological community can be manifest in two forms. First, spatial structure can be produced by interactions between organisms, such as competition, mutualism, behavior or morphologic traits (Tilman and Kareiva 1997, Dale 1999, Koenig 1999). Second, spatial structure can result when community members respond to aspects of the environmental factors that are themselves spatially structured (Rossi et al. 1992, Legendre 1993, Dale 1999). These two forms of spatial structure are termed *spatial autocorrelation* per se and *spatial dependence*, respectively (Legendre and Legendre 1998, Wagner 2003). Distinguishing between the effects of these two components of spatial structure may lead to a better understanding of the forces that structure biological communities.

Vegetation ecologists have developed statistical methods to explore the relationships between species composition and environmental factors (Whittaker 1967, ter Braak and Prentice 1988). Methods based on correspondence analysis (see Legendre and Legendre 1998) have been developed to accommodate the response of species to longer environmental gradients (e.g. Gauch 1982, Jongman et al. 1995) , the primary tool being canonical correspondence analysis(CCA, ter Braak 1986). The applicability of CCA has been expanded to enable partitioning variance into four components (Borcard et al. 1992), and more recently by Wagner (2003) with direct multiscale ordination (MSO), which provides a means to test for the existence of spatial dependence and residual autocorrelation in multivariate ecological data. MSO separates the spatial structure within a community into spatial dependence, which is explained by the explanatory variables, and residual spatial autocorrelation. The latter can be interpreted as the result of internal organization under the assumption that all relevant environmental factors have been included and measured at an appropriate scale. Prior to the development of this method, ordinations techniques were not adapted to the spatial paradigm that is emerging in ecology (Wagner 2003), i.e. the need to account for spatial structure or spatial autocorrelation.

One of the primary factors that can influence the spatial structure of a community is the mobility of organisms (Addicott et al. 1987, Wiens 1989). The spatial structure of plant communities, which are inherently sessile, is bound to be different from the spatial structure of very mobile organisms, such as birds. The structure of plant communities is highly dependent upon the location of resources. Mobile organisms, however, have the ability to respond to interactions with other organisms through moving, so their spatial distributions and the scales at which these distributions are expressed may be more immediately affected by interactions such as predation, competition or mutualism.

The spatial structure of a community is also influenced by the underlying environmental heterogeneity of a system (Kotliar and Wiens 1990, Milne 1991). In a homogenous environment (if such exists) the spatial distribution of organisms should reflect their interactions with other organisms. On the other hand, organisms in heterogeneous environments may respond more directly to the distribution of resources and the environmental matrix rather than to other organisms. The main problem is, thus, how to study the mobility of organisms without confounding it with the underlying environmental heterogeneity.

The study was conducted using three taxonomic groups of quite different mobilities: vascular plants, which are sessile, ground-dwelling beetles, which can move up to 5 m in 10 minutes in grassy habitat (Crist et al. 1992), to grassland birds which can easily range hundreds of meters in a minute. I selected four sites across a broad moisture gradient that encompassed a change from arid and relatively homogeneous to mesic and heterogeneous grasslands. This heterogeneity influences the distribution of resources that organisms are responding to (Kotliar and Wiens 1990) as well as influencing the movement patterns of different organisms (Crist et al. 1992, McIntyre 1997, McIntyre and Wiens 1999).

These two overarching factors, mobility and heterogeneity, provide the framework for this paper. Using this framework, the first goal is to determine the spatial structure of these three taxonomic groups across this moisture gradient. The second goal is to determine whether the spatial structure in the different taxonomic groups is due to spatial dependence or spatial autocorrelation per se. Finally, I determine whether these patterns change in a systematic fashion in relation to the broad gradient and to the varying mobilities of the different taxonomic groups.

Methods

Study Sites

This research was conducted at the Konza Prairie Long-Term Ecological Research site (LTER), Kansas; the Smoky Valley Ranch, Kansas and Fox Ranch, Colorado (Arikaree), both Nature Conservancy properties; and the Shortgrass Steppe LTER located within the Pawnee National Grasslands, Colorado (Fig. 3.1). These sites were selected because of their accessibility to research, because they represent locations that span a major environmental gradient, and because they are the locations of other regional research efforts. At each of these sites, two 2-km transects were established based on digitally available environmental data, including soil, topographic and vegetation maps (Table 3.1). The transects were established to encompass as much variation within the site as possible. The initial objective by which these transects were established was to determine gradients and thresholds in community composition within these sites. At several sites, transects encompassed uplands, valleys, and floodplains and on some occasions crossed streams. Along each transect, sampling stations were established every 50 m for a total of 40 sampling stations per transect. (More detailed descriptions of the transects can be found in Appendix I).

Biological data

Biotic data, including bird surveys, pitfall trapping for ground-dwelling beetles, and quadrat sampling of vegetation, were collected along each transect. At each sampling station, plant composition was surveyed in 1-m^2 quadrats during May and early June of 2002 to asses early season vegetation and August 2002 to incorporate late-season grasses and forbs. Within each quadrat, the abundance of each vascular plant species was recorded using seven cover classes (1 = <2%, 2 = 2 - 5%, 3 = 5 - 25%, 4 = 25 - 50%, 5 = 50 - 75%, 6 = 75 - 95%, 7 = 95 - 100%). These ordinal rankings were square-root transformed for use in analysis.

Beetles were sampled at each sampling location using pitfall traps during late May and early June 2000 and 2001. The pitfall traps (~8 cm diameter) were dug flush with the ground and allowed to settle for at least 10 days before sampling. The pitfall traps were then opened for 72 ± 2 h. Ethylene glycol was used as a killing and preserving agent in each pitfall trap. After 3 days, the traps were collected and taken into the laboratory for analysis. Beetles were counted and identified to morpho-species. Reference specimens for all the species from each site were pinned and labeled for consistency in identification. After all individuals had been examined at least twice, sample specimens of the most abundant families (Carabidae, Scarabaeidae, and Tenebrionidae) were sent to specialists to confirm identifications. Professors and students of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University identified all other beetle specimens to the lowest taxonomic level possible, typically to the level of genus.

Bird surveys were conducted along each transect to assess bird community composition. Each transect was surveyed once during the breeding seasons of 2000 and 2001. The surveys began at dawn and lasted approximately 3 h. The surveyors slowly walked each transect; when a bird was located and identified, visually or aurally, its location was determined by measuring the distance and angle from the surveyor to the bird as well as the distance to the next sampling station. Distance was measured using electronic range finders. Using this method (Buckland et al. 1993), the spatial location of each surveyed bird was defined and mapped. For analysis, each record was associated with the closest sampling location for the beetles and vegetation. This enabled the birds to be associated with the closest location where environmental variables were measured and not the location from which the bird was sighted.

For mobile organisms, such as beetles or birds, the effective area sampled by a pitfall trap or point surveys is difficult to assess due the different dispersal potentials or home ranges of different species. Also, for mobile organisms a complete census of the species present is rarely feasible. To more exhaustively portray the bird and beetles communities through time, the results from the 2 yr of sampling were combined. I considered joining the two years of data justified due to similarities in community structure across the two years based on canonical analysis. Both beetle and bird abundance data were transformed using the Napierian logarithm ([$y' = \ln(y + 1)$]) for analysis.

Environmental Data

At each sampling location along each transect, explanatory environmental data were collected at three scales. At the trap scale (1 m^2), I measured soil pH and texture, vegetation height, percent bare ground and soil hardness. For the three western sites, a hydrometer method was used to assess percent sand, silt and clay. The soil samples from Konza were analyzed by a private laboratory due to the high organic fraction in some of the samples. The mean and maximum of the vegetation height measured at each corner of the vegetation sampling quadrat were included in the analysis. Percent bare ground was estimated by visual assessment. The mean and standard deviation of soil hardness were calculated from four measurements obtained within each sampling quadrat.

At the local scale (10 m), I measured several aspects of the shrubs and cacti to assess their density and cover. Within a 5-m radius of each sampling location, I estimated the percent cover of each shrub and cactus species using seven cover classes (1 = <2%, 2 = 2 - 5%, 3 = 5 - 25%, 4 = 25 - 50%, 5 = 50 - 75%, 6 = 75 - 95%, 7 = 95 - 100%). For analysis, these ordinal rankings were converted to presence-absence data for analysis. Within a 30-m radius I measured the distance to the nearest cactus, shrub (<1 m in height), and large shrub / tree (1-3 m in height).

At a regional scale (30 m), I acquired satellite (Landsat 7 TM) imagery and digital elevation models (USGS 1998). The Landsat 7 images for each of the sites were taken in either May or June of 2000. The imagery and DEMs had 30 m^2 resolution. Based on the DEMs, I calculated elevation, slope and aspect. Considering the inappropriateness of using a single number to define aspect within a regression (i.e. 5 degrees and 355 degrees are only 10 degrees apart and not 250 degrees), two values for aspect were calculated: degrees from north and degrees from west. Using a GIS (ESRI 2002), I assigned all the Landsat band values (1-5, 6a, 6b, 7-8), elevation, aspect values, and slope to each sampling location.

The environmental variables were subjected to a forward selection process based on the amount of variance in community composition the variables explained. A selection process was necessary due to the fact that more environmental variables were measured than there were observations, which would violate the rules of CCA. Each variable was independently included in a CCA with each taxonomic group. The variable that explained the most variance was then tested for significance using an ANOVA-like permutation test (anova.cca in the vegan library of the statistical language R version 1.6.1), which tests for the joint effect of constraints in CCA (Legendre and Legendre 1998). The variable was selected if the p-value was less than 0.15 based on a pseudo F statistic. A liberal test statistic of 0.15 was used due to the ability of CCA to handle numerous, intercorrelated-explanatory variables. After the initial explanatory variable was selected using the previous method, the remaining variables were each combined with the initial variable and tested for the amount of variance explained. Again the variable that increased the explained variance by the largest amount was retained and tested for significance. Variables were added to the list to be included in the analysis until no more variables could be added that were significant. The environmental variables selected for each taxonomic group are listed in Table 2.5 of Chapter 2.

Statistical Analysis

For each transect I analyzed the beetle, bird, and plant community structure using multi-scale ordination with canonical correspondence analysis (MSO, Wagner 2003). MSO allows the partitioning by distance and the geostatistical interpretation of ordination results (Fig. 3.2). Separate multi-scale ordinations with CA and CCA were conducted for each combination of transect and taxonomic group to determine the degree of spatial autocorrelation per se and spatial dependence of the ground-dwelling beetle, breeding bird and vascular plant communities. The spatial partitioning of CA shows the total spatial structure in the community data. MSO of CCA results shows the spatial structure attributed to spatial dependence (explained or constrained variance) and to spatial autocorrelation (residual or unconstrained variance). A permutation test (R = 100, alpha = 0.1), as implemented in the R function "mso", was used to test for autocorrelation of the total variance (CA) and of the residual variance (CCA) for each distance class.

The mobility of organisms and the heterogeneity of the matrix in which the organisms live may both influence the spatial structure of communities, therefore I developed three primary questions to structure the analyses. First, at what scales are the different taxonomic groups showing significant autocorrelation (alpha = .01) and are these scales related to the mobility of these groups? I expected that plants would be significantly autocorrelated at the finest scales, with beetles at broader scales and birds at even broader scales. Second, is the spatial structure exhibited by these taxonomic groups a result of spatial dependence or spatial autocorrelation per se? With the increase in heterogeneity from the west to the east, I expected the patterns of spatial structure to be dominated by species interactions (spatial autocorrelation per se) in the more homogeneous sites and spatial dependence to be more prevalent at the eastern, more heterogeneous sites. Finally, are there systematic differences between the taxonomic groups in whether spatial structure can is best explained by spatial autocorrelation per se or spatial dependence? Due to the sessile nature of plants, I expected that the spatial structure in plant communities would be predominately a result of spatial dependence. On the other hand, because of the ability of birds and beetles to responds to interactions and environmental conditions with movement, I expected that their spatial structure would be more dominated by spatial autocorrelation per se than by spatial dependence.

To examine these trends in a more general way, the number of scales that were significantly autocorrelated were combined across transects to assess if the spatial structure of these communities was due to spatial dependence or spatial autocorrelation per se (Table 3.2). I also divided these results into the western sites, Pawnee and Arikaree, and the eastern sites, Smoky Valley and Konza (Table 3.2).

Results

To demonstrate the results of an MSO analysis, I explain an analysis of vascular plants along transect A1 in detail (Fig. 3.2). Figure 3.2A shows the overall spatial structure in the community data of the vascular plants of transect A1, i.e. the results of a CA partitioned by distance. Notice that there is significant autocorrelation from 50 – 250 m. Only the first 1000 m of the variance structure is shown in this figure due to the small sampling size above this scale, which confounds the interpretation just as in the analysis of a typical variogram (Rossi et al. 1992). Figure 3.2B shows the results of constraining the plant community of A1 by the selected environmental variables, i.e. the results of a CCA partitioned by distance. This figure has several key features that describe the spatial structure of this community. First, the variance explained by the environmental variables is shown. Second, the residual variance in the spatial structure of the community after accounting for environmental variables is shown along with the scales at which the residuals are significantly autocorrelated. In this figure there was significant autocorrelation at distances of 100 m, 250 m and 850 m. Notice that compared to Figure 3.2A, there is no longer significant autocorrelation at distances of 50 m, 150 m and 200 m. This suggests that the spatial structure at these three scales was explained by the environmental variables (spatial dependence). On the other hand, the significant residual autocorrelation at 100 m and 250 m suggests that this spatial structure was due to the interaction of organisms, assuming that all the influential environmental variables have been included in the analysis. The emergence of autocorrelation at 850 m after accounting for the environmental variables suggests that there was spatial autocorrelation among the organisms within this community that was masked by the patterns of the environmental variables. Figure 3.2B also includes a confidence interval of the total variance in the community composition

The equivalent of these two figures was created for each transect by community group. To simplify comparisons of these figures across communities and transects, only certain aspects of these graphs are shown. As in Figure 3.2A, Figure 3.3 depicts the variance and significant autocorrelation in overall community structure for each of the eight transects and three taxonomic groups. The residual variance and autocorrelation, after accounting for environmental variables, in each community by transect group is shown in Figure 3.4.

The spatial structure in plant communities across the eight transects shows that there was significant autocorrelation at fine scales (<200 m) along most transects, with occasional significant autocorrelation at broader scales (Fig. 3.3). At Pawnee, there was significant autocorrelation in plant community structure along both transects at the finest scale measured (50 m). These two transects differed, however, in the patterns at broader scales. Along transect P1, the majority of the significant autocorrelation was at fine scales, while along transect P2 significant autocorrelation was detected at scales ranging from 450 m to 750 m. Similar to transect P1, significant autocorrelation at the two transects at Arikaree was only detected at scales less than 400 m. At Smoky Valley, there was again significant autocorrelation at fine scales, but there was also some significant autocorrelation for plants at broader scales along transect S2. This pattern of significant autocorrelation at fine and broad scales was consistent within the two transects at Konza as well.

The patterns of spatial structure for beetles were very similar to those of plants at many transects, particularly at Pawnee and Arikaree. At the four transects at Pawnee and Arikaree the patterns of significant autocorrelation for beetles were almost identical to the patterns of the plants. These similarities did not hold at Smoky Valley and Konza. At Smoky Valley, there was significant autocorrelation at fine scales for beetles, but not at as many scales as the plants. The beetles also showed more significant autocorrelation at broader scales than did the plants. The beetles along transect S1 showed significant autocorrelation at scales of 550 m and 950 m and from 750 to 950 m along transect S2. At Konza, beetles were only significantly autocorrelated at scales <200 m along transect K1 and at scales of 50 m and 550 m along transect K2.

The spatial structure of the bird communities varied from transect to transect and rarely coincided with the patterns displayed by the other two taxonomic groups. The only noticeable pattern was that the bird communities showed autocorrelation at fewer scales across almost all transects than did either the beetle or plant communities. The only exception to this was transect S1, where beetles and plants were only significantly autocorrelated at three scales, while the bird community was significantly autocorrelated at five scales, including 100 to 200 m, 350 m and 1000 m.

Significance in the residuals for a community after accounting for environmental variables suggests spatial autocorrelation per se due to the interaction of organisms (Fig 3.4). The lack of significance at scales in which there was significance in the overall community structure (Fig. 3.3) suggests that the spatial structure that was evident in Figure 3.3 was accounted for by the environmental variables and thus due to spatial dependence. Along transect P1, the spatial structure that existed at fine scales for plants in the overall community structure was explained by the environmental variables, suggesting that the autocorrelation that existed at fine scales for plants was due to spatial dependence. At a few broader scales, however, the plants show significant autocorrelation in the residuals.

Beetles showed significant autocorrelation at fine scales along transect P1, with the addition of significant autocorrelation at scales of 350 m and 500 m. Along transect P2, almost all the significant autocorrelation that existed in the overall community structure in both plants and beetles was accounted for when these communities were constrained by the environmental variables.

As in transect P2, the significant autocorrelation in community structure for all taxonomic groups within the transects at both Arikaree and Smoky Valley was mostly accounted for when the variance in community structure was constrained by the environmental variables. This is exemplified by transect A2, where both beetles and plants had significant autocorrelation at scales ranging from 50 m to 350 m. After accounting for the environment, there was only a single scale less than 400 m for both plants and beetles that was significantly autocorrelated. Along transect S2, the broad-scale autocorrelation in community structure of the beetles was accounted for by the environmental variables, although, there was considerable autocorrelation in the residuals at scales less than 300 m.

At Konza, there were considerable differences in the spatial patterns displayed by the plant communities along the two transects. Along both transects, there was spatial autocorrelation in community structure at both fine (<200 m) and broad scales (700 – 900 m). After accounting for the environmental variables, however, there were only three scales that showed significant autocorrelation along transect K1, whereas there were seven scales that were significantly autocorrelated along transect K2. The scales that showed significant autocorrelation in overall plant community structure along transect K1 were all accounted for by the environmental variables. For birds at Konza, there was very little significant autocorrelation, especially along transect K2, where there were no scales at which the birds were significantly autocorrelated. The significant autocorrelation that existed for birds along transect K1 was not accounted for by the environmental variables, suggesting that it was a result of the interaction of the species.

When all the sites were combined the primary difference between the three taxonomic groups was that the plants were significantly autocorrelated at 40% more scales than either the beetles or the birds (Table 3.2). When considering the proportion of that autocorrelation that is explained by the environment, however, the difference is not significant (p=0.12). For plants, 86% of the significant autocorrelation in community structure could be attributed to spatial dependence. This pattern generally holds true at the two Arikaree transects and Pawnee, where for all three taxonomic groups at least 83%

of the significant autocorrelation in community structure was due to spatial dependence. There was a greater difference among taxonomic groups at Smoky Valley and Konza. At these sites, the significant autocorrelation in plant community composition was explained by the environmental variables 88% of the time. For beetles and birds, the environmental variables explained 71% and 60% of the significant autocorrelation, respectively.

Discussion

Accounting for spatial structure within communities, whether it is a result of spatial dependence upon environmental variables or the result of interactions between organisms (i.e. spatial autocorrelation per se) can help understand the influence of mobility and heterogeneity upon the structure of biological communities. This has implications for understanding how organisms respond to their environment, as well as the

The first question that I examined using MSO with CCA was whether or not the mobility of a taxonomic group influenced the scale at which these communities were spatially structured. When examining the differences in scale at which these three taxonomic groups are significantly autocorrelated, the only scale where there was an obvious difference between any groups was at the finest scale of analysis, 50 m. At this scale, along all eight transects, there was significant autocorrelation (Fig. 3.3) for plants, the beetles were significantly autocorrelated at seven of these transects, but the birds were only significantly autocorrelated at two of the transects. This supports the hypothesis that plants and beetles will be significantly autocorrelated at finer scales than birds. A scale of 50 m may be too broad to capture the internal organization within plant and beetle communities. At the next broader scale, the birds were significantly autocorrelated at half of the transects, suggesting that a scale of 100 m may be more indicative of the scale at which the bird communities are spatially structured.

The second question I asked addressed the potential for the heterogeneity of a site to influence the patterns of spatial dependence and spatial autocorrelation per se for three taxonomic groups. Across the moisture gradient from Pawnee to Konza, the most obvious pattern was the differences in the spatial structure of the vascular plants and ground-dwelling beetles. Within the transects at Pawnee and Arikaree, plants and beetles had very similar patterns of overall spatial structure. This trend was particularly evident at Arikaree, where both taxonomic groups were spatially autocorrelated at the same five scales along transect A1 and at six scales along transect A2. This coherence of patterns did not hold up along the transects of Smoky Valley and Konza.

The correspondence of patterns at Arikaree and Pawnee between plants and beetles suggests that similar processes or mechanisms maybe structuring these two communities. If this is the case, then the significant autocorrelation of these two communities should be accounted for by the same factors, either spatial dependence or spatial autocorrelation per se. For both plants and beetles, over 80% of the scales showing significant autocorrelation in their overall community structure were accounted for by the environmental variables (Table 3.2), indicating that both communities show strong spatial dependence along these transects. Both taxonomic groups, however, did have significant autocorrelation in the residuals of the CCA analyses (Figure 3.4) that does not follow similar patterns for the two taxonomic groups. This was most evident along transect P1, where there was significant spatial autocorrelation for beetles at three scales less than 250 m, whereas plants are only significantly autocorrelated at one scale in this range. The spatial dependence at transect P1 fits with the prediction that in an relatively homogenous landscape communities will be structured more by spatial dependence than by spatial autocorrelation per se. At Pawnee (Dodd et al. 2002) and in semi-arid systems in general (Sala et al. 1997), vegetation is known to be strongly correlated with soil texture and soil moisture. The existence of greater autocorrelation in the beetle community after accounting for the environmental variables suggests a response due to the interactions of the beetles. Beetle movements (and thus distributions) have been shown to be influenced by directed behavior at Pawnee, which was demonstrated for three species of darkling beetle (Tenebrionidae: *Eleodes*; Crist et al. 1992).

The differences in patterns in spatial structure between beetles and plants along the eastern transects suggests that these communities may be responding to the environmental heterogeneity of these sites in different ways. Konza prairie is the most heterogeneous site I sampled in terms of elevation changes as well as in complexity of vegetation structure, particularly when looking at the quantity and diversity of shrubs. Chapter II describes a method for quantifying heterogeneity based on Landsat imagery and clearly showed the increase in heterogeneity across the gradient I sampled. At Konza the overall plant communities of the two transects were spatially autocorrelated at both fine- (< 200m) and broad- (800-900m) scales (Fig. 3.3). This spatial autocorrelation was accounted for by the environmental variables indicating spatial dependence (Fig. 3.4).

Again, however, as at Pawnee, there were several scales at which the residuals of the CCA analysis were significantly autocorrelated that were not autocorrelated in the overall community analysis. The broad scale patterns of autocorrelation at Konza may correspond to the scale of the hills and valleys that are present along the two transects.

The third question I addressed was whether there were systematic differences between the taxonomic groups in terms of the proportion of the significant autocorrelation that existed in the overall community that could be attributed to spatial dependence or spatial autocorrelation per se. The expectations were that the vascular plants would tend toward spatial dependence, while the more mobile taxonomic groups would be dominated by spatial autocorrelation. To address this question I combined the results for each taxonomic group across all transects, as well as, within eastern and western sites. The results shown in Table 3.2 suggest that across all sites there is little difference between the taxonomic groups in terms of the proportion of the spatial structure in community composition that is explained by spatial dependence. However, when I compared the eastern sites and the western sites there was more significant autocorrelation in beetles and birds in western sites compared to the plants. This supports the expectation that the spatial structure of plant communities was structured more by spatial dependence in comparison to more mobile taxonomic groups, such as beetles and birds.

Literature Cited

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods - scaling environmental patterns. Oikos **49**:340-346.

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

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman & Hall. New York.

Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes - an experiment with *Eleodes* beetles in shortgrass prairie. Functional Ecology **6**:536-544.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge.

Dodd, M. B., W. K. Lauenroth, I. C. Burke, and P. L. Chapman. 2002. Associations between vegetation patterns and soil texture in the shortgrass steppe. Plant Ecology **158**:127-137.

ESRI. 2002. ArcGIS version 7.1. ESRI, Redlands, CA.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press. Cambridge.

Jongman, R. H., C. J. F. ter Braak, and O. F. R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press. Cambridge.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution **14**:22-26.

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

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

Legendre, P., and L. Legendre. 1998. Numerical ecology, 2nd English edition. Elsevier Science B.V. Amsterdam,

McIntyre, N. E. 1997. Scale-dependent habitat selection by the darkling beetle *Eleodes hispilabris* (Coleoptera: Tenebrionidae). American Midland Naturalist **138**:230-235.

McIntyre, N. E., and J. A. Wiens. 1999. How does habitat patch size affect animal movement? An experiment with darkling beetles. Ecology **80**:2261-2270.

Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscapes. Pages 69-84 *in* T. F. H. Allen, editor. Ecological Heterogeneity. Springer-Verlag, New York.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs **62**:277-314.

Sala, O. E., W. K. Lauenroth, and R. A. Golluscio. 1997. Plant functional types in ternerpate semi-arid regions. Pages 217-233 *in* F. I. Woodward, editor. Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge.

ter Braak, C. J. F. 1986. Canonical correspondence analysis - a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research **18**:271-317.

Tilman, D., and P. M. Kareiva. 1997. Spatial ecology : the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.

USGS. 1998. U.S. Geological Survey DEM 7.5 Quadrangel. U.S. Geological Survey, Reston, VA, USA.

Wagner, H. H. 2003. Direct multiscale ordination with canonical correspondence analysis. Ecology.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Reviews of the Cambridge Philosophical Society **42**:207-264.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385-397.

Table 3.1: Site descriptions, including location, average precipitation and dominant vegetation.

Site	State	County	Latitude	Longitude	Average Precipitation	Dominant Vegetation
Pawnee National Grasslands Long Term Ecological Research Station	Colorado	Weld	40°47′N	104°42′W	320 mm	*Bouteloua gracilis* *Buchloe dactyloides*
Fox Ranch (Arikaree) The Nature Conservancy	Colorado	Yuma	39°44′N	102°28′W	448 mm	*Bouteloua gracilis* *Stipa comata*
Smoky Valley Ranch The Nature Conservancy	Kansas	Logan	38°50′N	100°58′W	533 mm	*Artemesia filifolia* *Bouteloua gracilis*
Konza Prairie Long Term Ecological Research Station	Kansas	Riley	39°04′N	96°34′W	835 mm	*Andropogon gerardi* *Sorghastrum nutans*

Table 3.2: The number of scales at which the three different taxonomic groups were significantly autocorrelated across all transects, within the western transects and within the eastern transects. I report the number of time these communities were significantly autocorrelated after a canonical analysis was conducted (SA after CA, from Figure 3.3), the number of these occurrences of autocorrelation that were explained by environmental variables (Explained), suggesting spatial dependence, and the total number of scales at which these taxonomic groups were significantly autocorrelated after accounting for the environment (SA after CCA), suggesting spatial autocorrelation per se.

		SA after CA	Explained	SA after CCA
All Sites	Plants	50	43	24
	Beetles	35	28	23
	Birds	22	17	18
Western Sites	Plants	24	20	10
	Beetles	21	18	11
	Birds	12	11	8
Eastern Sites	Plants	26	23	12
	Beetles	14	10	12
	Birds	10	6	10

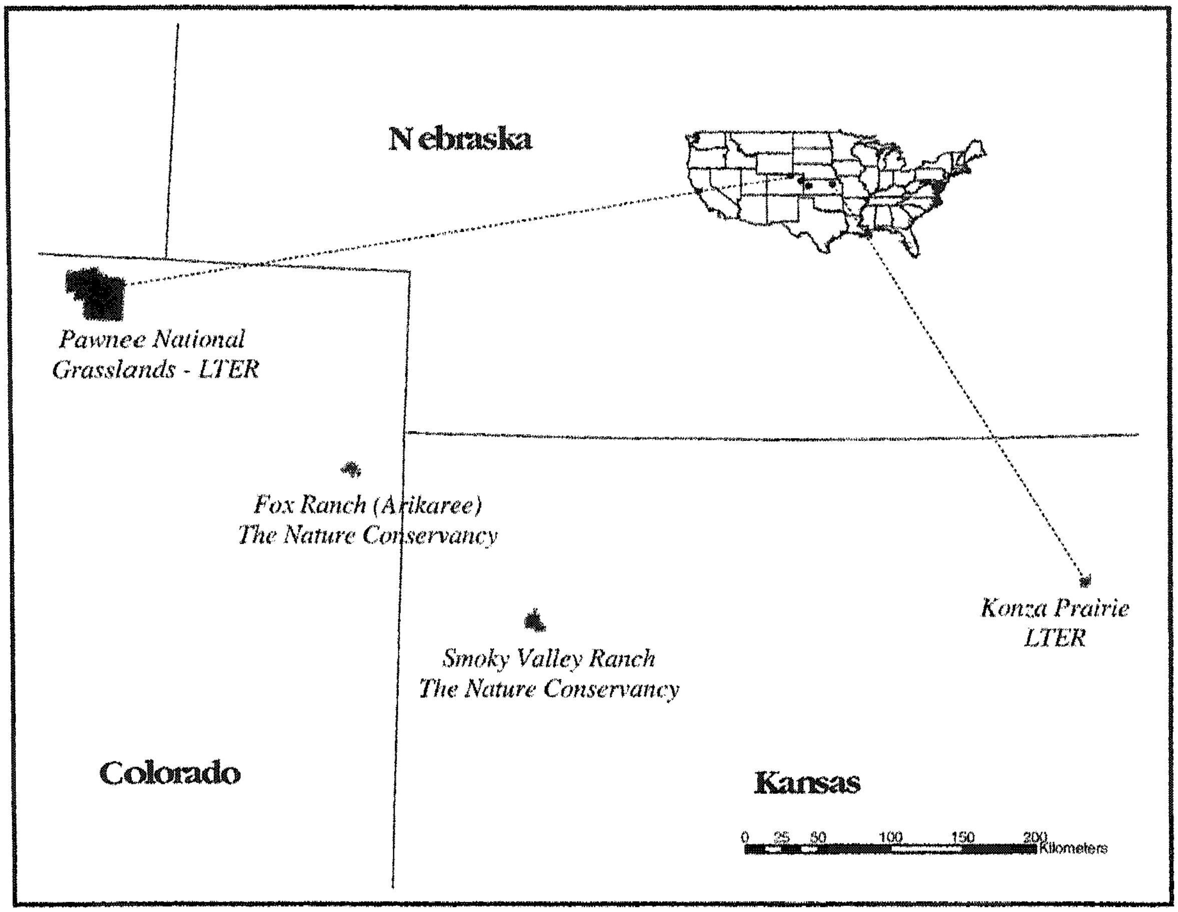


Figure 3.1: Study Sites

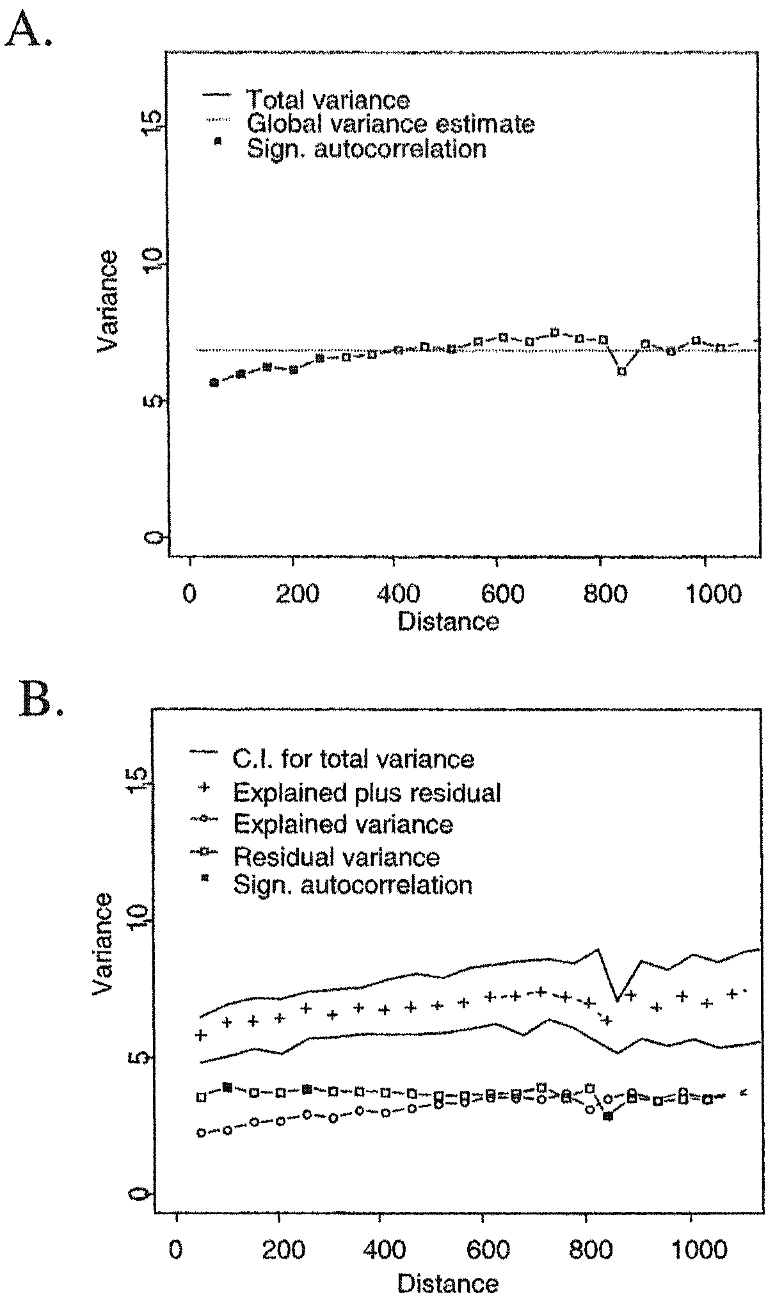


Figure 3.2: An example of the results of a multi-scale ordination with CCA using the plant community of transect A1 at Arikaree. Figure 3.2A shows the variance in plant community composition partitioned by distance after a canonical analysis. The solid squares indicate scales at which the variance in community composition is significantly (alpha <= 0.10) autocorrelated. Figure 3.2B represents results of a MSO. The circles indicate the variance in community composition explained by environmental variables. The squares represent the residual variance in community composition after accounting for the environmental variables. The solid squares indicate scales at which there is significant autocorrelation in the residuals. The crosses are the sum of the explained and residual variances. The solid lines indicate the 95% confidence interval of total variance.

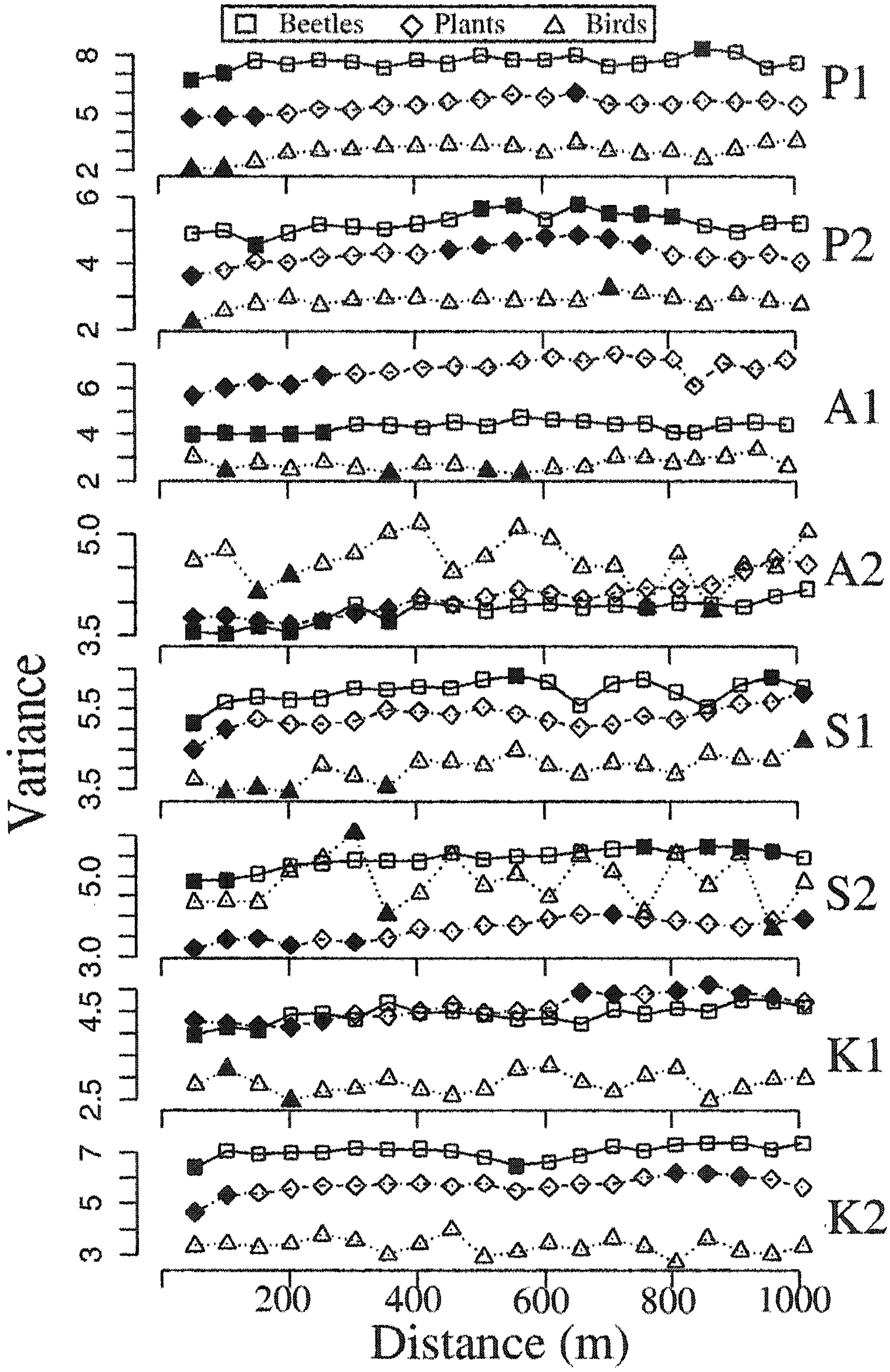


Figure 3.3: The results of CAs partitioned by distance, for beetle (squares), bird (triangles) and plant (circles) communities of eight transects at four sites: Pawnee National Grasslands, Colorado; Arikaree, Colorado; Smoky Valley Ranch, Colorado and Konza Prairie, Kansas. The solid symbols indicate significant autocorrelation ($\alpha <= 0.10$) within community structure at that particular distance class or scale.

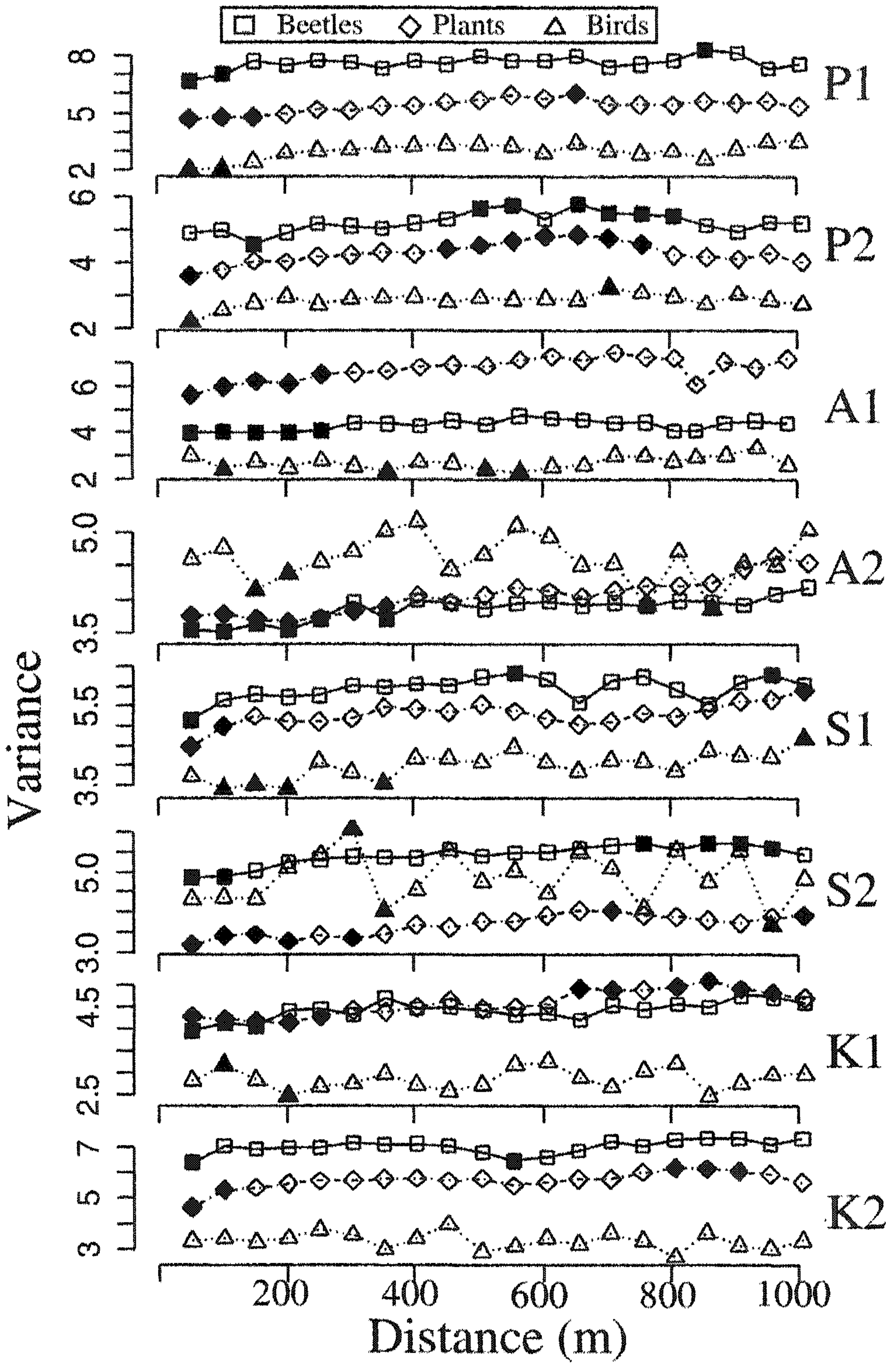


Figure 3.4: Results of multi-scale ordinations with CCA for beetle (squares), bird (triangles) and plant (circles) communities along eight transects at four locations: Pawnee National Grasslands, Colorado; Arikaree, Colorado; Smoky Valley Ranch, Colorado and Konza Prairie, Kansas. The symbols indicate the residual variance in community structure after the community structure has been constrained by environmental variables, i.e. subjected to a CCA. The solid symbols indicate significant autocorrelation ($\alpha <= 0.10$) within these residual values at that particular distance class or scale.

CHAPTER 4: PREDICTING BIODIVERSITY ACROSS A REGIONAL GRADIENT.

Abstract

Understanding how species richness varies with scale and among habitats is essential to conserving and managing biodiversity. I examine the scale-dependent relationships between species richness and habitat heterogeneity by addressing three questions: 1) Can species-accumulation curves be predicted at specific locations as well as across a region using area sampled and heterogeneity as explanatory variables?; 2) Can species-area-heterogeneity relationships developed across a region be used to predict the scale-dependent patterns of species richness at a specific location?; and 3) Does the incorporation of an objective measure of heterogeneity, such as spectral variance, improve the predictability of species-accumulation curves? To address these questions, I surveyed breeding bird, ground-dwelling beetle and vascular plant communities along two 2-km transects at each of four sites in 2000 and 2001. The sites span the transition from short-grass steppe to tallgrass prairie in Colorado and Kansas. The species-accumulation curves of these transects were modeled using three alternative models based on area, heterogeneity and the interaction between area and heterogeneity. The results show that along specific transects individual species-accumulation curves are highly correlated with both area and heterogeneity ($r^2 > 0.73$). When data were combined across the entire region, the ability of heterogeneity to explain the variance in these

relationships was drastically reduced ($r^2 < 0.43$), while area was still highly correlated ($r^2 > 0.73$) for all taxonomic groups. Incorporating heterogeneity, as measured here, into models did not improve the ability to predict species-accumulation curves across a region. Despite this, spectral variance provides one objective measure of heterogeneity, which can be used to model species richness on a local scale.

Introduction

Biodiversity preservation has become the primary goal of conservation biology (Noss 1990, Rosenzweig 1999, Myers et al. 2000) and of conservation organizations such as The Nature Conservancy and Conservation International. Considering the vast number of preserves and number of species that occur at these locations, quick and reliable assessments of biodiversity would significantly enhance efforts to preserve biodiversity (Oliver and Beattie 1993). Both area and habitat heterogeneity have been used as predictors of species-accumulation curves.

The increase in species number with area has been demonstrated in hundreds of studies (Rosenzweig 1995, Lomolino 2001). The species-area relationship has been used as a means to estimate the biodiversity of large regions (Williams 1964, May 1988, Palmer 1990), as a means for designing preserves (Terborgh 1974, Diamond and May 1981) and as the central focus of the SLOSS (Single Large Or Several Small) debate (Terborgh 1974, Simberloff and Abele 1976, Wilcox 1980, Simberloff and Abele 1982, Boecklen 1986).

The importance of habitat heterogeneity in determining species richness within a site has also long been a focus of species-accumulation studies, since the number of habitats often increases as a function of area (MacArthur and MacArthur 1961, Williams 1964, Whittaker 1998). Thus, considerable effort has been made to test and separate the effects of area and habitat heterogeneity upon species richness (e.g. Williams 1964, Kitchener et al. 1980a, Kitchener et al. 1980b, Boecklen and Gotelli 1984, Ricklefs and Lovette 1999, Tjorve 2002, Johnson et al. 2003). The interaction between area and habitat has also been used to fit species-accumulation curves more accurately. Triantis et al. (2003) indicate that the incorporation of the number of habitat types increases the variance explained in almost all studies reviewed.

The unfortunate aspect of the term "habitat" and how it has been used in most assessments of species-area-habitat relationships is that "habitat" is often viewed from the perspective of a single taxonomic group (Ricklefs and Lovette 1999) and as a categorical variable. "Habitat" has been quantified in several ways in order to predict species richness, including soil type (e.g. Simberloff and Gotelli 1984, Le Brocque 1998, Wohlgemuth 1998), elevation (Picton 1979, Rahbek 1997), and vegetation type (e.g. Kohn and Walsh 1994, Ricklefs and Lovette 1999, Triantis et al. 2003). Classifying habitat, however, results in a loss of information corresponding to continuous changes in an environmental variable or in heterogeneity.

Because of the difficulties in defining habitat heterogeneity (Simberloff 1976), I have attempted to measure environmental heterogeneity in a more objective way that is not tailored to a specific taxonomic group, does not infer a particular "habitat" type, and can be used to assess heterogeneity at a variety of scales. Boecklen (1986) used principal component analysis to generate an objective value of heterogeneity, although there was still only a single value of heterogeneity for a particular site. Within a particular site, it has been proposed that there is a link between spectral heterogeneity and biodiversity, which was termed the spectral variation hypothesis (Palmer et al. 2000, Palmer et al. 2002) This suggests that heterogeneity within an image, such as a Landsat 7 TM band or Normalized Difference Vegetation Index (NDVI), can be used as a measure of habitat heterogeneity. Variation within the image measured with different window sizes reflects heterogeneity at several scales, permitting an analysis of the effects of environmental heterogeneity to be measured at fine or broad scales.

Habitat-area relationships are known to be excellent predictors of species richness for entire regions (e.g. Williams 1964, Abbott 1978, Palmer 1990). Most predictions based on species-area relationships are based on predicting the total number of species at a location. For example, the number of species on different sized islands could be modeled using the species-area relationship and then used to predict the number of species on other islands. This method, however, does not predict the species accumulation curves that occur within each island. Having the ability to predict not only the total number of species within a region, but also the form of the species accumulation curves within a location, can provide insight into the influence of area and heterogeneity upon species richness. Here, I assess how well area and habitat heterogeneity predict species richness across scales at a location, based on relationships derived from several other locations.

The primary questions addressed in this paper are: 1) Can species accumulation curves be fit at specific locations as well as across a region using area and heterogeneity? 2) Can species-area-heterogeneity relationships developed across a region be used to predict the scale-dependent patterns of species richness of a specific location? and, 3)

Does the incorporation of an objective measure of heterogeneity, such as spectral variance, increase the variance explained by species accumulation curves? To answer these questions I studied three taxonomic groups, birds, ground-dwelling beetles and plants, at four locations along the moisture gradient that defines the transition from shortgrass steppe in eastern Colorado to the tallgrass prairie in central Kansas.

Methods

Study Sites

This research was conducted at the Konza Prairie Long-Term Ecological Research site (LTER); the Smoky Valley and Fox Ranches (Arikaree), both Nature Conservancy properties; and the Short-grass Steppe LTER located within the Pawnee National Grasslands (Fig. 4.1). At each of these designated sites, two 2-km transects were established based on digitally available environmental data, including soil, topographic and vegetation maps. The transects were established to encapsulate as much of the variation that exists within the site as possible. At several sites, transects encompassed uplands, valleys, and floodplains and on some occasions crossed streams or rivers. Along each transect, sampling stations were established every 50 m for a total of 40 sampling stations per transect. Table 4.1 lists the location, dominant vegetation and precipitation information for these five sites. (More detailed descriptions of the transects can be found in Appendix I).

Biological data

Biotic data, including bird surveys, pitfall trapping for ground-dwelling beetles, and quadrat sampling of vascular plants, were collected along each transect. At each sampling station, plant species presence was surveyed within a 1-m^2 quadrat during May and early June 2000 to assess early-season vegetation and August 2000 to incorporate late-season grasses and forbs.

Beetles were sampled at each sampling location using pitfall traps during late May and early June 2000 and 2001. The pitfall traps (~ 8 cm diameter) were dug flush with the ground and allowed to settle at least 10 days before sampling. The pitfall traps were then opened for 72 ± 2 h. Ethylene glycol was used as a killing and preserving agent in each pitfall trap. After 3 days, the traps were collected and taken into the laboratory for analysis. Beetles were counted and identified to morpho-species. Reference specimens for all the species from each site were pinned and labeled for consistency in identification. After all individuals had been examined at least twice, sample specimens of the most abundant families (Carabidae, Scarabaeidae, and Tenebrionidae) were sent to specialists to confirm identifications. Professors and students of the C.P. Gillette Museum of Arthropod Diversity of Colorado State University identified all other beetle specimens to the lowest taxonomic level possible, typically to the level of genus.

Bird surveys were conducted along each transect in May or early June in 2000 and 2001 to assess bird community composition. The surveys began at dawn and lasted approximately 3 h. The surveyor slowly walked each transect until a bird was located and identified, visually or aurally. The bird's location was then determined by measuring the distance and angle from the surveyor to the bird, as well as the distance to the next sampling station. Distance was measured using laser range finders. Using this method, the actual spatial location of each surveyed bird was defined and mapped. To more exhaustively portray the bird and beetles communities through time the results from the two years of sampling were combined.

Species-Accumulation Curves

To generate scale-dependent species-accumulation curves for beetles, plants and birds, the average number of species sampled was calculated using a moving window analysis. For consistency between taxonomic groups, birds were assigned to the nearest sampling location of beetles and vegetation. In terms of species-area relationships, I combined the data from neighboring sampling locations as a surrogate for increasing area or scale. Because this sampling method does not directly equate to area, the accumulation curves are based on an increased number of samples. Using a moving window I systematically increased the window size from the initial state, where each sampling location was considered independent, to the aggregation of all 40 sampling locations along a transect. For each window size, the mean number of species was calculated over all possible windows (allowing for windows to overlap). In this way, I was able to calculate the average species richness for 40 scales. Thus, for example, for the scale of two there were 39 points corresponding to the average number of species found in each neighboring pair of sampling locations.

Heterogeneity Index

In order to create a scale-dependent and objective measurement of habitat heterogeneity, I measured the heterogeneity of an image based on Landsat data. The Landsat images used were from late spring 2000 and had a resolution of 30 m^2. The near-infrared (NIR; band 4) and the visible light (VIS; band 3) bands of the Landsat 7 TM images for each site were combined to generate NDVI based on the following equation:

NDVI = (NIR-VIS) / (NIR+NIS). Using these NDVI images, a heterogeneity index was calculated based on the spectral variation hypothesis developed by Palmer et al. (2002). The spectral variation approach asserts that plant species richness is positively correlated with this heterogeneity index. To calculate the heterogeneity index, the variance of the NDVI values was calculated within a particular window size for each grid cell in the image. To generate a scale-dependent heterogeneity index, this process was conducted for windows ranging in size from 360 m^2 to just under 4 km^2 (Table 4.2). This range of window sizes corresponds to the scales of the accumulation curves. For example, a 360-m^2 window has dimensions of 60 x 60 m or approximately the spacing of the sampling stations, so I equated this with the scale of a single sampling station. A 90 x 90 m window can incorporate two sampling stations, so it was equated to the scale of 2. Window sizes were systematically increased until a window was large enough to contain all 40 points of a transect. Values for scales not directly calculated from Landsat images were estimated based on a spline-smoothing algorithm in S-Plus . ArcGIS 8.2 (ESRI 2002) was used for the moving-window analysis to calculate the values for the heterogeneity index. Based on this process, a new image was created for each window size analyzed. The new images or grids were then resampled for each sampling location, providing a scale-dependent heterogeneity value for each sampling location. To compare this heterogeneity index to the species-accumulation curves, the values from each location were averaged for each scale of heterogeneity index (Figure 4.2).

Statistical Analysis

To model species richness I used models based on area and heterogeneity (Het) using the following three models:

Area model: $\text{Log(Species Richness)} = \beta_1 \text{Log(Area)} + \beta_0$ (1)

Heterogeneity model: $\text{Log(Species Richness)} = \beta_1 \text{Log(Het)} + \beta_0$ (2)

Interaction model: $\text{Log(Species Richness)} = \beta_1 \text{Log(Area)} + \beta_2 \text{Log(Het)} + \beta_3(\text{Log(Area)} * \text{Log(Het)}) + \beta_0$ (3)

These models were used to fit the species-accumulation curves for each taxonomic group along each transect individually. I also pooled all data for a taxonomic group from all sites to model the fit of these models across the entire region.

These models were then used to predict species-accumulation curves. For each transect by taxonomic group, I predicted the species-accumulation curve based on the combined data for that group from the other seven transects and each of the three alternative models (equations 1, 2 and 3). For example, to predict the bird-species-accumulation curve of transect P1, I first fit three models, based on area, heterogeneity and the interaction between area and heterogeneity to the combined data of the other seven transects. Using the coefficients of these three models, three predictions were made for the species- accumulation curve for birds of transect P1.

The predictions for each transect and taxonomic group were then compared to the observed data. I measured the accuracy of the predictions in two ways (Fig. 4.3). First, an envelope was calculated based on the observed average species richness ± 10%. The predictions could then be tested in relation to the proportion of the predicted curves that fell within this envelope. Second, I calculated the average difference between the number of species predicted by the models and the observed number of species for each scale of analysis. This second method was used to characterize models for which predictions were not within the 10% envelope, but accurately mimicked the shape or form of the observed curves.

Results

The species-accumulation curves for each of the transects (Fig. 4.4) show the differences in the number of species of each taxonomic group at different transects and across the sites studied. At all locations, the number of bird species was significantly ($p<0.001$) less than the number of plant or beetle species. More beetle species than plant species were detected at three of the four sites (Pawnee, Arikaree and Smoky Valley). The birds were the only taxonomic group that reached an asymptote in species richness within the scales I sampled.

Heterogeneity for each of the sites increased from west to east, corresponding to the increase in precipitation and biomass. NDVI is a measure of productivity, thus this increase is expected. Also, the index of heterogeneity for Konza reaches a sill, while heterogeneity seems to be continually increasing beyond the scales I measured for the western three sites. For most sites, the differences in heterogeneity between the two transects were not significant (paired t-test, alpha=0.05; Fig. 4.2). The transects at Arikaree, however, were significantly different ($p<0.001$). Across all scales, the heterogeneity index for transect A2 was higher than that for transect A1. Heterogeneity did increase from west to east across the sites and with scale.

To fit the species-richness curves for each taxonomic group along each of the transects, I developed models based on area, heterogeneity, and the interaction between area and heterogeneity. These models all explained at least 73% of the variance in the species accumulation curves within each transect (Table 4.3). The area model explained at least 79% of the variance of each species-accumulation curve. The heterogeneity model did not fit the species-accumulation curves as well as the area model in general, but at S1 and K1 heterogeneity explained more variance in the bird accumulation curves than did area. Along all transects and for all taxonomic groups, the interaction model explained over 76% of the variance of each species-accumulation curve.

At the level of the individual transect, there was considerable fit of the three alternative models to the observed data, but when the data were combined across transects, the accuracy of the models was reduced. The area model explained at least 73% of the variance in species richness for each of the taxonomic groups. However, the heterogeneity model had considerably lower R^2 values, with only 14% of the variance explained for birds and 18% and 42% of the variance explained for beetles and plants, respectively.

The area and interaction models were considerably more accurate than the heterogeneity models in terms of the average difference between the observed species richness and the predictions for beetles, birds and plants (Table 4.4). There were several instances in which the heterogeneity model provided more accurate predictions in terms of the proportion of the predicted curves that were within the 10% envelope of the observed data. This was often a function of the shape of the predicted curve and not of the accuracy of the predictions (Table 4.4). In almost all predictions, the heterogeneity model predictions crossed through the 10% envelope, whereas the other models typically had a similar shape to that of the observed distribution (Figs. 4.5, 4.6, 4.7).

For beetles, the area and interaction models typically predicted accumulation curves that were similar in shape to the observed data (Fig 4.5). The predictions made by the area and the interaction models for Arikaree and Smoky Valley were almost perfect (i.e. the average difference between observations and predictions was < 1). The area models were more accurate than the interaction model at both Pawnee and Konza. Along transect P1, the area model predictions were within the 10% envelope for 100% of the predictions, suggesting that area was a better predictor of beetle accumulation curves than heterogeneity.

The predicted species-accumulation curves for birds were similar to the beetle curves in that the area and the interaction models were very similar and the heterogeneity models made poor predictions (Fig. 4.6). The primary differences between the area and interaction models were at Pawnee and Konza. At Pawnee, the predictions of the interaction models were lower than the area models at fine scales but higher at broad scales. The opposite occurred at Konza, where the interaction models were higher at fine scales and lower at broad scales compared to the area model predictions.

As with the other two taxonomic groups, the area and interaction models for the species-accumulation curves of plants were noticeably different at Pawnee and Konza, but very similar at Arikaree and Smoky Valley (Fig. 4.7).

Discussion

Species-area-habitat relationships are a useful tool for predicting the number of species at certain locations (Rosenzweig 1995, Lomolino 2001). Here, I discuss three aspects of the results. First, area is a better predictor of species-accumulation curves across a broad region than is heterogeneity. Even though models based on area and heterogeneity may fit accumulation curves at specific locations, the ability of these models to accurately predict the form of accumulation curves at other locations is often very limited. Second, I assess the practicality of using the spectral variance approach to model accumulation curves for several taxonomic groups across the regional moisture gradient. Finally, I consider the implications of these methods for predicting species-accumulation curves in grassland systems.

Habitat diversity has long been considered an important predictor of species richness (MacArthur and MacArthur 1961, Williams 1964, Whittaker 1998). Along individual transects, these data show that species-accumulation curves of ground-dwelling beetles, breeding birds and vascular plants in grassland ecosystems can be explained with a high degree of accuracy based on area and heterogeneity (Table 4.3). Considering this strong relationship, I expected these relationships to hold across the entire region. However, when all the transects were combined, the relationship between heterogeneity and species richness was considerably weaker. The relationships between species richness and area and the interaction between area and heterogeneity still remained strong on a regional basis.

Triantis et al. (2003) recently proposed an additional method for incorporating habitat diversity into predictions of species-accumulation curves, by modeling the interaction between area and the number of habitats, such that Log(Species) = Log (Area * Number of Habitats), which they termed the *choros* model. Triantis et al. (2003) showed that the interaction of area and habitat diversity explained more variance in species-accumulation curves than did area alone in 20 studies found in the literature.

These results confirm the assessment of Triantis et al. (2003), although in this analysis and the analysis of Triantis et al. (2003) the models including heterogeneity rarely explained more than 5% more variance than did models based on area alone, and in only 6 of 22 examples (Triantis et al. 2003) was the slope of the *choros* model prediction significantly different from the models based solely on area. Thus, habitat heterogeneity does influence the number of species within a location and the shape of species-accumulation curves, but the primary predictor of species-accumulation curves remains the area studied. Even though several studies have shown the importance of habitat heterogeneity in predicting the biodiversity of a particular location (e.g. Williams 1964, Abbott 1978, Palmer 1990), focusing just on area would be sufficient for explaining species richness in grassland systems.

When I used area and heterogeneity to predict species-accumulation curves, there were consistent differences between the three taxonomic groups in terms of which models were the most accurate. For beetles, models based on area alone were almost always more accurate than were models based on heterogeneity only (Table 4.4). Including heterogeneity as an interaction variable with area rarely improved this accuracy. Along several of the transects, however, the inclusion of heterogeneity increased the goodness of fit for both birds and plants (Table 4.4). This was especially true for plants, where seven of the eight species-accumulation curves were most accurately predicted by either the heterogeneity model or the interaction model. This may be indicative of the measure of heterogeneity that I used and relationship between vegetation and NDVI.

The spectral variance approach was developed based on evidence that plant species richness increases with an increase in the variance in a satellite image or aerial photograph. The expectation was that beetle and bird species richness would also increase with spectral variance, which was supported by the results at specific sites. The ability of heterogeneity to explain the variance in species-accumulation curves across a region, however, was not as successful. The predictions of species-accumulation curves of beetles on a regional scale do not support the spectral variance hypothesis, but rather indicate that area alone is a good predictor of beetle species richness. For birds and plants, however, the results support the spectral variance approach and indicate that this method can aid in predicting species-accumulation curves for these taxonomic groups. The resolution and aspects of the landscape quantified by NDVI may be inappropriate measures of heterogeneity for beetle communities but may be indicative of factors influencing the species richness of plant and bird communities. "Habitats" are artificial constructs associated with researchers' perception of broad categories that organisms are responding to, but spectral variance is able to capture continuous changes in landscape structure, which is unfeasible with the use of categorical data and may be indicative of ecotones or rare habitats important to rare species.

One aspect to consider in using spectral variance to predict species-accumulation curves across a region is the potential inconsistency in the variance at different sites. The heterogeneity index at Konza was three to six times higher than the index at Pawnee (Fig. 4.2). There is not an equivalent increase in the number of species across this gradient, nor would there likely be an equivalent difference in the number of habitats if habitat had been measured in a more traditional manner, such as based on vegetation classes (e.g.

Kohn and Walsh 1994, Ricklefs and Lovette 1999). The only taxonomic group that showed an increase in species richness across the regional gradient was plants, which increased slightly from west to east (p=0.079). This pattern gives more evidence for why heterogeneity was more influential in predicting species-accumulation curves for plant communities. Plant species richness seemed to be related more to the productivity gradient than either beetle or bird species richness. Identifying a measure of heterogeneity that increases with scale but remains constant across a regional gradient may be more appropriate for modeling species richness patterns on such a regional basis.

For heterogeneity to be an important factor in predicting species richness on a regional scale, sampling may have to be conducted on a stratified basis, with an emphasis on rare habitats (Barnett and Stohlgren 2003). Focusing on rare habitats, however, may hinder attempts to survey multiple taxa in such a way as to enable analyses to be conducted in the same manner. The sampling transects crossed broad gradients and potentially undersampled rare habitats or rare species within the study sites, but the design enabled us to analyze multiple taxa in the same manner. The modified-Whitaker sampling method (Stohlgren et al. 1995, Barnett and Stohlgren 2003) is a useful method for understanding the relationship between plant community richness and the influence of area and heterogeneity, but adapting these techniques to mobile taxa such as beetles and birds is a challenge.

Conclusions

Habitat heterogeneity has frequently been shown to be an effective predictor of species richness (Williams 1964, Abbott 1978, Palmer 1990). The analyses, however, show that on a regional basis area is a more important predictor of species richness than is heterogeneity. Despite the low predictive power of heterogeneity on a regional basis using the spectral variance approach (Palmer et al. 2000, Palmer et al. 2002), I believe that this method is nonetheless useful in defining heterogeneity in an objective manor. Environmental heterogeneity has typically been defined in terms of taxon-specific habitats (i.e. discrete maps of habitat for specific organisms), whereas spectral variance uses a single measure of heterogeneity that can be related to numerous taxa. I suggest that objective measures of environmental heterogeneity will not only increase the knowledge of species-habitat-area relationships, but enable more accurate assessments of overall biodiversity in heterogeneous landscapes.

Literature Cited

Abbott, I. 1978. Factors determining number of land bird species on islands around Southwestern Australia. Oecologia **33**:221-233.

Barnett, D. T., and T. J. Stohlgren. 2003. A nested-intensity design for surveying plant diversity. Biodiversity and Conservation **12**:255-278.

Boecklen, W. J. 1986. Effects of habitat heterogeneity on the species area relationships of forest birds. Journal of Biogeography **13**:59-68.

Boecklen, W. J., and N. J. Gotelli. 1984. Island biogeographic theory and conservation practice - species-area or specious-area relationships. Biological Conservation **29**:63-80.

Diamond, J. M., and R. M. May. 1981. Island biogeography and the design of natural reserves. Pages 163-186 *in* R. M. May, editor. Theoretical ecology : principles and applications. Sinauer Associates, Sunderland, MA.

ESRI. 2002. ArcGIS version 7.1. ESRI, Redlands, CA.

Johnson, M. P., N. J. Frost, M. W. J. Mosley, M. F. Roberts, and S. J. Hawkins. 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. Ecology Letters **6**:126-132.

Kitchener, D. J., A. Chapman, J. Dell, and B. G. Muir. 1980a. Lizard assemblage and reserve size and structure in the western Australian wheatbelt - Some implications for conservation. Biological Conservation **17**:25-62.

Kitchener, D. J., A. Chapman, B. G. Muir, and M. Palmer. 1980b. The conservation value for mammals of reserves in the western Australian wheatbelt. Biological Conservation **18**:179-207.

Kohn, D. D., and D. M. Walsh. 1994. Plant-species richness - the effect of island size and habitat diversity. Journal of Ecology **82**:367-377.

Le Brocque, A. F. 1998. Richness of species and growth-forms within sclerophyll and mesophyll vegetation in eastern Australia. Australian Journal of Ecology **23**:168-176.

Lomolino, M. V. 2001. The species-area relationship: new challenges for an old pattern. Progress in Physical Geography **25**:1-21.

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

May, R. M. 1988. How many species are there on earth. Science **241**:1441-1449.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853-858.

Noss, R. F. 1990. Indicators for monitoring biodiversity - a hierarchical approach. Conservation Biology **4**:355-364.

Oliver, I., and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. Conservation Biology **7**:562-568.

Palmer, M. W. 1990. The estimation of species richness by extrapolation. Ecology **71**:1195-1198.

Palmer, M. W., P. G. Earls, B. W. Hoagland, P. S. White, and T. Wohlgemuth. 2002. Quantitative tools for perfecting species lists. Environmetrics **13**:121-137.

Palmer, M. W., T. Wohlgemuth, P. G. Earls, J. R. Arévalo, and S. D. Thompson. 2000. Opportunities for long-term ecological research at the Tallgrass Prairie Preserve, Okalahoma. Pages 123-128 *in* K. Vanderbilt, editor. Cooperation in Long Term Ecological Research in Central and Eastern Europe: Proceedings of the ILTER Regional Workshop. Oregon State University, Corvallis, OR.

Picton, H. D. 1979. Application of insular biogeographic theory to the conservation of large mammals in the Northern Rocky Mountains. Biological Conservation **15**:73-79.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. American Naturalist **149**:875-902.

Ricklefs, R. E., and I. J. Lovette. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology **68**:1142-1160.

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

Rosenzweig, M. L. 1999. Ecology - Heeding the warning in biodiversity's basic law. Science **284**:276-277.

Simberloff, D. 1976. Experimental zoogeography of islands - effects of island size. Ecology **57**:629-648.

Simberloff, D., and L. G. Abele. 1982. Refuge design and island biogeographic theory - effects of fragmentation. American Naturalist **120**:41-50.

Simberloff, D., and N. Gotelli. 1984. Effects of insularization on plant-species richness in the prairie-forest ecotone. Biological Conservation **29**:27-46.

Simberloff, D. S., and L. G. Abele. 1976. Island biogeography and conservation - strategy and limitations. Science **193**:1032-1032.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117**:113-121.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction-prone species. Bioscience **24**:715-722.

Tjorve, E. 2002. Habitat size and number in multi-habitat landscapes: a model approach based on species-area curves. Ecography **25**:17-24.

Triantis, K. A., M. Mylonas, K. Lika, and K. Vardinoyannis. 2003. A model for the species-area-habitat relationship. Journal of Biogeography **30**:19-27.

Whittaker, R. J. 1998. Island biogeography: ecology, evolution, and conservation. Oxford University Press. Oxford.

Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95-117 *in* B. A. Wilcox, editor. Conservation biology : an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Mass.

Williams, C. B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, New York.

Wohlgemuth, T. 1998. Modelling floristic species richness on a regional scale: a case study in Switzerland. Biodiversity and Conservation **7**:159-177.

Table 4.1: Site descriptions, including location, average precipitation and dominant vegetation.

Site	State	County	Latitude	Longitude	Average Precipitation	Dominant Vegetation
Pawnee National Grasslands Long Term Ecological Research Station	Colorado	Weld	40°47′N	104°42′W	320 mm	*Bouteloua gracilis* *Buchloe dactyloides*
Fox Ranch (Arikaree) The Nature Conservancy	Colorado	Yuma	39°44′N	102°28′W	448 mm	*Bouteloua gracilis* *Stipa comata*
Smoky Valley Ranch The Nature Conservancy	Kansas	Logan	38°50′N	100°58′W	533 mm	*Artemesia filifolia* *Bouteloua gracilis*
Konza Prairie Long Term Ecological Research Station	Kansas	Riley	39°04′N	96°34′W	835 mm	*Andropogon gerardi* *Sorghastrum nutans*

Table 4.2: Scale and window sizes used to develop a scale dependent measure of heterogeneity based on an NDVI image. The dimensions correspond to the window size in pixels or cells of an image. The resolution of the NDVI images was 30 m^2.

Scale	Dimensions (Number of Cells)	Length of one side of Window (m)
1	2 x 2	60
2	3 x 3	90
4	6 x 6	180
7	11 x 11	330
8	13 x 13	360
11	18 x 18	540
14	23 x 23	690
17	28 x 28	840
20	33 x 33	990
28	46 x 46	1380
36	60 x 60	1800
40	66 x 66	1980

Table 4.3: Proportion of variance in species accumulation curves of beetle, birds and plants explained by three alternative models, namely the Area model (Area), the Heterogeneity model (Het), and the Interaction model (Int) at four sites: P – Pawnee National Grasslands, Colorado; A – Arikaree (Fox Ranch), Colorado; S - Smoky Valley Ranch, Kansas; and K –Konza Prairie, Kansas. Two transects were analyzed at each site, and the pooled data from all transects were analyzed (All Data). For the Interaction model, a superscript of 1 indicates that area was not a significant variable, a superscript of 2 indicates heterogeneity was not a significant variables and a superscript of 3 indicates the interaction term was not significant.

	Beetles			Birds			Plants		
Transects	Area	Het	Int	Area	Het	Int	Area	Het	Int
All Data	0.88	0.18	0.88	0.73	0.14	0.74	0.78	0.42	0.86
P1	0.93	0.92	$0.93^{1,2}$	0.75	0.74	$0.76^{1,2,3}$	0.79	0.79	0.80
P2	0.96	0.90	$0.96^{1,2}$	0.83	0.77	$0.83^{1,2,3}$	0.9	0.82	0.91^{1}
A1	0.94	0.90	0.94^{2}	0.73	0.74	0.76^{2}	0.93	0.92	0.93
A2	0.88	0.88	$0.89^{1,2}$	0.79	0.78	$0.79^{2,3}$	0.85	0.85	0.86
S1	0.89	0.84	$0.89^{2,3}$	0.81	0.82	0.83^{1}	0.86	0.79	0.86^{3}
S2	0.85	0.83	$0.85^{2,3}$	0.74	0.74	0.75^{1}	0.92	0.90	0.92^{1}
K1	0.94	0.90	$0.94^{2,3}$	0.73	0.79	0.80	0.9	0.88	0.90^{3}
K2	0.90	0.76	0.90	0.76	76	0.80^{1}	0.96	0.80	0.96^{3}

Table 4.4: The average difference between the observed species richness for three taxonomic groups and the predictions across all scales at eight transect at four sites, using three alternative models: the Area model (Area), the Heterogeneity model (Het) and the Interaction model (Int). The numbers in parentheses represent the proportion of the predicted curve that falls within a 10% envelope of the observed accumulation curves. Analyses in which the predicted curves were within the 10% envelope 90% of the time are in bold. The four sites are: P – Pawnee National Grasslands, Colorado, A – Arikaree (Fox Ranch), Colorado, S - Smoky Valley Ranch, Kansas, and K –Konza Prairie, Kansas.

	Beetles			Birds			Plants		
	Area	Het	Int	Area	Het	Int	Area	Het	Int
P1	**2.2(100%)**	24.6(3%)	4.1(45%)	0.5(80%)	3(5%)	0.6(68%)	6.1(0%)	13(8%)	**1.8(100%)**
P2	8.7(0%)	15.7(8%)	10.8(0%)	0.8(45%)	4.1(5%)	0.8(60%)	7.3(0%)	13(8%)	2.1(60%)
A1	2.4(78%)	17.4(10%)	2.3(78%)	1(33%)	1.3(33%)	0.9(28%)	7(8%)	15.6(8%)	7.3(3%)
A2	4.7(43%)	15.4(8%)	4.5(43%)	0.8(60%)	3.3(10%)	0.8(58%)	7.7(20%)	6.5(13%)	4.8(25%)
S1	**0.9(95%)**	15.5(10%)	**0.9(95%)**	0.8(45%)	2.4(10%)	0.8(28%)	**2.5(90%)**	7.6(20%)	3.8(43%)
S2	6.2(23%)	19.6(5%)	5.8(28%)	1.5(0%)	1.3(25%)	1.3(8%)	3(53%)	5.4(20%)	4.4(40%)
K1	2.3(85%)	11.2(43%)	5(55%)	1.3(28%)	1.1(63%)	0.9(33%)	7.7(3%)	7.6(50%)	**2.1(98%)**
K2	**1.5(90%)**	12.4(18%)	1.7(80%)	0.7(63%)	1.2(58%)	**0.3(93%)**	12.7(0%)	11.6(18%)	5.5(45%)

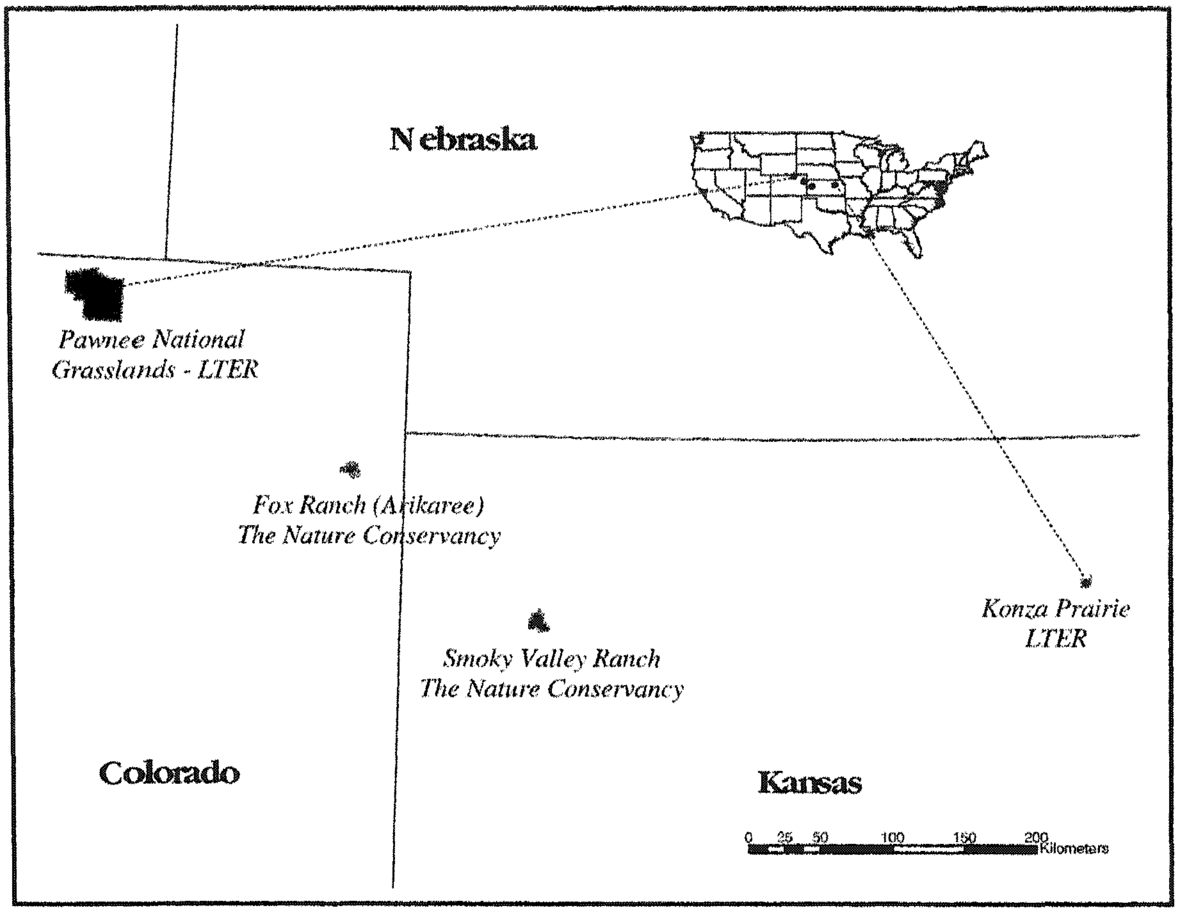


Figure 4.1: Location of study sites.

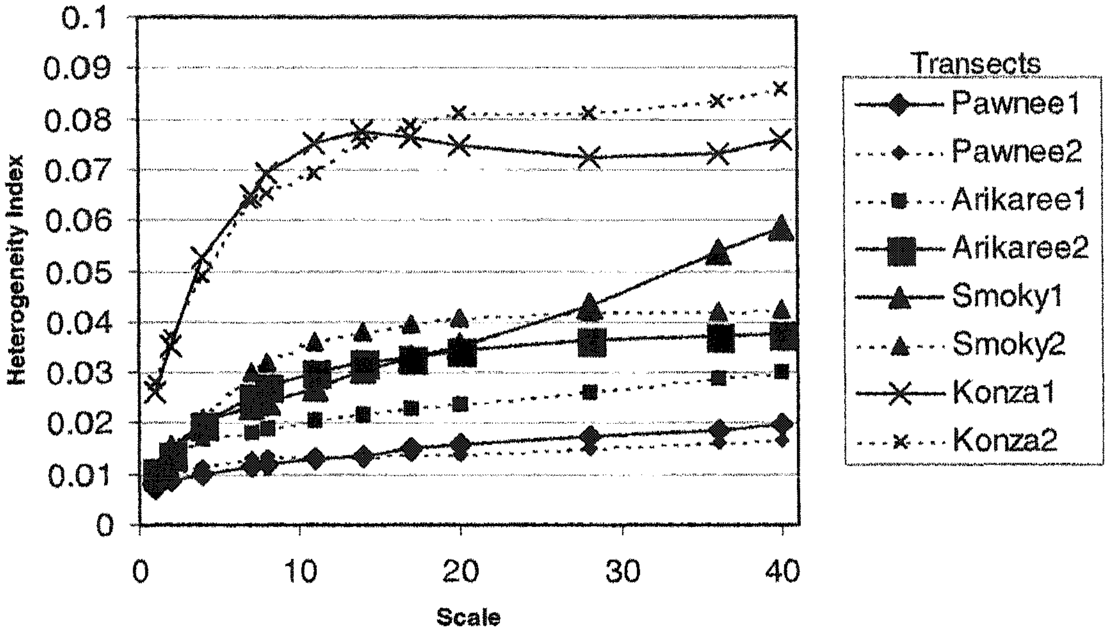


Figure 4.2: Heterogeneity-scale curves for each of eight transects at four sites: P – Pawnee National Grasslands, Colorado, A – Arikaree (Fox Ranch), Colorado, S - Smoky Valley Ranch, Kansas, and K –Konza Prairie, Kansas. The heterogeneity index was based on the spectral variance of an NDVI image at different scales.

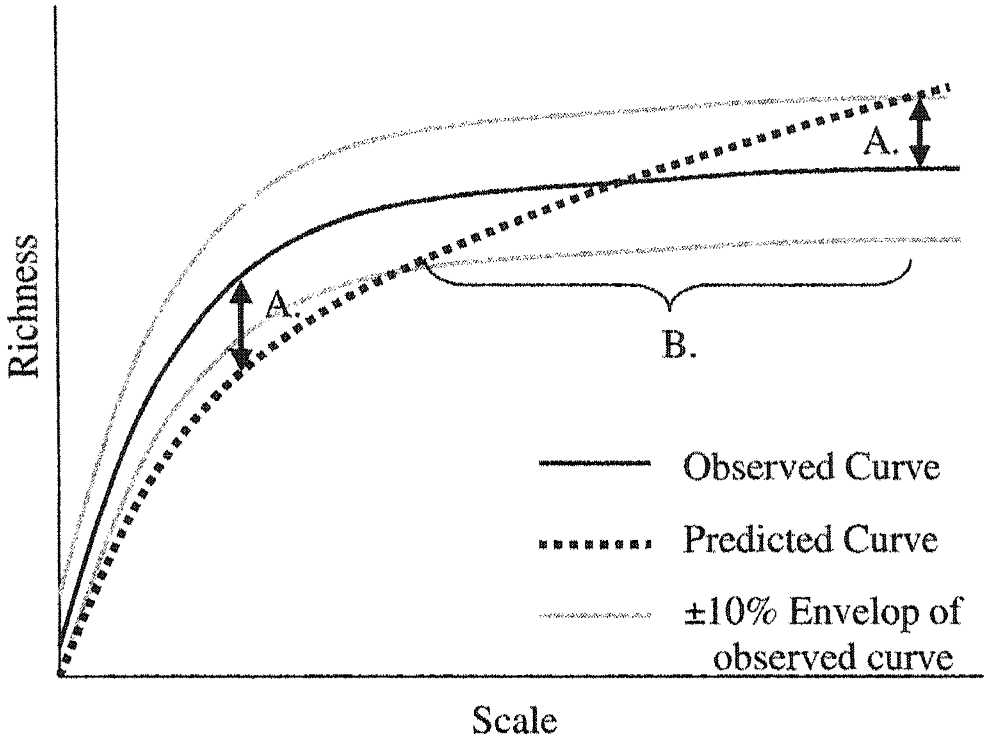


Figure 4.3: Methods to determine the accuracy of the model predictions compared to the observed values. The letter As indicate the measurement of the differences between the number of species predicted and the number observed at a particular scale. B indicates the proportion of the predicted curve that lies within an envelope calculated based on the observed value ± 10%.

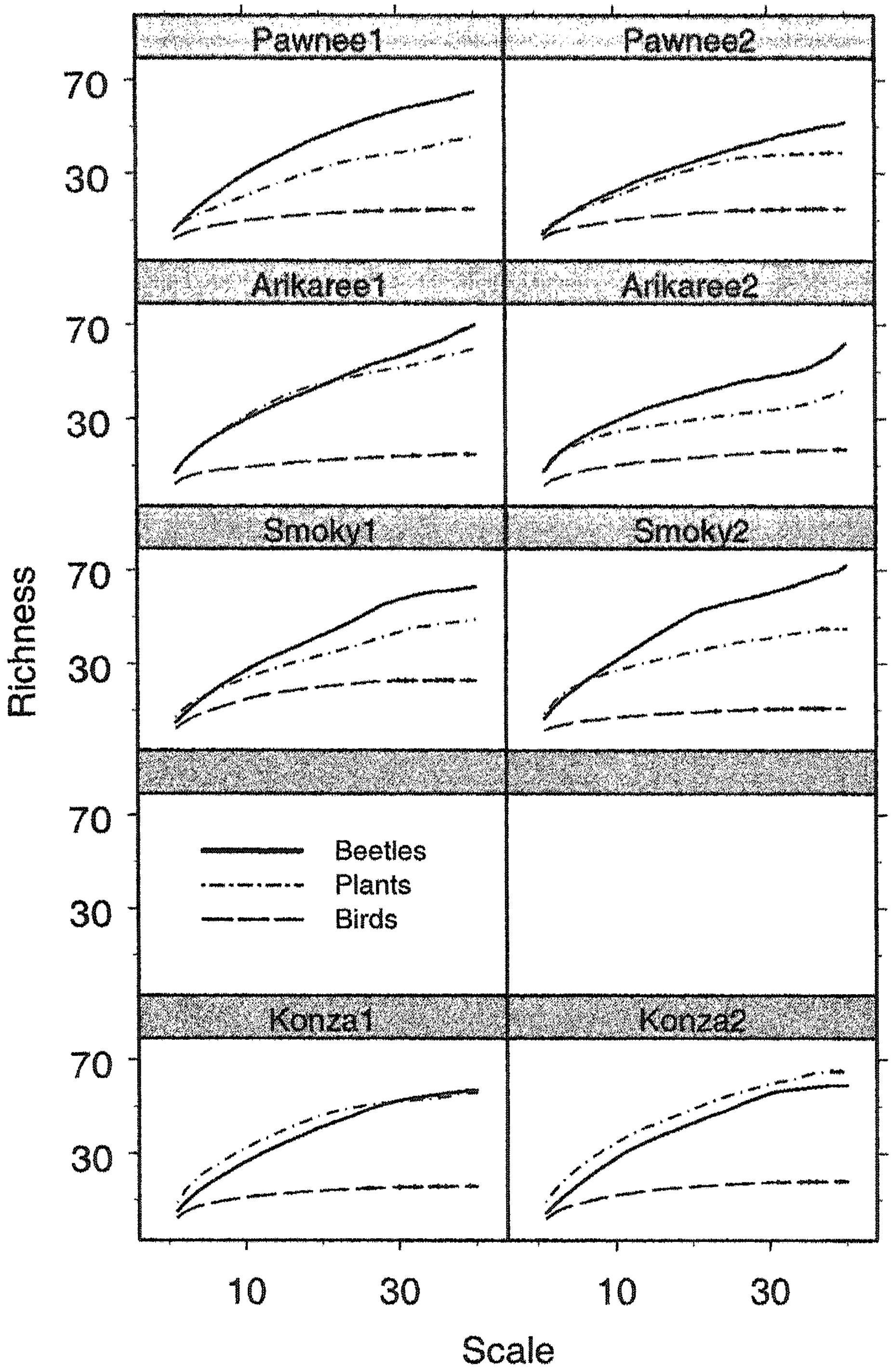


Figure 4.4: Species-area(scale) curves for birds (dashed line),beetles (solid line) and plants (dash – dot line) for each eight transects at four sites based on a moving window analysis of 40 sampling locations along 2 km transects. The four sites are: P – Pawnee National Grasslands, Colorado; A – Arikaree (Fox Ranch), Colorado; S - Smoky Valley Ranch, Kansas; and K –Konza Prairie, Kansas.

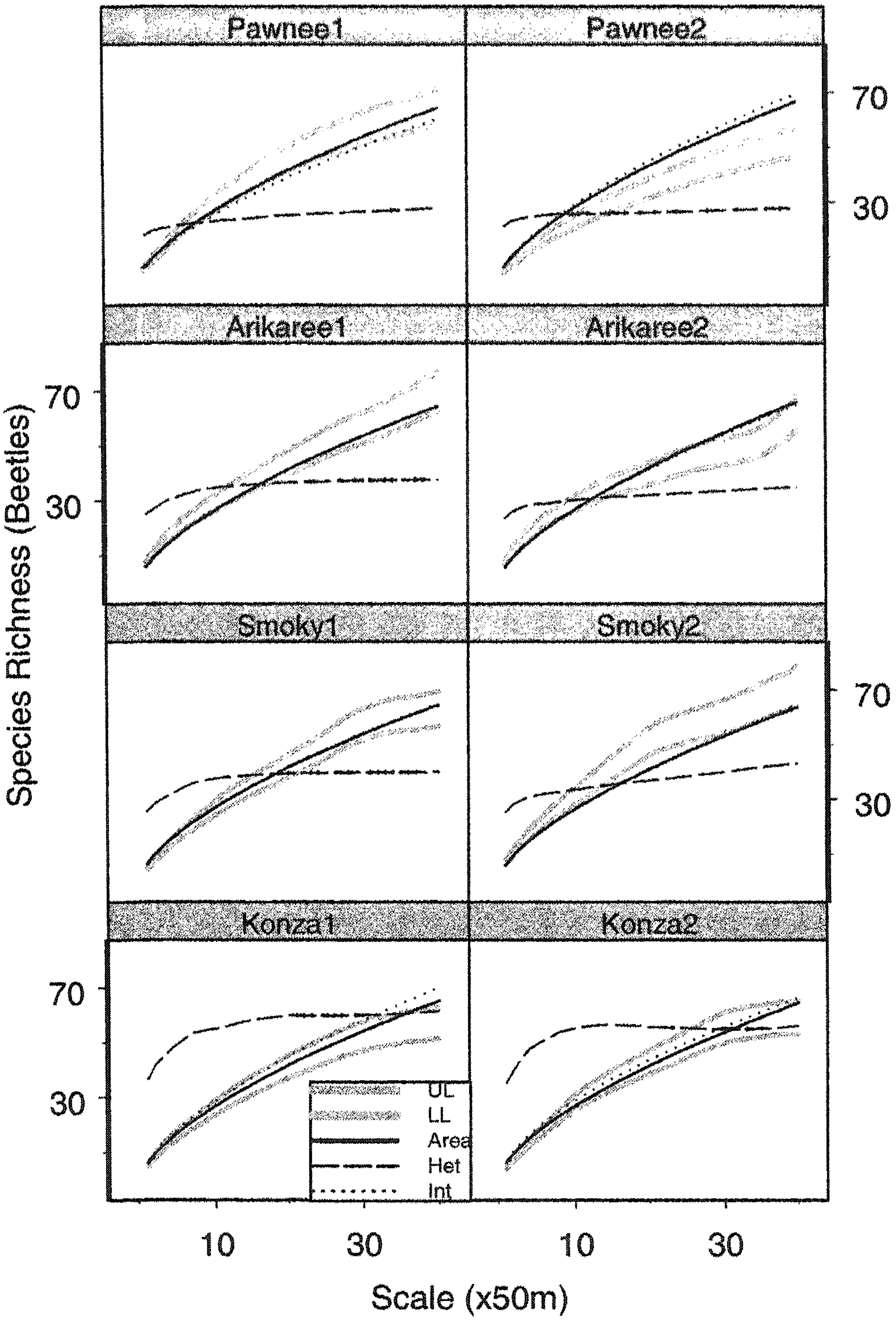


Figure 4.5: Area (solid line), heterogeneity (dashed line) and interaction (dotted line) model predictions of beetle-species-accumulation curves for eight transects at four sites. UL and LL define the upper and lower limits of the 10% envelope of the observed curves. The four sites are: P – Pawnee National Grasslands, Colorado; A – Arikaree (Fox Ranch), Colorado; S - Smoky Valley Ranch, Kansas; and K –Konza Prairie, Kansas.

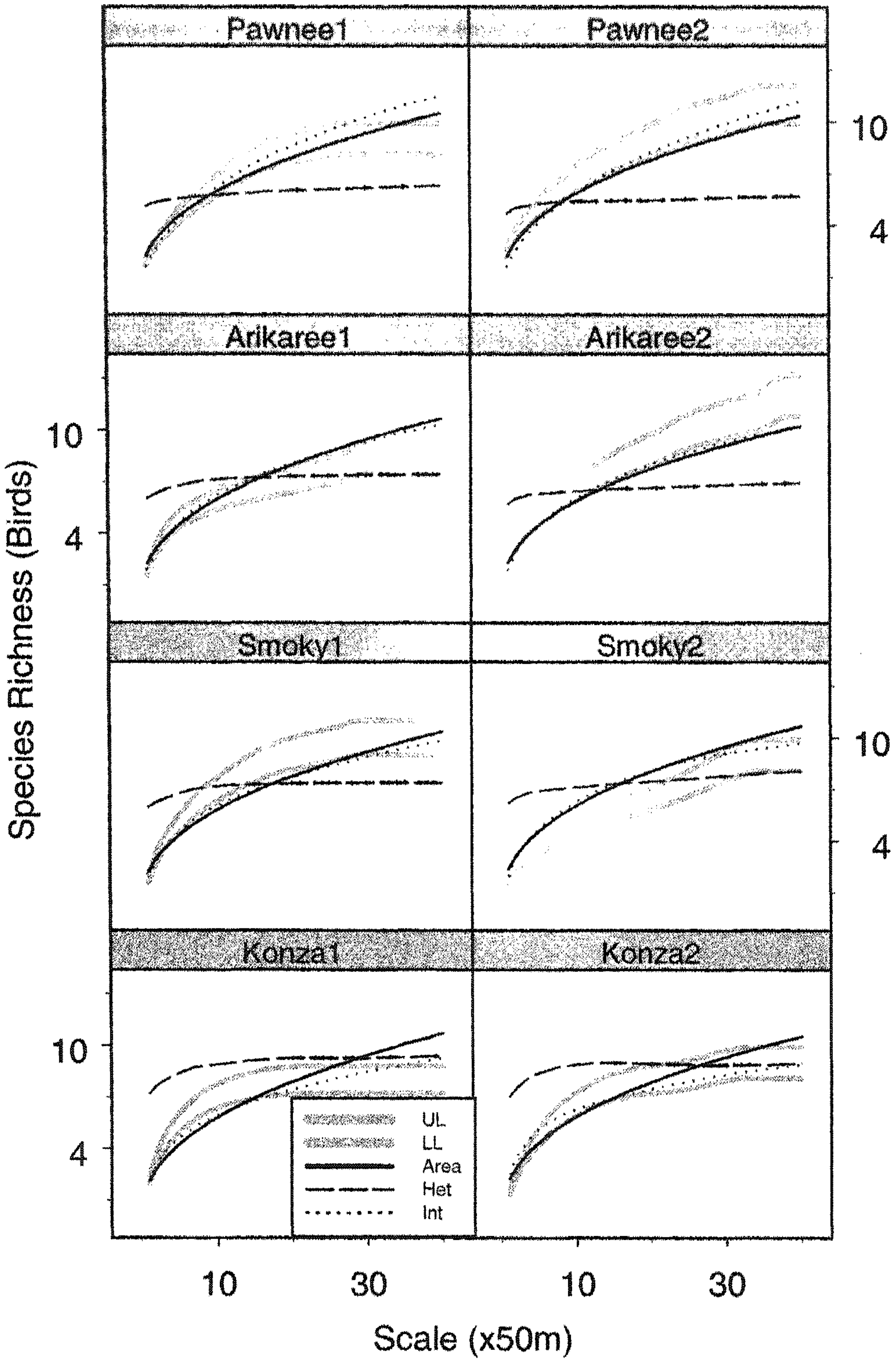


Figure 4.6: Area (solid line), heterogeneity (dashed line) and interaction (dotted line) model predictions of bird-species-accumulation curves for eight transects at four sites. UL and LL define the upper and lower limits of the 10% envelope of the observed accumulation curves along each of these transects. The four sites are: P – Pawnee National Grasslands, Colorado; A – Arikaree (Fox Ranch), Colorado; S - Smoky Valley Ranch, Kansas; and K –Konza Prairie, Kansas.

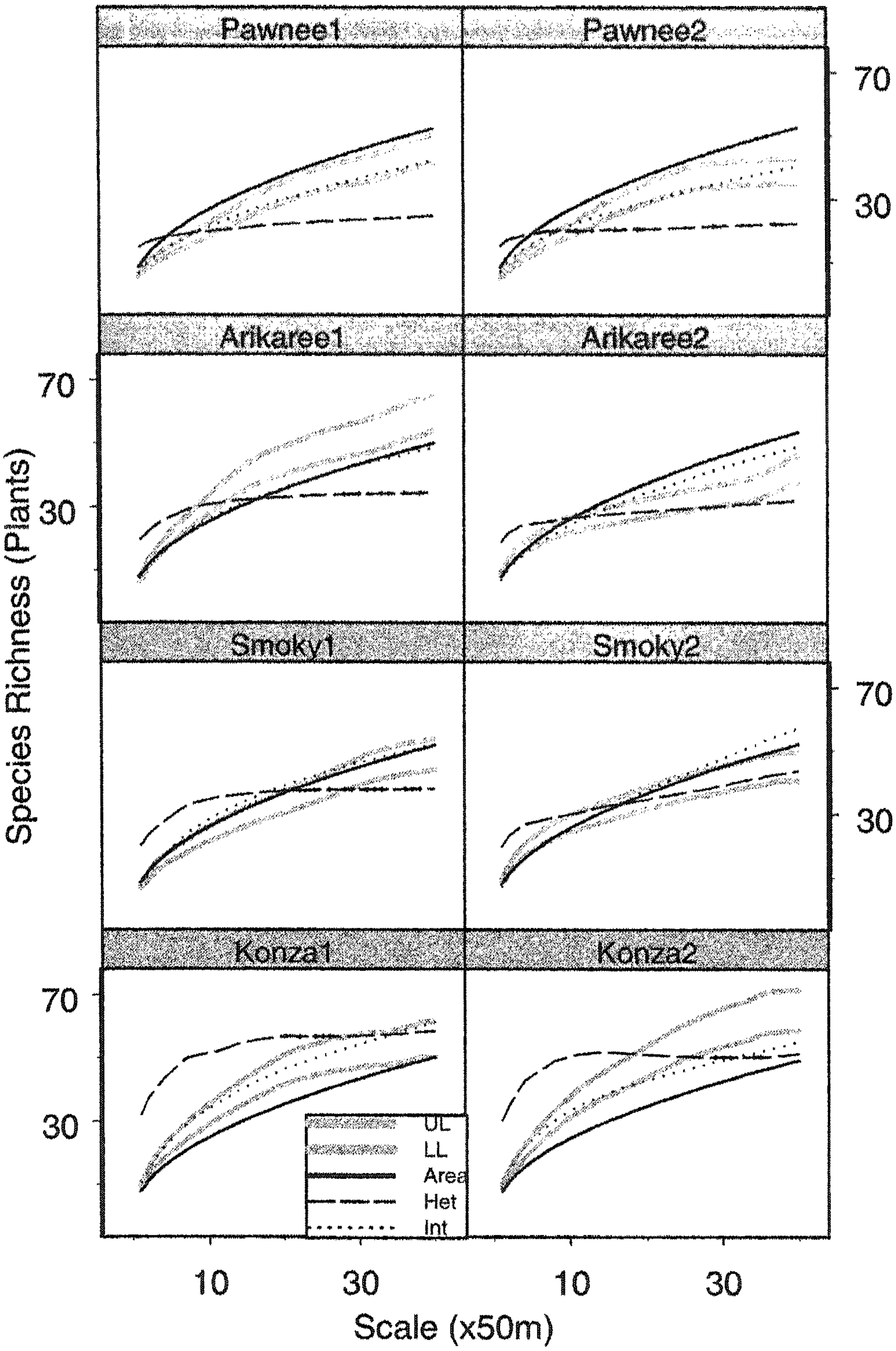


Figure 4.7: Area (solid line), heterogeneity (dashed line) and interaction (dotted line) model predictions of plant-species-accumulation curves. UL and LL define the upper and lower limits of the 10% envelope of the observed accumulation curves along each of these transects. The four sites are: P – Pawnee National Grasslands, Colorado; A – Arikaree (Fox Ranch), Colorado; S - Smoky Valley Ranch, Kansas; and K –Konza Prairie, Kansas.

CHAPTER 5: CONCLUSIONS

In *The Ecology of Bird Communities*, John Wiens notes, "Because species respond to environmental conditions in different ways, changing the place one studies a community is likely to lead to differences in the composition or structure of the community encountered" (1989a). With a focus on regional planning and biodiversity, ecologists and conservation practitioners must begin to understand how and why these changes in structure occur as one changes locations. Within this dissertation I presented a regional analysis using three different methods on three different taxonomic groups in order to understand these relationships. Based on these analyses I have shown: 1) that there are systematic and predictable differences in community structure across a regional gradient, which are related to changes in heterogeneity. 2) the differences between taxonomic groups at specific sites and across the region are not consistent and underscore the limitations of using "indicator" taxa to predict overall biodiversity. 3) how the three methods used in this dissertation highlight current progress in understanding scale-dependent species-environment relationships.

Across the moisture gradient that defines the shift from short-grass steppe to tallgrass prairie there are significant changes in the composition of the biotic communities and in the environmental context in which these organisms live. The western sites are semi-arid and relatively homogeneous, while the eastern sites, in particular Konza Prairie, are mesic and much more heterogeneous in terms of vegetation structure and shrub diversity. This transition from arid to mesic landscapes influences the structure of bird, beetles and plant communities in several ways as shown in the analyses. One similarity between these communities across this gradient was the predominance of spatial dependence in explaining the presence of significant autocorrelation in these communities. There were, however, several differences between taxonomic groups across this gradient. For example, the beetles and plants show very similar patterns of spatial structure in community composition in the western sites I studied, while this synchrony dissipates as the underlying heterogeneity of the environment increase (Chapter III). The variables used to explain the variance in community composition in the three taxonomic groups studied also systematically changes from west to east. In the arid west, variables associated with soil hardness, percent bareground and cactus are important in explaining variance in community composition, while in the mesic east, variables associated with vegetation structure and shrub diversity become the predominate explanatory variables (Chapter II). The changes across this moisture gradient may seem obvious when walking through these different locations, however, these differences are important to highlight considering the implications of regional management. These differences emphasize the dangers of transplanting management plans throughout a region without identifying the differences within that region.

Differences between taxonomic groups also highlight potential problems with managing or studying "indicator" taxa or species when attempting to manage or preserve biodiversity. In some instances the different taxonomic groups studied responded in similar manners, thus suggesting that these communities are being structure by the same underlying forces, however, this did not hold true for all communities and across all sights. One of the primary differences between the three taxonomic groups I studied was the differences in mobility. From sessile plants to the highly mobile birds, forces structuring and variables explaining this structures are expected to be and were shown to be different. In the conservation literature, significant attention has been focused on identifying and using "indicators" for quantifying and monitoring biodiversity (e.g. Noss 1990, McGeoch 1998.). However, the results show that depending on the site, patterns of community structure and significant explanatory variables changes across the different taxonomic groups. Along transect 1 at Pawnee, beetles and plants show similar spatial structure (Chapter III) and have a similar suite variables that explain the variance in that community structure (Chapter II), however, these similarities to not hold at different sites. Thus, at Pawnee beetles community structure may be an appropriate indicator of plant community structure, but this relationship may not hold at different locations. Even though beetles and plants showed similarities in structure and explanatory variables, the ability to predict species richness at Pawnee varied between the two taxonomic groups. Again along transect P1, the model that predicted the species accumulation curve of beetle richness most accurately was the model based solely on area, while including heterogeneity as a interaction term, decreased the predictability. On the other hand, inclusion of heterogeneity as a predictor of plant species richness increased the accuracy the model predictions (Table 4.4).

The influences of scale on patterns of species distributions and community structure has become a predominate paradigm in ecology (Allen and Starr 1982, Addicott et al. 1987, O'Neill et al. 1989, Wiens 1989b). The introduction of methods such as multi-scale ordination with canonical correspondence analysis (MSO; Wagner 2003), hierarchical variance partitioning (Cushman and McGarigal 2002) and quantifying scale-dependent measures of heterogeneity using spectral variance (Palmer et al. 2000, Palmer et al. 2002) have added new tools for community ecologist to build a credible body of theory by which to understand the relationships between the biota, the environment and the geographic space in which interactions and processes occur. The chapters of this dissertation were the first applications of these methods on a multi-taxa and regional basis. The results using these methods showed the importance of scale in several manners. First, using hierarchical variance partitioning indicated the importance of measuring environmental variables at several scales in order to explain the structure of communities, even for communities such as plants or beetles that may be expected to be merely responding to fine-scale processes. Second, the scale-dependence of autocorrelation within communities could be identified using MSO, thus enabling hypotheses to be developed based on the mobility of organisms and the heterogeneity of the environment. Finally, using a scale-dependent measure of heterogeneity, such as spectral variance, enabled more accurate predictions of species accumulation curves for plant communities. Finding a similar measure of heterogeneity that is related to multiple taxonomic groups would substantially increase the applicability of this method.

The development and application of new methods and theory to understand the relationships between organisms, the environment and geographic space is essential to understanding regional patterns of biodiversity. The analyses of ground-dwelling beetles, breeding birds and vascular plants within this dissertation provide a glimpse of the possibilities of understanding that can be achieved by embracing the importance of scale-dependence and resolution-dependence in species-environment relationships.

Literature Cited

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods - scaling environmental patterns. Oikos **49**:340-346.

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

Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology **17**:637-646.

McGeoch, M. 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews **73**:181-201.

Noss, R. F. 1990. Indicators for monitoring biodiversity - a hierarchical approach. Conservation Biology **4**:355-364.

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.

Palmer, M. W., P. G. Earls, B. W. Hoagland, P. S. White, and T. Wohlgemuth. 2002. Quantitative tools for perfecting species lists. Environmetrics **13**:121-137.

Palmer, M. W., T. Wohlgemuth, P. G. Earls, J. R. Arévalo, and S. D. Thompson. 2000. Opportunities for long-term ecological research at the Tallgrass Prairie Preserve, Okalahoma. Pages 123-128 *in* K. Lahtha and K. Vanderbilt, editors. Cooperation in Long Term Ecological Research in Central and Eastern Europe: Proceedings of the ILTER Regional Workshop. Oregon State University, Corvallis, OR.

Wagner, H. H. 2003. Spatial covariance in plant communities: Integrating ordination, geostatistics, and variance testing. Ecology **84**:1045-1057.

Wiens, J. A. 1989a. The ecology of bird communities. Vol. 2. Processes and variations. Cambridge University Press, Cambridge.

Wiens, J. A. 1989b. Spatial scaling in ecology. Functional Ecology **3**:385-397.

APPENDIX 1: TRANSECT DESCRIPTIONS

The Pawnee National Grasslands (Pawnee), in Northeast Colorado is an arid short-grass prairie, in which cattle graze the vast majority of the site. Pawnee is dominated by *Bouteloua gracilis* and *Buchloe dactyloides* and receives 320 mm of precipitation on average (http://sgs.cnr.colostate.edu). The two transects sampled at the PNG were separated by approximately 3 km, but were both situated in similar context. Both transects began at or near the top of hill, descended and crossed Owl Creek and continued on past Owl Creek into relatively level terrain. Both of these regions are grazed by cattle and are predominately short grasses with interspersed shrubs, primarily saltbush and yucca. The major differences between the two transects are that the northern transect (P1) had large willow trees within the floodplain, while the southern transect (P2) had none and P2 ended in a prairie dog town, which can significantly modify the community composition of many taxonomic groups.

The Fox Ranch (Arikaree) is classified as short-grass steppe habitat in northeastern Colorado, near the Colorado/Kansas border. The preserve is bisected by the Arikaree River, is grazed throughout much of the grassland and has more topographical variation than Pawnee. The Fox Ranch receives 448 mm of precipitation and is dominated *Bouteloua gracilis* and *Stipa comata*. The two transects sampled at this site meet at the Arikaree River to make a combined transect 4 km in length. Transect A1 is on the south side of the river, where the soils are loamy and the dominate shrub is yucca. The northern side of the river, where transect A2 was located, is dominated by sandy soils, which corresponds to a high abundance of sand-sage habitat. Both transects at the Fox Ranch are grazed by cattle. The sections of transects closest to the rivers are in areas used for calving, while the upslope regions are grazed the remainder of the year.

The Smoky Valley Ranch is a short-grass prairie located in western Kansas, and is grazed by both buffalo and cattle. It is similar to Fox Ranch in vegetation and topography. Smoky Valley Ranch vegetation is dominated by *Artemesia filifolia* and *Bouteloua gracilis* and receives 533 mm of precipitation on average. Transect S1 begins in a region dominated by short-grass vegetation and is close to a region of chalk bluffs. The transect descends into the flood plain of the Smoky Hill River, which is ephemeral along this stretch, where there is approximately an 150 m swath of willow forest. On the west side of the forest and out of the flood plain the soils remain sandy and the transect enters a stretch of dense sand-sage habitat. The last third of transect S1, is again in an upland area that is predominately short-grass vegetation with some yucca shrubs. Transect S2 does not cross the Smoky Hill River and is almost exclusively in short-grass vegetation with only sparse cover of shrubs. The transect begins in a prairie dog down, descends through a small gully, where there is more shrub cover, but then rises to a flat upland dominated by grasses.

The Saline Experimental Range (Hays) is a heavily grazed mixed grass prairie that has numerous crude oil wells throughout the experimental range. The Saline Range is owned and managed by Kansas State University. The vegetation is dominated by *Pascopyrum smithii* and *Bouteloua curtipendula*. The average precipitation is 577 mm.

The two transects established at Hays, begin in lower elevations, and cross rolling hills, but continually increase in elevation. Transect H1 crosses more roads and appears to have been impacted more heavily by human alteration through road construction and drilling for oil than transect H2. Transect H1, was not included in the analysis presented in this paper due to a lack of a bird survey from the spring of 2001.

Konza Prairie is a tall grass prairie located in the Flint Hills area of northeast Kansas and is also a LTER site. It is grazed by both buffalo and cattle and is periodically burned under a controlled burning regime. The vegetation of Konza Prairie is dominated by *Andropogon gerardi* and *Sorghastrum nutans* and receives 835 mm of precipitation annually. Transect K1 is located within an area that is grazed by bison. The first several hundred meters of K1 is in a flat prairie dominated by tall grasses. The transect then continually descends through a region dominated by taller shrubs, primarily dogwood, it crosses a stream and the end of the transect is in a flat region with shallow soils and dominated by grasses. Transect K2 is in an ungrazed region and begins mid-way up a bluff. The transect proceeds up the bluff, which is primarily dominated by grasses with a few patches of dogwood. At the peak of the bluff, the transect crosses a steep gully dominated by shrubs. After the gully, the transect descends slowly through more gently rolling hills, in which the higher regions are dominated by grasses and the lower sections dominated by shrubs.

APPENDIX 2: BEETLE SPECIES LISTS

Beetles species identified at the Pawnee National Grasslands, Colorado along four transects during June 2000 and 2001. During the first year (2000), 160 pit-fall traps were used to sample beetles for a three day period. During 2001, 104 pit-fall traps were sampled.

- Anobiidae
    - *Tricorynus* sp.
- Anthicidae
    - *Anthicus* spp.
    - *Formicilla* sp.
    - *Ischyropalpus* sp.
    - *Notoxus* sp.
- Cantharidae
    - *Malthodes* sp.
- Carabidae
    - *Acupalpus partiarius*
    - *Amara convexa*
    - *Amara obesa*
    - *Amara rubrica*
    - Amara sp.
    - *Bembidion quadrimaculatum*
    - *Bembidion rapidum*
    - *Cratacanthus dubius*
    - *Cyclotrachelus incisa*
    - *Discoderus* sp.
    - *Euryderus grossus*
    - *Geopinus incrassatus*
    - *Harpalus compar*
    - *Harpalus* sp.
    - *Pasimachus elongatus*
    - *Piosoma setosum*
    - *Selenophorus planipennis*
    - *Stenolophus conjunctus*
    - 2 unidentified spp.
- Chrysomelidae
    - *Brachycoryna* sp.
    - *Brachypnoea* sp.
    - *Chaetocnema* sp.
    - *Glyptoscelis* sp.
    - *Pachybrachis* sp.
    - *Phyllotreta* sp.
    - *Systena* sp.
- Cicindelidae
    - *Cicindela punctulata*
- Cleridae
    - *Enoclerus cordifer*
- Coccinellidae
    - *Coccinella septempunctata*
    - *Hyperaspidius* spp.
    - *Hyperaspis* sp.
    - 1 unidentifed sp.
- Corylophidae
    - 1 unidentifed sp.
- Curculionidae
    - *Cylindrocopturus* sp.
    - *Gerstaeckeria* sp.
    - *Otiorhynchus ovatus*
    - *Pantomorus* sp.
    - *Sphenophorus* sp.
    - 13 unidentified spp.
- Elateridae
    - *Aeolus* sp.
    - *Agrypnus rectangularis*
- Histeridae
    - *Euspilotus* sp.
    - *Hister* sp.
    - *Spilodiscus* sp.
- Latridiidae
    - 1 unidentifed sp.
- Leiodidae
    - *Leiodes* sp.

- Lyctidae
  - 1 unidentifed sp.
- Meloidae
  - *Epicauta parvula*
- Mordellidae
  - *Mordella* sp.
  - *Mordellistena* sp.
- Nitidulidae
  - *Carpophilus pallipennis*
  - *Carpophilus* sp.
  - *Nitidula* sp.
- Phalacridae
  - 1 unidentifed sp.
- Scarabaeidae
  - *Aphodius concavus*
  - *Aphodius scabriceps*
  - *Canthon viridis*
  - *Orizabus pyriformis*
  - *Phyllophaga mucoreus*
  - *Rhyssemus sonatus*
  - *Serica curvata*
  - 1 unidentified sp.
- Scydmaenidae
  - 1 unidentified sp.
- Silphidae
  - *Nicrophorus sayi*
- Staphylinidae
  - *Baeocera* sp.
  - 5 unidentified spp.
- Tenebrionidae
  - *Blapstinus substriatus*
  - *Coniontis obesa*
  - *Edrotes rotundus*
  - *Eleodes carbonarius*
  - *Eleodes extricata*
  - *Eleodes fusiformis*
  - *Eleodes hispilabris*
  - *Eleodes obscura*
  - *Eleodes opaca*
  - *Eleodes suturalis*
  - *Eleodes tricostata*
  - *Embaphion muricata*
  - *Embaphion planum*
  - *Trimytis pruinosa*
  - 1 unidentified sp.

Beetles species identified at the Fox Ranch (Arikaree), Colorado along four transects during June 2000 and 2001. During the first year (2000), 160 pit-fall traps were used to sample beetles for a three day period. During 2001, 104 pit-fall traps were sampled.

- Anobiidae
  - *Megorama* sp.
- Anthicidae
  - *Anthicus* sp.
  - *Mecynotarsus* sp.
  - *Notoxus* sp.
- Bruchidae
  - *Acanthoscelides* sp.
- Cantharidae
  - *Malthodes* sp.
- Carabidae
  - *Acupalpus partiarius*
  - *Amara carinata*
  - *Amara* sp.
  - *Anisodactylus merula*
  - *Bembidion quadrimaculatum*
  - *Chlaenius tomentosus*
  - *Cratacanthus dubius*
  - *Cyclotrachelus incisa*
  - *Cyclotrachelus torvus*
  - *Diplocheila obtusa*
  - *Discoderus* sp.
  - *Dyschirius globulosus*
  - *Euryderus grossus*
  - *Harpalus caliginosus*
  - *Harpalus compar*
  - *Harpalus pensylvanicus*
  - *Harpalus* sp.
  - *Helluomorphoides texanus*
  - *Microlestes linearis*
  - *Pasimachus duplicatus*
  - *Pasimachus elongatus*

  - *Selenophorus planipennis*
- Cerambycidae
  - *Moneilema annulata*
- Chrysomelidae
  - *Brachypnoea* sp.
  - *Chaetocnema* sp.
  - *Gastrophysa* sp.
  - *Metachroma* spp.
  - *Monoxia* sp.
  - *Pachybrachis* spp.
  - *Phyllotreta* sp.
  - *Systena* sp.
  - *Zygograma disrupta*
  - 4 unidentified spp.
- Cicindelidae
  - *Cicindela lengi*
  - *Cicindela punctulata*
  - *Cicindela scutellaris*
- Coccinellidae
  - *Hyperaspidius sp.*
  - 2 unidentified spp.
- Corylophidae
  - 1 unidentified sp.
- Curculionidae
  - *Ophryastes vittatus*
  - *Otiorhynchus ovatus*
  - *Pantomorus* sp.
  - *Spenophorus* sp.
  - *Sphenophorus maidis*
  - 16 unidentified sp.
- Elateridae
  - *Aeolus* spp.
  - *Agrypnus rectangularis*
  - *Conoderus vespertinus*
  - *Hemicrepidius memnonius*
- Geotrupidae
  - *Geotrupes opacus*
- Glaresidae
  - *Glaresis* sp.
- Histeridae
  - *Euspilotus* spp.
  - *Saprinus* sp.
  - *Spilodiscus* sp.
- Latridiidae
  - 3 unidentified spp.
- Lyctidae
  - 1 unidentified sp.
- Meloidae
  - *Epicauta sericans*
- Mordellidae
  - *Hoshihananomia* sp.
  - *Mordella* spp.
  - *Mordellaria* spp
  - *Mordellistena* spp.
- Nitidulidae
  - *Carpophilus* sp.
  - *Glischrochilus* sp.
- Phalacridae
  - 2 unidentified spp.
- Ptiliidae
  - 1 unidentified sp.
- Scarabaeidae
  - *Aphodius fimetarius*
  - *Aphodius scabriceps*
  - *Canthon ebenus*
  - *Canthon viridis*
  - *Hoplia laticollis*
  - *Melanocanthon nigricornis*
  - *Phyllophaga lanceolata*
  - *Phyllophaga mucorea*
  - *Rhyssemus sonatus*
  - *Serica curvata*
  - 2 unidentified spp.
- Scraptiidae
  - *Canifa* sp.
- Scydmaenidae
  - 1 unidentified sp.
- Silphidae
  - *Nicrophorus carolina*
  - *Nicrophorus sayi*
- Silvanidae
  - *Ahasverus* sp.
- Staphylinidae
  - 3 unidentified spp.
- Tenebrionidae
  - *Blapstinus substriatus*
  - *Blapstinus vestitus*
  - *Eleodes acuta*
  - *Eleodes extricata*
  - *Eleodes fusiformis*
  - *Eleodes hispilabris*

- *Eleodes opaca*
- *Eleodes suturalis*
- *Eleodes tricostatus*
- *Embaphion muricata*
- *Lobometopon fusiformis*
- Trogidae
  - *Omorgus punctatus*

Beetles species identified at the Smoky Valley Ranch, Kansas along four transects during June 2000 and 2001. During the first year (2000), 160 pit-fall traps were used to sample beetles for a three day period. During 2001, 104 pit-fall traps were sampled.

- Anobiidae
  - *Megorama* sp.
- Anthicidae
  - *Anthicus* sp.
  - *Euvacusus* sp.
  - *Notoxus* sp.
  - *Squamanotoxus* sp.
  - *Vacusus* sp.
  - 1 unidentified sp.
- Bruchidae
  - *Acanthoscelides* sp.
- Carabidae
  - *Acupalpus partiarius*
  - *Amara* sp.
  - *Anisodactylus ovularis*
  - *Apenues sinuatus*
  - *Calosoma marginale*
  - *Calosoma obsoletum*
  - *Chlaenius tomentosus*
  - *Cratacanthus dubius*
  - *Cyclotrachelus incisa*
  - *Cyclotrachelus torvus*
  - *Diplocheila obtusus*
  - *Discoderus* sp.
  - *Dyschirius globulosus*
  - *Euryderus grossus*
  - *Harpalus caliginosus*
  - *Harpalus pennsylvanicus*
  - *Microlestes pusio*
  - *Pasimachus californicus*
  - *Pasimachus elongatus*
  - *Selenophorus planipennis*
  - *Stenolophus conjunctus*
  - *Syntomus americanus*
- Chrysomelidae
  - *Brachypnoea* sp
  - *Chaetocnema* sp.
  - *Disonycha sp.*
  - *Epitrix* sp.
  - *Glyptina* sp.
  - *Monoxia* sp.
  - *Pachybrachis* sp.
  - *Phyllotreta* spp.
- Cicindelidae
  - *Amblycheila cylindriformis*
  - *Cicindela lengi*
  - *Cicindela punctulata*
- Coccinellidae
  - *Hyperaspidius* sp.
  - 1 unidentified sp.
- Corylophidae
  - 1 unidentified sp.
- Cryptophagidae
  - 1 unidentified sp.
- Curculionidae
  - *Pantomorus* sp.
  - *Spenophorus* sp.
  - *Sphenophorus màidis*
  - 19 unidentified spp.
- Elateridae
  - *Aeolus* spp.
  - *Agrypnus rectangularis*
  - *Melanotus* sp.
  - *Paradonus pectoralis*
- Eucinetidae
  - *Eucinetus terminalis*
- Histeridae
  - *Euspilotus* sp.
  - *Hister* sp.
  - *Saprinus* sp.

  - *Spilodiscus* sp.
- Hydrophilidae
  - *Cercyon* sp.
  - 1 unidentified sp.
- Latridiidae
  - 1 unidentified sp.
- Meloidae
  - *Epicauta segmenta*
- Melyridae
  - 1 unidentified sp.
- Monotomidae
  - *Monotoma* sp.
  - 1 unidentified sp.
- Mordellidae
  - *Mordellistena* spp.
- Mycetophagidae
  - *Litargus* sp.
- Nitidulidae
  - *Carpophilus* sp.
- Phalacridae
  - 1 unidentified sp.
- Scarabaeidae
  - *Aphodius erraticus*
  - *Aphodius fimetarius*
  - *Aphodius vittatus*
  - *Canthon ebenus*
  - *Canthon viridis*
  - *Cremastocheilus knochii*
  - *Diplotaxis frondicola*
  - *Diplotaxis rudis*
  - *Diplotaxis thoracica*
  - *Omorgus puncutus*
  - *Onthophagus pennsylvanicus*
  - *Phaneus vindex*
  - *Phyllophaga lanceolata*
  - *Phyllophaga mucorea*
  - *Phyllophaga submucida*
  - *Rhyssemus sonatus*
  - 1 unidentified sp.
- Scraptiidae
  - *Canifa* sp.
- Scydmaenidae
  - *Euconnus* spp.
  - 1 unidentified sp.
- Silphidae
  - *Nicrophorus sayi*
- Silvanidae
  - *Ahasverus* sp.
- Staphylinidae
  - *Scaphisoma sp.*
  - 10 unidentifed spp.
- Tenebrionidae
  - *Blapstinus fortis*
  - *Blapstinus substriatus*
  - *Blapstinus vestitus*
  - *Eleodes fusiformis*
  - *Eleodes opaca*
  - *Eleodes suturalis*
  - *Eleodes tricostata*
  - *Embaphion muricata*

Beetles species identified at the Saline Experimental Range, Kansas along two transects during June 2000 and 2001. During the first year (2000), 80 pit-fall traps were used to sample beetles for a three day period. During 2001, 104 pit-fall traps were sampled.

- Anthicidae
  - *Vacusus* sp.
- Carabidae
  - *Cyclotrachelus incisa*
  - *Discoderus* sp.
  - *Euryderus grossus*
  - *Harpalus caliginosus*
  - *Microlestes pusio*
  - *Pasimachus californicus*
  - *Pasimachus elongatus*
  - *Scarites quadriceps*
  - *Selenophorus planipennis*
- Cerambycidae
  - 1 unidentified sp.
- Chrysomelidae
  - *Brachypnoea* spp.
  - *Chaetocnema* sp.
  - *Glyptoscelis* sp.
  - *Jonthonota nigripes*
  - *Kuschelina* sp.

  - *Mychrous* sp.
  - *Pachybrachis* sp.
  - *Zygogramma exclamationis*
- Coccinellidae
  - 1 unidentified sp.
- Corylophidae
  - 1 unidentified sp.
- Cryptophagidae
  - 1 unidentified sp.
- Curculionidae
  - *Pantomorus* sp.
  - *Spenophorus* sp.
  - *Sphenophorus maidis*
  - 11 unidentified spp.
- Elateridae
  - *Aeolus* spp.
  - *Melanotus* spp.
  - *Paradonus pectoralis*
- Histeridae
  - *Hister* sp.
  - *Hypocaccus* sp.
- Latridiidae
  - 3 unidentified spp.
- Leiodidae
  - *Leiodes* sp.
- Phalacridae
  - 1 unidentified sp.
- Scarabaeidae
  - *Ataenius spretulus*
  - *Canthon ebenus*
  - *Canthon viridis*
  - *Diplotaxis frondicola*
  - *Euphoria fulgida*
  - *Euphoria sepulcralis*
  - *Phyllophaga lanceolata*
  - *Rhyssemus sonatus*
- Scraptiidae
  - *Canifa* sp.
- Scydmaenidae
  - *Stenichnus* sp.
  - 1 unidentified sp.
- Silvanidae
  - *Ahasverus* sp.
- Staphylinidae
  - 6 unidentified spp.
- Tenebrionidae
  - *Blapstinus substriatus*
  - *Eleodes suturalis*
  - *Opatrinus aciculatus*

Beetles species identified at the Konza Prairie, Kansas along three transects during June 2000 and 2001. During the first year (2000), 120 pit-fall traps were used to sample beetles for a three day period. During 2001, 104 pit-fall traps were sampled.

- Anthicidae
  - *Ischyropalpus* sp.
  - 1 unidentified sp.
- Carabidae
  - *Anisodactylus merula*
  - *Calathus opaculus*
  - *Chlaenius tomentosus*
  - *Cyclotrachelus incisa*
  - *Cyclotrachelus sodalis*
  - *Harpalus compar*
  - *Helluomorphoides texanus*
  - *Micrixys distinctus*
  - *Pasimachus californicus*
  - *Pasimachus elongatus*
  - *Poecilus lucublanda*
  - *Polyderis laevis*
  - *Pterostichus permunda*
  - *Pterostichus ventralis*
- Cerambycidae
  - *Typocerus octonotatus*
  - 1 unidentified sp.
- Chrysomelidae
  - *Blepharida rhois*
  - *Brachypnoea* sp.
  - *Chaetocnema* sp.
  - *Epitrix* sp.
  - *Mychrous* sp.
  - *Pachybrachis* sp.
  - *Paria* sp.
  - *Phyllotreta* sp.

- *Systena* sp.
- 4 unidentified spp.

Cleridae
- *Isohydnocera* sp.

Coccinellidae
- *Hyperaspidius* sp.
- 2 unidentified spp.

Corylophidae
- 2 unidentified spp.

Curculionidae
- *Spenophorus* sp.
- 10 unidentified spp.

Elateridae
- *Aeolus* spp.
- *Melanotus* sp.

Histeridae
- *Hister* sp.
- *Hypocaccus* sp.

Hydrophilidae
- 1 unidentified sp.

Latridiidae
- 4 unidentified spp.

Mordellidae
- *Mordella* sp.
- *Mordellistena* spp.

Phalacridae
- 1 unidentified sp.

Ptilodactylidae
- *Ptilodactyla* sp.
- 1 unidentified sp.

Scarabaeidae
- *Ataenius strigatus*
- *Canthon viridis*
- *Copris fricator*
- *Dialytellus* sp.
- *Diplotaxis frondicola*
- *Euphoria sepulcharis*
- *Onthophagus knausi*
- *Onthophagus pennsylvanicus*
- *Phyllophaga rubiginosa*
- *Platytomus* sp.
- *Rhyssemus sonatus*
- 1 unidentified sp.

Geotrupidae
- *Bolbocerosoma bruneri*

Scraptiidae
- *Canifa* sp.

Scydmaenidae
- *Stenichnus* sp.
- 1 unidentified sp.

Staphylinidae
- *Baeocera* sp.
- *Scaphisoma* sp.
- 16 unidentified spp.

Tenebrionidae
- *Blapstinus substriatus*
- *Eleodes suturalis*

APPENDIX 3: BIRD SPECIES LISTS

Bird species identified at the Pawnee National Grasslands, Colorado during May and June of 2000 and 2001 along four 2 km transects.

Agelaius phoeniceus	Redwinged Blackbird
Ammodramus savannarum	Grasshopper Sparrow
Anas platyrhynchos	Mallard
Athene Cunicularia	Burrowing Owl
Calamospiza melanocorys	Lark Bunting
Calcarius mccownii	McGown's Longspur
Charadrius melodus	Piping Plover
Charadrius vociferus	Killdeer
Chondestes grammacus	Lark Sparrow
Chordeiles minor	Common Nighthawk
Circus cyaneus	Northern Harrier
Eremophila alpestris	Horned Lark
Hirundo pyrrhonata	Cliff Swallow
Hirundo rustica	Barn Swallow
Melanerpes erythrocephalus	Red-Headed Woodpecker
Molothrus ater	Brown-Headed Cowbird
Pooecetes gramineus	Vesper Sparrow
Spizella breweri	Brewer's Sparrow
Sturnella neglecta	Western Meadowlark
Turdus migratorinus	American Robin
Tyrannus verticalis	Western Kingbird
Zenaida macroura	Mourning Dove

Bird species identified at the Fox Ranch (Arikaree), Colorado during May and June of 2000 and 2001 along four 2 km transects.

Agelaius phoeniceus	Redwinged Blackbird
Aimophia cassinii	Cassin's Sparrow
Ammodramus savannarum	Grasshopper Sparrow
Bartramia longicauda	Upland Sandpiper
Buteo jamaicensis	Redtailed Hawk
Calamospiza melanocorys	Lark Bunting

Charadrius vociferus	Killdeer
Chondestes grammacus	Lark Sparrow
Chordeiles minor	Common Nighthawk
Colaptes auratus	Flicker
Colinus virginianus	Bob-white
Eremophila alpestris	Horned Lark
Hirundo pyrrhonata	Cliff Swallow
Hirundo rustica	Barn Swallow
Melanerpes erythrocephalus	Red-Headed Woodpecker
Molothrus ater	Brown-Headed Cowbird
Picoides villosus	Hairy Woodpecker
Pooecetes gramineus	Vesper Sparrow
Sturnella neglecta	Western Meadowlark
Troglodytes aedon	Wren
Tryannus verticalis	Western Kingbird
Turdus migratorinus	American Robin
Tyrannus tyrannus	Eastern Kingbird
Zenaida macroura	Mourning Dove

Bird species identified at the Smoky Valley Ranch, Kansas during May and June of 2000 and 2001 along four 2 km transects.

Ammodramus savannarum	Grasshopper Sparrow
Athene cunicularia	Burrowing Owl
Buteo jamaicensis	Redtailed Hawk
Buteo swainsoni	Swainson's Hawk
Calamospiza melanocorys	Lark Bunting
Carduelis tristis	American Goldfinch
Cathartes aura	Turkey Vulture
Charadrius vociferus	Killdeer
Chondestes grammacus	Lark Sparrow
Chordeiles minor	Common Nighthawk
Colaptes auratus	Flicker
Eremophila alpestris	Horned Lark
Hirundo pyrrhonata	Cliff Swallow
Melanerpes erythrocephalus	Red-Headed Woodpecker
Molothrus ater	Brown-Headed Cowbird
Riparia riparia	Bank Swallow
Spizella pusilla	Field Sparrow
Sturnella neglecta	Western Meadowlark
Tyrannus tyrannus	Eastern Kingbird
Tyrannus verticalis	Western Kingbird
Zenaida macroura	Mourning Dove

Bird species identified at the Saline Experimental Range, Kansas during May and June of 2000 and 2001 along two 2 km transects.

Agelaius phoeniceus	Redwinged Blackbird
Ammodramus savannarum	Grasshopper Sparrow
Buteo swainsoni	Swainson's Hawk
Charadrius vociferous	Killdeer
Chordeiles minor	Common Nighthawk
Falco columbarius	Merlin
Hirundo pyrrhonata	Cliff Swallow
Hirundo rustica	Barn Swallow
Molothrus ater	Brown-Headed Cowbird
Riparia riparia	Bank Swallow
Sayornis phoebe	Eastern Phoebe
Spiza Americana	Dickcissel
Sturnella magna	Eastern Meadowlark
Sturnella neglecta	Western Meadowlark
Tyrannus tyrannus	Eastern Kingbird
Zenaida macroura	Mourning Dove

Bird species identified at the Konza Prairie, Kansas during May and June of 2000 and 2001 along three 2 km transects.

Ammodramus savannarum	Grasshopper Sparrow
Bartramia longicauda	Upland Sandpiper
Cardinalis cardinalis	Northern Cardinal
Carduelis tristis	American Goldfinch
Cathartes aura	Turkey Vulture
Chordeiles minor	Common Nighthawk
Colinus virginianus	Bob-white
Corvus brachyrhynchos	American Crow
Dumetella carolinensis	Gray Catbird
Geothlypis trichas	Common Yellow Throat
Guiraca caerulea	Blue Grosbeak
Hirundo rustica	Barn Swallow
Melospiza melodia	Song Sparrow
Molothrus ater	Brown-Headed Cowbird
Spiza Americana	Dickcissel
Spizella pusilla	Field Sparrow
Sturnella magna	Eastern Meadowlark
Toxostoma rufum	Brown Thrasher
Tyrannus tyrannus	Eastern Kingbird
Vireo griseus	White-eyed Vireo
Zenaida macroura	Mourning Dove

APPENDIX 4: PLANT SPECIES LISTS

Plant species identified at the Pawnee National Grasslands, Colorado along four 2 km transects. Plant species presence was surveyed within 1-m^2 quadrats at 50 m intervals during May and early June 2000 to assess early-season vegetation and August 2000 to incorporate late-season grasses and forbs.

Agropyron smithii	Western wheatgrass
Allium canadense	Wild onion
Amaranthus retroflexus	Rough pigweed
Ambrosia psilostachya	Western ragweed
Argemone polyanthemos	Prickly poppy
Aristida purpurea	Three-Awn
Artemisia frigida	Pasture sagebrush
Artemisia ludoviciana	Prairie sage, White sage
Aster ericoides	White Aster
Astragalus gracilis	Slender Milk-vetch
Astragalus mollissimus	Woolly locoweed
Atriplex canescens	Four-winged saltbrush
Bouteloua curtipendula	Sidoats grama
Bouteloua gracilis	Blue grama
Bromus tectorum	Cheatgrass, Downy brome
Buchloe dactyloides	Buffalo-grass
Calylophus serrulatus	Plains yellow primrose
Carex filifolia	Theadleaf sedge
Chenopodium leptophyllum	Narrowleaf goosefoot
Chrysothamnus nauseosus	Rabbitbrush
Cirsium altissimum	Tall or Roadside thistle
Cirsium undulatum	Wavy-leaved thistle
Comandra umbellata	Bastard toadflax
Dalea candida	White prairie clover
Delphinium virescens	Prairie larkspur
Distichlis spicata	Saltgrass, Inland saltgrass
Equisetum laevigatum	Smooth scouring rush
Erigeron pumilus	Low daisy
Eriogonum effusum	Bushy eriogonum, Spreading wild buckwheat
Euphorbia spathulata	warty spurge
Evolvulus nuttallianus	Nuttall's Evolvulus, Shaggy dwarf morning-glory
Gaura coccinea	Scarlet gaura

Grindelia squarrosa	Curly-top gumweed
Gutierrezia sarothrae	Broom snakeweed
Haplopappus spinulosus	Cutleaf ironplant
Helianthus rigidus	Stiff sunflower
Hordeum jubatum	Foxtail barley
Hymenopappus filifolius	Fineleaf hymenopappus
Hymenoxys acaulis	
Iopmopsis laxiflora	Looseflowered gilia
Juncus balticus	Baltic rush
Kochia scoparia	Kochia, Fire-weed, Summer or mock cypress
Lappula spp.	
Lathyrus polymorphus	Hoary peavine, Hoary vetchling
Lepidium densiflorum	Peppergrass
Liatris punctata	Dotted gay-feather, Blazing star
Linum rigidum	Yellow flax
Lygodesmia juncea	Skeleton weed
Macaranthea tenacetifolia	
Melilotus officinalis	Yellow sweet-clover
Mirabilis linearis	Narrowleaf four o'clock
Oenothera coronopifolia	Cut-leaf evening primrose
Opuntia macrorhiza	Plains prickly pear
Opuntia polyacantha	Starvation cactus, Plains prickly pear
Oryzopsis hymenoides	Ricegrass
Oxytropis sericea	White locoweed
Picradeniopsis oppositifolia	Plains bahia
Plantago patagonica	Woolly plantain, Patagonian plantain
Psoralea lanceolata	Lemon scurf-pea
Psoralea tenuiflora	Wild alfalfa, Scurfy pea
Ratibida columnifera	Prairie coneflower
Salsola iberica	Russian-thistle, tumbleweed
Schedonnardus paniculatus	Tumblegrass
Scutellaria brittonii	Skullcap, Britton's skullcap
Senecio tridenticulatus	Prairie Groundsel
Sitanion hystrix	Squirreltail
Sonchus asper	Prickly sow thistle
Sophora nuttaliana	White loco
Sphaeralcea coccinia	Copper mallow, Red false mallow
Sporobolus cryptandrus	Sand dropseed
Stipa comata	Needle-and-thread
Talinum parviflorum	Fame-flower, Prairie fameflower
Taraxacum officinale	Common dandelion
Thelesperma filifolium	Greenthread
Thelesperma megapotamicum	Rayless greenthread
Tradescantia occidentalis	Spiderwort

Tragopogon dubius	Goat's beard, Western salsify
Verbena bracteata	Prostrate vervain
Vicia americana	American vetch
Vulpia octoflora	Sixweeks fescue
Yucca glauca	Spanish bayonet

Plant species identified at the Fox Ranch (Arikaree), Colorado along four 2 km transects. Plant species presence was surveyed within 1-m^2 quadrats at 50 m intervals during May and early June 2000 to assess early-season vegetation and August 2000 to incorporate late-season grasses and forbs.

Agropyron smithii	Western Wheatgrass
Ambrosia psilostachya	Western Ragweed
Ambrosia tomentosa	Perennial Bursage
Andropogon gerardii	Big Blustern
Andropogon scoparius	Little Bluestern
Apocynum cannabinum	Indian Hemp Dogbane, Prairie Dogbane
Argemone polyanthemos	Prickly Poppy
Aristida purpurea	Three-Awn
Artemisia filifolia	Silvery wormwood, Sand Sagebrush
Artemisia ludoviciana	Prairie Sage, White Sage
Asclepias speciosa	Showy Milkweed
Aster Ericoides	White Aster
Aster sericeus	Silky Aster
Astragalus mollissimus	Woolly Locoweed
Bouteloua curtipendula	Sidoats Grama
Bouteloua gracilis	Blue Grama
Bouteloua hirsuta	Hairy Grama
Bromus tectorum	Cheatgrass, Downy Brome
Buchloe dactyloides	Buffalo-Grass
Calylophus serrulatus	Plains Yellow Primrose
Cenchrus longispinus	Sandbur
Chenopodium album	Lamb's Quarters
Chenopodium leptophyllum	Narrowleaf Goosefoot
Chenopodium spp.	
Chrysopsis villosa	Golden Aster
Cirsium undulatum	Wavy-Leaved Thistle
Comandra umbellata	Bastard Toadflax
Cucurbita foetidissima	Buffalo Ground
Dalea purpurea	Purple Prairie Clover
Digitaria sanguinalis	Hairy Crabgrass
Distichlis spicata	Saltgrass, Inland Saltgrass
Equisetum laevigatum	Smooth Scouring Rush

Erigeron pumilus	Low Daisy
Euphorbia spathulata	Warty spurge
Evolvulus nuttallianus	Evolvulus, Nuttall's Evolvulus
Gaura coccinea	Scarlet Gaura
Geranium fremontii	
Grindelia squarrosa	Curly-Top gumweed
Gutierrezia sarothrae	Broom snakeweed
Haplopappus spinulosus	Cutleaf Ironplant
Hedeoma hispida	Rough Falso Pennyroyal
Helianthus annuus	Common sunflower
Helianthus rigidus	Stiff sunflower
Hordeum jubatum	Foxtail barley
Hymenopappus filifolius	Fineleaf Hymenopappus
Hymenopappus scabiosaeus	Old Plainsman
Hymenoxys acaulis	Stemless Hymenoxys
Kochia scoparia	Kochia, Fire-Weed, Summer or Mock Cypress
Koeleria pyramidata	Junegrass
Lactuca serriola	Prickly lettuce
Lepidium densiflorum	Peppergrass
Lesquerella ludoviciana	Silvery Bladder-Pod, Bladderpod
Leucelene ericoides	Rose heath
Liatris punctata	Dotted Gay-Feather, Blazing Star
Linum rigidum	Yellow Flax
Lithospermum incisum	Narrow-Leaved Puccoon
Lygodesmia juncea	Skeleton Weed
Muhlenbergia spp.	
Opuntia macrohiza	Plains Prickly Pear
Oryzopsis hymenoides	Ricegrass
Panicum virgatum	Switchgrass
Paspalum setaceum	Thin paspalum
Penstemon albidus	White penstemmon, White Beardtongue
Physalis pumila	Prairie Ground Cherry
Plantago patagonica	Woolly Plantain, Patagonian Plantain
Polygonum aviculare	Devil's Shoestrings, Knotweed
Populus deltoides	Cottonwood
Psoralea lanceolata	Lemon Scurf-Pea
Psoralea tenuiflora	Wild Alfalfa, Scurfy Pea
Rumex venosus	Veiny Dock, Wild Begonia
Salsola iberica	Russian-thistle, Tumbleweed
Sitanion hystrix	Squirreltail
Sonchus asper	Prickly Sow thistle
Sorghastrum nutans	Indian Grass
Sphaeralcea coccinia	Copper Mallow, Red False Mallow
Sporobolus cryptandrus	Sand Dropseed

Stipa comata	Needle-and-Thread
Talinum parviflorum	Fame-Flower, Prairie Fameflower
Thelesperma filifolium	Greenthread
Thelesperma megapotamicum	Rayless Greenthread
Toxicodendron radicans	Poison ivy
Tradescantia occidentalis	Spiderwort
Tragopogon dubius	Goat's Beard, Western Salsify
Viola Nuttallii	Nuttall's Violet, Yellow Prairie Violet
Vulpia octoflora	Sixweeks fescue
Yucca glauca	Spanish Bayonet

Plant species identified at the Smoky Valley Ranch, Kansas along four 2 km transects. Plant species presence was surveyed within 1-m^2 quadrats at 50 m intervals during May and early June 2000 to assess early-season vegetation and August 2000 to incorporate late-season grasses and forbs.

Agropyron smithii	Western wheatgrass
Allium canadense	Wild onion
Ambrosia psilostachya	Western ragweed
Andropogon gerardii	Big bluestem
Andropogon scoparius	Little bluestem
Aristida purpurea	Three-awn
Artemisia filifolia	Silvery wormwood, Sand sagebrush
Artemisia ludoviciana	Prairie sage, white sage
Asclepias verticillata	Whorled milkweed
Aster ericoides	White aster
Astragalus mollissimus	Woolly locoweed
Astragalus spp.	
Bouteloua curtipendula	Sidoats grama
Bouteloua gracilis	Blue grama
Bouteloua hirsuta	Hairy grama
Bromus tectorum	Cheatgrass, Downy brome
Buchloe dactyloides	Buffalo-grass
Callirhoe involucrata	Purple poppy mallow
Calylophus serrulatus	Plains yellow primrose
Carex nebrascensis	Nebraska sedge
Chenopodium album	Lamb's quarters
Chenopodium leptophyllum	Narrowleaf goosefoot
Chenopodium spp.	
Cirsium undulatum	Wavy-leaved thistle
Dalea candida	White prairie clover
Delphinium virescens	Prairie larkspur, plains larkspur?
Digitaria sanguinalis	Hairy crabgrass
Distichlis spicata	Saltgrass, Inland saltgrass

Euphorbia marginata	Snow-on-the-mountain
Euphorbia spathulata	Warty spurge
Gaillardia pulchella	Indian blanket
Gaura coccinea	Scarlet gaura
Grindelia squarrosa	Curly-top gumweed
Gutierrezia sarothrae	Broom snakeweed
Haplopappus spinulosus	Cutleaf ironplant
Hedeoma hispida	Rough false pennyroyal
Helianthus annuus	Common sunflower
Helianthus rigidus	Stiff sunflower
Hordeum jubatum	Foxtail barley
Hymenopappus scabiosaeus	Old plainsman
Hymenoxys acaulis	
Kochia scoparia	Kochia, Fire-weed, Summer or mock cypress
Lactuca serriola	Prickly lettuce
Lappula occidentalis	Flatspine stickseed
Lappula spp.	
Lepidium densiflorum	Peppergrass
Lesquerella ludoviciana	Silvery bladder-pod, Bladderpod
Leucelene ericoides	Rose heath
Liatris punctata	Dotted gay-feather, Blazing star
Linum rigidum	Yellow flax
Lomatium foeniculaceum	Wild parsley
Lygodesmia juncea	Skeleton weed
Melilotus officinalis	Yellow sweet-clover
Mentzelia decapetala	Giant evening-star, Ten-petal mentzelia
Opuntia macrorhiza	Plains prickly pear
Panicum virgatum	Switchgrass
Plantago patagonica	Woolly plantain, Patagonian plantain
Polygonum aviculare	Devil's shoestrings, Knotweed
Polypogon monspeliensis	Rabbitfoot grass
Populus deltoides	Cottonwood
Psoralea argophylla	Silver-leaf scurf-pea
Psoralea esculenta	Breadroot scruf-pea, prairie-turnip
Psoralea lanceolata	Lemon scurf-pea
Psoralea tenuiflora	Wild alfalfa, scurfy pea
Ratibida columnifera	Prairie coneflower
Salsola iberica	Russian-thistle, tumbleweed
Schedonnardus paniculatus	Tumblegrass
Senecio plattensis	Prairie ragwort
Sitanion hystrix	Squirreltail
Sonchus asper	Prickly sow thistle
Sphaeralcea coccinia	Copper mallow, Red false mallow
Sporobolus cryptandrus	Sand Dropseed

Talinum parviflorum	Fame-flower, Prairie fameflower
Thelesperma filifolium	Greenthread
Thelesperma megapotamicum	Rayless greenthread
Tragopogon dubius	Goat's beard, Western salsify
Viola nuttallii	Nuttall's violet, Yellow prairie violet
Vulpia octoflora	Sixweeks fescue
Yucca glauca	Spanish bayonet

Plant species identified at the Saline Experimental Range, Kansas along two 2 km transects. Plant species presence was surveyed within 1-m^2 quadrats at 50 m intervals during May and early June 2000 to assess early-season vegetation and August 2000 to incorporate late-season grasses and forbs.

Achillea millefolium	Yarrow
Agropyron smithii	Western wheatgrass
Allium canadense	Wild Onion
Ambrosia psilostachya	Western ragweed
Amorpha canescens	Lead plant
Andropogon gerardii	Big bluestem
Andropogon ischaemum	King ranch bluestem, Turkestan bluestem
Andropogon scoparius	Little bluestem
Apocynum cannabinum	Indian hemp dogbane, Prairie dogbane
Aristida purpurea	Three-Awn
Artemisia ludoviciana	Prairie sage, White sage
asclepias viridis	Spider milkweed
Aster ericoides	White aster
Aster laevis	Smooth blue aster
Bouteloua curtipendula	Sidoats grama
Bouteloua gracilis	Blue grama
Bouteloua hirsuta	Hairy grama
Bromus tectorum	Cheatgrass, Downy brome
Buchloe dactyloides	Buffalo-grass
Callirhoe involucrata	Purple poppy mallow
Calyophus serrulatus	Plains yellow primrose
Chenopodium leptophyllum	Narrowleaf goosefoot
Cirsium altissimum	Tall of Roadside thistle
Cirsium undulatum	Wavy-leaved thistle
Dalea purpurea	Purple prairie clover
Delphinium virescens	Prairie larkspur
Dichanthelium oligosanthes	Heller's rosette grass
Distichlis spicata	Saltgrass, Inland saltgrass
Echinacea angustifolia	Purple coneflower
Eleocharis spp.	
Elymus canadensis	Canada wild rye

Erigeron strigosus	Daisy fleabane
Eupatorium altissimum	Tall thoroughwort
Euphorbia marginata	Snow-on-the-mountain
Euphorbia spathulata	Warty spurge
Festuca octoflora	Six-weeks Fescue
Gaura coccinea	Scarlet gaura
Gutierrezia sarothrae	Broom snakeweed
Hedyotis hispida	Rough false pennyroyal
Helianthus annuus	Common sunflower
Helianthus rigidus	Stiff sunflower
Hordeum jubatum	Foxtail barley
Hymenopappus scabiosaeus	Old plainsman
Koeleria pyramidata	Junegrass
Lappula spp	
Lepidium densiflorum	Peppergrass
Leucelene ericoides	Rose heath
Liatris punctata	Dotted gay-feather, Blazing star
Linum rigidum	Yellow flax
Lithospermum incisum	Narrow-leaved puccoon
Lomatium foeniculaceum	Wild parsley
Medicago lupulina	Black medic
Melilotus officinalis	Yellow sweet-clover
Opuntia macrohiza	Plains prickly pear
Oxytropis campestris	Field locoweed
Panicum virgatum	Switchgrass
Plantago patagonica	Woolly plantain, Patagonian plantain
Poa compressa	Canada bluegrass
Poa pratensis	Kentucky bluegrass
Polygala verticillata	Whorled milkwort
Psoralea argophylla	Silver-leaf scurf pea
Psoralea esculenta	Breadfoot scurf-pea, Prairie turnip
Psoralea tenuiflora	Wild alfalfa, scurfy pea
Ratibida columnifera	Prairie coneflower
Rhus aromatica	Fragrant Sumac, Polecat Bush
Rhus glabra	Smooth sumac
Schrankia nuttallii	Sensitive brier
Scutellaria resinosa	Sticky skullcap
Senecio plattensis	Prairie ragwort
Sitanion hystrix	Squirreltail
Solanum rostratum	Buffalo-bur, Kansas thistle
Solidago canadensis	Canada goldenrod
Solidago rigida	Rigid or Stiff goldenrod
Sonchus asper	Prickly sow thistle
Sorghastrum nutans	Indian Grass

Spermolepis inermis	Scale-seed
Sphaeralcea coccinia	Copper mallow, Red false mallow
Sphenopholis obtusata	Wedgegrass
Sporobolus asper	Rough dropseed
Stenosiphon linifolius	False gaura
Symphoricarpos orbiculatus	Coralberry, Buckbrush
Tragopogon dubius	Goat's beard, Western Salsify
Vicia americana	American Vetch
Vitis riparia	River-bank grape
Yucca glauca	Spanish Bayonet

Plant species identified at the Konza Prairie, Kansas along three 2 km transects. Plant species presence was surveyed within 1-m^2 quadrats at 50 m intervals during May and early June 2000 to assess early-season vegetation and August 2000 to incorporate late-season grasses and forbs.

Achillea millefolium	Yarrow
Agropyron smithii	Western wheatgrass
Ambrosia psilostachya	Western ragweed
Amorpha canescens	Lead plant
Andropogon gerardii	Big bluestem
Andropogon scoparius	Little bluestem
Artemisia ludoviciana	Prairie sage, White sage
Asclepias speciosa	Showy milkweed
Asclepias tuberosa	Butterfly milkweed
Asclepias verticillata	Whorled milkweed
Asclepias viridis	Spider milkweed
Aster ericoides	White aster
Aster laevis	Smooth blue aster
Aster oblongifolius	Aromatic aster
Baptisia australis	Blue false indigo
Bouteloua curtipendula	Sidoats grama
Bouteloua gracilis	Blue grama
Bouteloua hirsuta	Hairy grama
Bromus tectorum	Cheatgrass, Downy brome
Buchloe dactyloides	Buffalo-grass
Callirhoe involucrata	Purple poppy mallow
Calyophus serrulatus	Plains yellow primrose
Carex (heliophylum)	
Ceanothus herbaceus	New Jersey tea
Cirsium altissimum	Tall or Roadside thistle
Cirsium undulatum	Wavy-leaved thistle
Comandra umbellata	Bastard toadflax
Cornus drummondii	Rough-leaved dogwood

Dalea candida	White prairie clover
Dalea multiflora	Round-headed prairie clover
Dalea purpurea	Purple prairie clover
Descurainia sophia	Flixweed
Dichanthelium oligosanthes	Heller's rosette grass
Distichlis spicata	Saltgrass, Inland saltgrass
Echinacea angustifolia	Purple coneflower
Eleocharis spp.	
Elymus canadensis	Canada wild rye
Eragrostis spectabilis	Purple lovegrass
Erigeron strigosus	Daisy fleabane
Eupatorium altissimum	Tall thoroughwort
Euphorbia marginata	Snow-on-the-mountain
Euphorbia spathulata	Warty spurge
Galium circaezans	Woods bedstraw
Gleditsia triacanthos	Honey locust
Hedeoma hispida	Rough false pennyroyal
Hedyotis nigricans	Narrowleaf bluet
Helianthus rigidus	Stiff sunflower
Hordeum jubatum	Foxtail barley
Hymenopappus scabiosaeus	Old plainsman
Koeleria pyramidata	Junegrass
Kuhnia eupatorioides	False boneset
Lepidium densiflorum	Peppergrass
Lespedeza capitata	Round-headed lespedeza
Lespedeza violacea	Prairie lespedeza
Liatris aspera	Gay-feather, Rough blazing star
Liatris punctata	Dotted gay-feather, Blazing star
Linum rigidum	Yellow flax
Lomatium foeniculaceum	Wild parsely
Oenothera macrocarpa	Bigfruit evening-primrose
Oenothera speciosa	Showy white evening-primrose, pinkladies
Oxalis stricta	Yellow wood sorrel
Panicum virgatum	Switchgrass
Physalis pumila	Prairie ground cherry
Plantago patagonica	Woolly Plantain, Patagonian Plantain
Psoralea argophylla	Silver-leaf scurf-pea
Psoralea esculenta	Breadroot scurf-pea, Prairie-turnip
Psoralea tenuiflora	Wild alfalfa, scurfy pea
Ratibida columnifera	Prairie coneflower
Rhus aromatica	Fragrant sumac, Polecat bush
Rhus glabra	Smooth sumac
Rosa arkansana	Prairie wild rose
Rubus spp.	

Ruellia humilis	Fringeleaf ruellia
Schrankia nuttallii	Sensitive brier
Senecio plattensis	Prairie ragwort
Silphium laciniatum	Compass plant
Solidago canadensis	Canada goldenrod
Solidago carolinense	Carolina horse-nettle
Solidago missouriensis	Prairie goldenrod
Solidago ridiga	Rigid or Stiff goldenrod
Sorghastrum nutans	Indian grass
Spermolepis inermis	Scale-seed
Sporobolus asper	Rough dropseed
Sporobolus cryptandrus	Sand Dropseed
Sporobolus heterolepis	Prairie dropseed
symphoricarpos orbiculatus	Coralberry, buckbrush
Teucrium canadense	American germander, Wood sage
Tragia betonicifolia	Noseburn
Triodanis leptocarpa	Venus's looking glass
Vernonia baldwinii	Western ironseed
Vicia americana	American vetch
Vitis riparia	River-bank grape