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Research Article

Taxon-dependent scaling: beetles, birds, and vegetation at four North American grassland sites

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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. We consider whether the relative importance of different scales is associated with organism mobility, and whether this relationship is independent of landscape characteristics. We observed abundances of particular species 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 central Colorado to tallgrass prairie in central 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. Plant, beetle and bird community composition was explained by environmental factors measured at all three scales. 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. We conclude that, independent of the mobility of a taxonomic group, factors at several scales are important in explaining community composition. The importance of different scales shifts along a regional gradient, and the variability between sites is high even for nearby sites.

Introduction

A primary goal of community ecology is to understand the species–environmental relationships underlying ecological patterns. Accordingly, it might be expected that defining these associations at one location would provide insights into the patterns that exist across a region or even at a location just down the road. If regional planning is to be effective for managing and conserving different taxonomic groups, developing predictions across sites and taxonomic groups are essential.

Hansen and Urban (1992) showed that bird communities from distinct biomes respond differently to structural aspects of the landscape, such as patch size and distance to forest edge, and McCulley and Burke (2004) describe changes in microbial communities across a regional moisture gradient. Regional changes in species richness and community composition have been documented for both plants and animals and attributed to climate and historical factors (Whittaker 1975; Brown and Lomolino 1998). In general, however, there is a paucity of analyses assessing changes in community response to landscape structure across a regional gradient.

The issue is complicated because individuals of a species may respond to different features of the environment at different scales (Brown 1984; Ricklefs 1987; McIntyre 1997; Ohmann and Spies 1998), and different taxa exhibit different scaling responses (Allen and Starr 1982; Addicott et al. 1987; Wiens 1989; Schneider 1994; Cushman and McGarigal 2002). For example, Cushman and McGarigal (2002) measured environmental variables at three scales, thus enabling the explained variance of bird communities in the Oregon Coast Range US to be partitioned among different hierarchical scales. Using hierarchical variance partitioning, hypotheses can be generated concerning the scale of response of different organisms or taxonomic groups. This approach enables 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. Most studies, however, have 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.

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

Methods

Study sites

This research was conducted at the Konza Prairie Long-Term Ecological Research site, which is owned by The Nature Conservancy and managed by Kansas State University; the Smoky Valley and Fox Ranches (Arikaree), both Nature Conservancy properties; and the Shortgrass Steppe Long-Term Ecological Research site located within the Pawnee National Grasslands (Figure 1). These sites cross an environmental gradient ranging from tallgrass praire in the east at Konza with average precipitation of 835 mm to shortgrass prairie in the west with an average of 320 mm precipitation. 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 transects randomly, they were positioned to encompass a wide range of the variation that exists within each site in order to assess the influence of local variation on biological communities. 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.

Biological data

Data on vegetation, ground-dwelling beetles, and birds were collected along each transect (Table 1). Plant composition at each sampling station 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. Species that were unidentifiable in the field were collected and identified using specimens at the herbaria of Konza prairie and Colorado State University. 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 analysis.

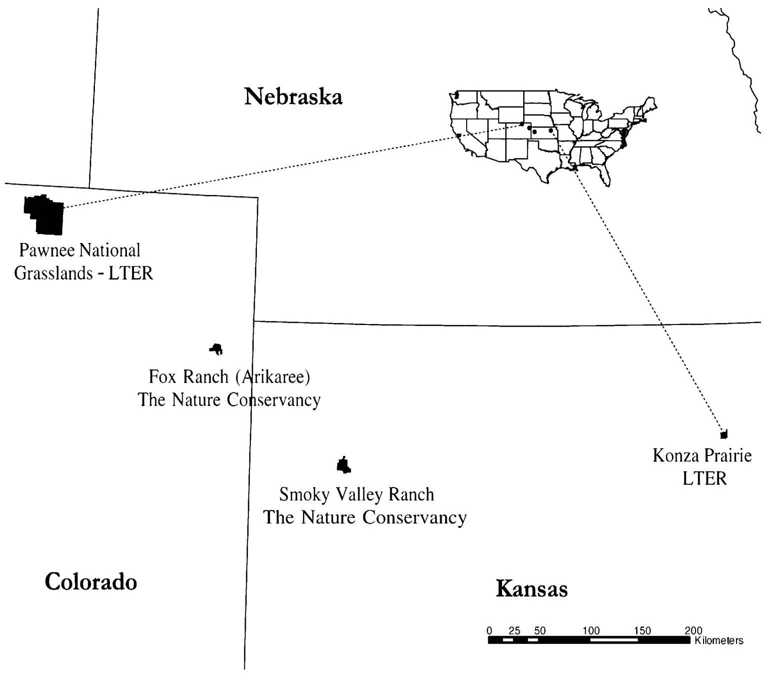

Figure 1. Location of study sites.

Table 1. Number of species identified for each taxonomic group along eight transects.

	P1	P2	A1	A2	S1	S2	K1	K2
Plants	46	39	60	42	49	45	56	65
Beetles	39	30	48	40	37	37	46	55
Birds	9	11	9	12	10	9	8	9

The transects are identified as P1/P2 – the Pawnee National Grasslands, A1/A2 – the Fox Ranch (Arikaree), S1/S2 – the Smoky Valley Ranch, and K1/K2 – the Konza Prairie.

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 preserved 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 to assess bird community composition. Each transect was surveyed once during May and early June 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 and later mapped by measuring the distance and angle from the surveyor to the bird as well as the distance to the next sampling station (Buckland et al. 1993). Distance was measured using electronic range finders. 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, rather than 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 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. Canonical analysis showed that bird and beetle community structure were similar in the 2 years, so we combined the results from both years in order to portray the bird and beetle communities through time more accurately. 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 (see Appendix 1 for descriptions). At the trap scale (1 m^2), we sampled soil, vegetation height, percent bare ground, and soil hardness. Soil samples were returned to the laboratory to measure soil pH and percent sand, silt, and clay for each location. The soil samples used for texture and pH were from a single sample at each station of the top 15 cm of soil. For the three western 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. We also measured soil hardness four times at each location using a soil penetrometer.

At the local scale, we 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, we estimated the percent cover of each shrub and cactus species. Within a 30-m radius we measured the distance to the nearest cactus, shrub (< 1 m in height), and large shrub/tree (1–3 m in height) in each quadrant.

At a regional scale, we 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 2000. The imagery and digital elevation models had 30 m resolution. Based on the digital elevation models, we 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, not 350 degrees) two values for aspect were calculated: degrees from north and degrees from west. Using a geographic information system (ESRI 2002), each sampling location was associated with the Landsat band values (1–5, 6a, 6b, 7–8), elevation, aspect values, and slope. The geographic location (UTM x and y coordinates) of each sampling station was also included in the analysis.

Because different processes act at different scales, comparisons conducted across scales necessarily employ different variables. For instance, a variable such as percent cover of a shrub species would be meaningless at 1 m^2 and would not accurately portray the differences in shrub density at different sites. We compared the explanatory power of variables at different scales using those variables that we considered to be most appropriately measured at a particular scale.

Statistical analysis

Canonical correspondence analysis (Terbraak 1986) is one commonly used method for determining the environmental factors that are related to community structure. Canonical correspondence analysis is a direct ordination technique that uses environmental and biological data to examine species–environment relationships (Palmer 1993). 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. More recently, Cushman and McGarigal (2002) extended this model by introducing hierarchical canonical variance partitioning which partitions the explained variance (constrained inertia) of a canonical correspondence analysis by the different scales at which the environmental variables were measured.

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, we used hierarchical canonical variance partitioning with the addition of geographic space (i.e. UTM x and y coordinates) as explanatory variables. 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, geographic coordinates were also included to account for spatial autocorrelation, so for each of the seven components there is an additional partition corresponding to the variance explained by both the component listed above and by geographic space. A 15th component is the variance explained by geographic space. Combing hierarchical canonical variance partitioning with geographic coordinates thus results in 15 components of variance. These 15 components were used to compare the variance explained in community composition by different scales of environmental variables and geographic location (i.e. spatial autocorrelation).

To reduce the number of explanatory environmental variables, the 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 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; http://www.r-project.org/), 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. A liberal test statistic of 0.15 was used due to the ability of canonical correspondence analysis to handle numerous, intercorrelated explanatory variables. 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. These selected variables were then analyzed using hierarchical canonical variance partitioning.

Based on the results of these analyses, we made two primary comparisons. First, we compared the amount of variance of each community along each transect explained by the environmental variables alone, by environmental variables plus geographic space, and by geographic space alone. Second, we 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 explaining variance within a particular transect, we also compared the specific variables chosen at different locations and for different taxa to assess the similarities in these explanatory variables.

Results

At least 33% of the variance in community composition was explained for each community analyzed using canonical correspondence analysis (Figure 2). The maximum variance explained for any community was 72% for the vascular plants along transect 2 of Konza (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

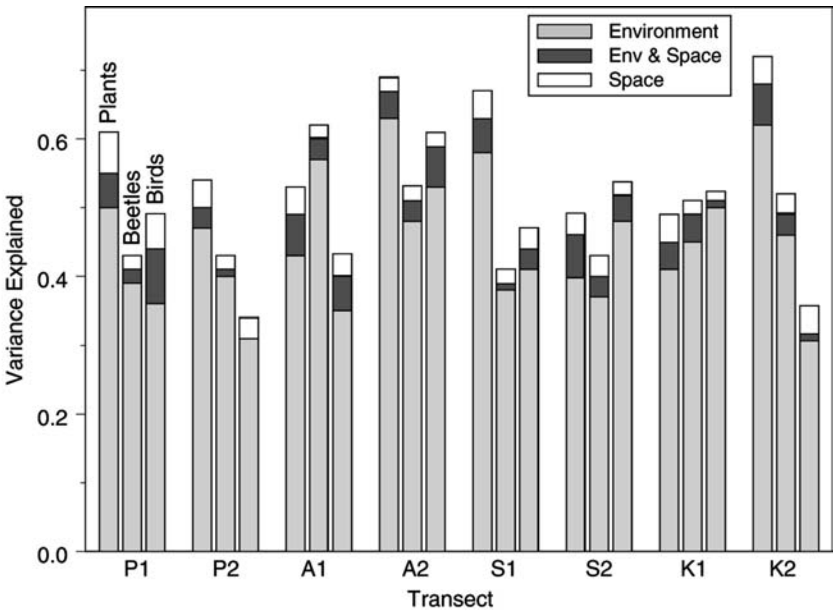

Figure 2. Amount of variance explained for plant, beetle, and bird communities at eight transects using canonical correspondence analysis. In each set of bars the first bar refers to plants, the second bar refers to beetles, and the third bar refers to birds. The variance has been partitioned by environmental variables and geographic space. The transects are identified as P1/P2 – the Pawnee National Grasslands, A1/A2 – the Fox Ranch (Arikaree), S1/S2 – the Smoky Valley Ranch, and K1/K2 – the Konza Prairie.

was explained for the vascular plants. For birds and 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 (Figure 2). In only two instances (birds and plants along transect 1 of Pawnee) was the explained variance increased by more than 5%. For the beetle communities, incorporating geographic space only increased the explained variance by an average of 2.3%. The limited explanatory power of geographic space in these analyses suggests that the 50-m spacing of sampling locations in these systems produced largely independent samples.

At Pawnee, the partitioning of explained variance among scales was very similar for the two transects for both the vascular plants and beetles (Figure 3 and Table 2). Comparing the three taxonomic groups along transect P1, the local-scale variables explained 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. The explained variance along transect P2 was more evenly distributed among the three scales than P1, with the landscape-scale variables explaining the most variance.

None of the transects at Arikaree showed a clear pattern or dominance of one scale of variables in explaining variance in community composition. Compared to Pawnee, however, the trap-scale variables at Arikaree contributed more to the amount of variance explained for all taxonomic groups. Along transect A2 the trap-scale 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, 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, we expected that there

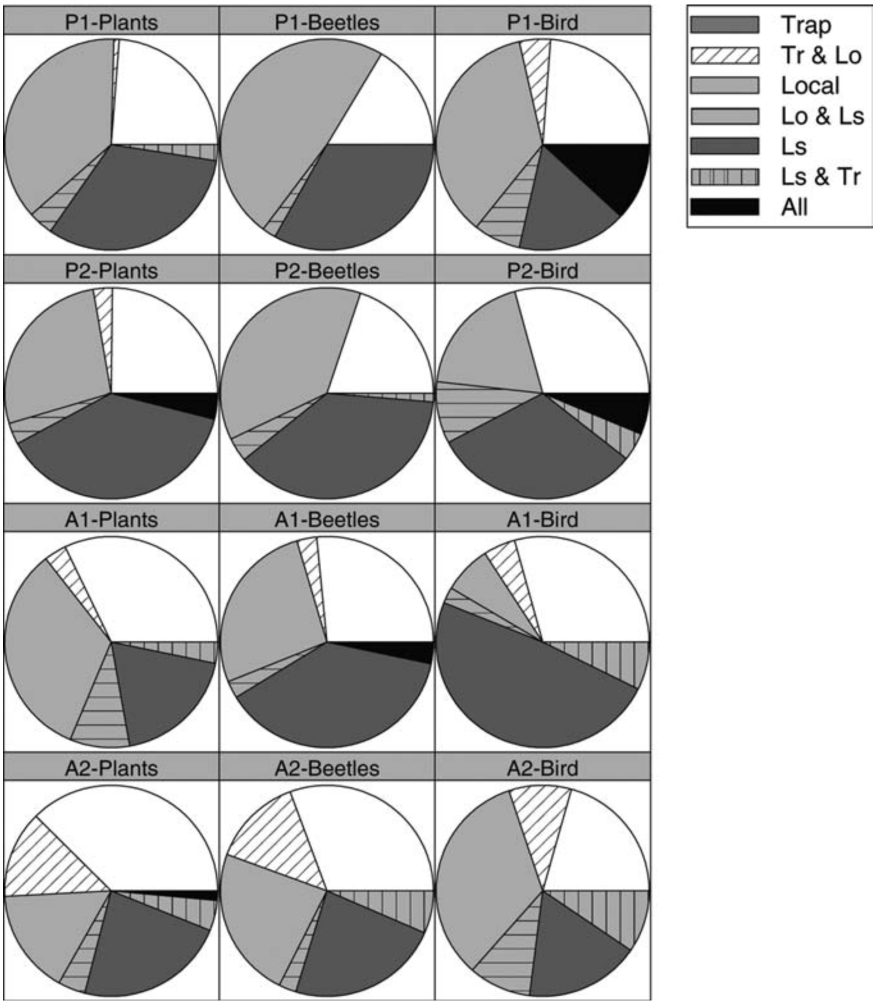

Figure 3. Proportion of the total variance explained by different scales of environmental variables using hierarchical canonical variance partitioning for plant, beetle, and bird communities at eight transects. The actual amount of variance explained by each scale is listed in Table 2. In certain instances portions of variance were explained by more than one scale of environmental variables or even all three scales. 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 P1/P2, transects at the Pawnee National Grasslands, A1/A2 – transects at the Fox Ranch (Arikaree), S1/S2 – the transects at the Smoky Valley Ranch, and K1/K2 – transects at the Konza Prairie.

would be systematic shifts in the response of different taxonomic groups to the scale of environmental variables. However, 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. 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, our 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. These results suggest no systematic shift in the scale of explanatory variables for any of these taxonomic groups.

One pattern that is evident at different sites is the amount of variance that is explained by more than one scale of environmental variables. Along many of these transects, but particularly at Arikaree and Smoky Valley there was overlap in

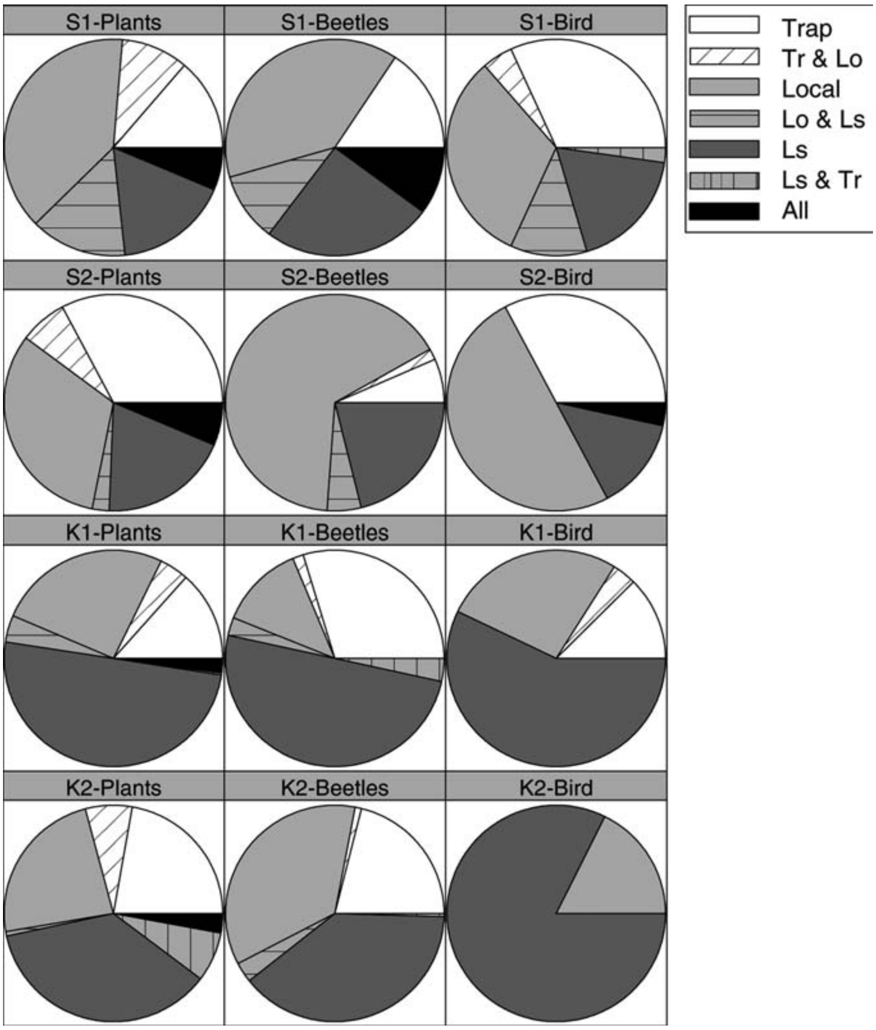

Figure 3. Continued.

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.

Beyond examining the scale at which birds, beetles, and plants respond to environmental heterogeneity, we also examined the specific variables that were included in the analysis (See Appendix 2 for details). 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 our 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. Of the 11 variables selected for analysis of beetle community composition on transect P1, seven 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 the two transects. For the analysis of beetles from the two transects at Pawnee, only three of the variables, all of which were associated with the presences of cactus, occurred in both.

Table 2. Amount of variance explained for plant, beetle, and bird communities at eight transects using hierarchical canonical variance partitioning for plant, beetle, and bird communities.

Scale	Plants	Beetles	Birds	Plants	Beetles	Birds
	P1			P2		
Trap	0.13	0.07	0.10	0.13	0.08	0.09
Trap & local	0.00	0.00	0.02	0.01	0.00	−0.01
Local	0.20	0.20	0.15	0.14	0.15	0.06
Landscape & local	0.02	0.01	0.03	0.02	0.02	0.03
Landscape	0.18	0.14	0.07	0.19	0.15	0.10
Trap & landscape	0.01	0.00	0.00	0.00	0.01	0.01
All scales	0.00	0.00	0.05	0.02	0.00	0.02
	A1			A2		
Trap	0.16	0.16	0.12	0.25	0.16	0.13
Trap & local	0.02	0.02	0.02	0.09	0.07	0.06
Local	0.16	0.16	0.03	0.11	0.12	0.21
Landscape & local	0.04	0.02	0.01	0.03	0.01	0.06
Landscape	0.09	0.23	0.20	0.15	0.12	0.11
Trap & landscape	0.02	0.00	0.03	0.03	0.03	0.06
All scales	−0.01	0.02	−0.01	0.01	0.00	−0.01
	S1			S2		
Trap	0.09	0.06	0.14	0.15	0.03	0.19
Trap & local	0.00	0.00	0.01	−0.01	0.00	−0.01
Local	0.11	0.10	0.08	0.09	0.08	0.08
Landscape & local	0.09	0.04	0.05	0.01	0.02	−0.01
Landscape	0.25	0.15	0.14	0.15	0.26	0.29
Trap & landscape	0.06	0.00	0.02	0.03	0.01	−0.01
All scales	0.04	0.04	0.00	0.03	0.00	0.02
	K1			K2		
Trap	0.06	0.15	0.07	0.15	0.10	0.00
Trap & local	0.00	0.02	−0.03	0.05	0.00	0.00
Local	0.23	0.24	0.32	0.25	0.19	0.28
Landscape & local	0.02	0.01	0.00	0.00	0.01	−0.01
Landscape	0.12	0.06	0.15	0.16	0.17	0.06
Trap & landscape	0.02	0.01	0.02	0.05	0.00	0.00
All scales	0.01	0.00	−0.02	0.02	0.00	0.00

In certain instances portions of variance were explained by more than one scale of environmental variables or even all three scales. 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 P1/P2 – the Pawnee National Grasslands, A1/A2 – the Fox Ranch (Arikaree), S1/S2 – the Smoky Valley Ranch, and K1/K2 – the Konza Prairie.

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: mean vegetation height, percent silt, proportion of quadrats containing shrubs < 1 m tall, 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 by the landscape-scale variables, there was very little similarity among the taxonomic 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, five of the same variables were selected for the analyses of beetles and plants along transect K1; four of these were local-scale variables. Eight variables were selected for both beetles and plants for transect K2, of which three were trap-scale, two were local-scale and three were landscape-scale variables.

Discussion

This research highlights two primary issues that confront research and conservation efforts aimed at a regional scale. In particular, we have shown that: (1) measuring environmental variables at multiple scales is important for explaining the variance in community composition for a variety of taxonomic groups, and (2) community–environment relationships between different taxonomic groups across a regional gradient change in a manner that limits regional management planning due to the uniqueness of individual locations.

As expected, some taxonomic groups in our 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-scale variables explained more variance in community structure along all of our transects than did the trap-scale variables. This result is consistent with our expectations for two reasons. First, individual birds perceive the landscape at a broader scale and are more mobile than either plants or ground-dwelling beetles. Second, the trap-scale 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 bird communities.

In contrast to the birds, we 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. Our results showed that all three scales were important in explaining variance in the community structure of these communities. The disparity between our expectations and the scales that did contribute to explaining the variance in community composition highlights the importance of including explanatory variables beyond those typically expected.

The influence of local-scale variables at Konza for all taxonomic groups is an obvious departure from the more equal distribution of explanatory variables across scales exhibited at the other sites. Konza is at the western edge of the tallgrass prairie, is dominated by tallgrass species such as big bluestem (*Andropogon gerardii)*, and is much more diverse in shrubs and woody plants than the other sites studied. 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 occurred at Konza. The greater number of shrub species at Konza consequently increased the number of possible variables to be selected for the suite of local variables.

Across the moisture gradient encompassed by our 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 for beetles and plants 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 factors describing vegetation structure, such as vegetation height and percent cover of particular shrub species, rather than to 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 or 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 the scaling relationships of different taxonomic groups. The need for different management plans at Pawnee and Konza is obvious considering these sites represent two categorically different grassland types, i.e. the shortgrass steppe and the tallgrass prairie. The differences between Arikaree and Smoky Valley are, however, not so apparent. These two sites are less than 200 km apart and can both be described as mixed-grass prairies, yet our results suggest that the scaling relationships for beetle and plant communities are different between these two similar locations.

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. Our results, however, 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 emphasize several taxonomic groups rather than species of special interest.

Regional approaches, however, come at a cost. Sampling designs such as the long transects used in this study may 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

Our 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, respond only to environmental variables measured at fine scales or that larger and more mobile species, such as birds, respond only 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. Such regional approaches 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. Our study has shown that finding specific factors that explain variance in communities across taxonomic groups and throughout a region will require a concerted effort to understand the influence of processes acting at multiple scales.

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Appendix 1. Environmental variables measured at one of three scales, which were used to explain the variance in community composition of beetles, birds, and vegetation.

Scale	Variable(s)	Code(s)
Trap	Soil pH	ph
	Mean soil hardness (based on four measurements)	mhard
	Soil hardness – standard deviation	sdhard
	Soil texture	Sand
		Silt
		Clay
	Percent bareground	brgd
	Mean vegetation height (based on four 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

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-scale variables were obtained via satellite imagery and digital elevation models.

Appendix 2. Environmental parameters selected as explanatory variables for canonical correspondence analyses of three taxonomic communities along eight transects at four grassland sites.

Transect	Trap variables			Local variables			Landscape variables		
	Plants	Beetles	Birds	Plants	Beetles	Birds	Plants	Beetles	Birds
P1	brgd	mxvght	clay	cact1	cact1	nearcac	ls6a	ls6a	ls6b
	mxvght	brgd	brgd	nearcac	yucc3	atri2	ls5	ls8	
	sand			atri2	prop1		slp	ls2	
	stvght			prop1	propcac		ls3	ls1	
				propcac	nearcac				
				near1					
P2	sdhard	sdhard	silt	propcac	propcac	propcac	ls7	ls7	ls6b
	mhard	silt	brgd	atri2	atri2		ls2	ls4	elev
	silt			atri1	cact1		ls6a	ls5	
	ph				nearcac		wasp	elev	
							ls4	ls8	

Appendix 2. Continued.

Transect	Trap variables			Local variables			Landscape variables		
	Plants	Beetles	Birds	Plants	Beetles	Birds	Plants	Beetles	Birds
A1	clay	mvght	stvght	prop1	near1	cact1	ls7	elev	elev
	brgd	ph	brgd	near1	nearcac		ls4	slp	ls1
	ph	brgd		yucc1	atri2		ls5	ls6b	ls6a
	silt	sdhard			cact2		yucc2	ls8	ls6b
	mhard	mhard			yucc3		yucc3	ls3	
								ls4	
								ls1	
A2	mvght	mvght	mvght	near1	prop1	prop1	ls62	ls7	ls7
	silt	sdhard	silt	prop1	near1	atri1	nasp	slp	ls1
	clay	silt	brgd	nearcac	nearcac	nearcac	ls7	ls1	slp
	sdhard	mhard		atri2	propcac	atri4	ls8	ls2	
	mhard						ls5		
							ls6a		
S1	silt	brgd	stvght	nearcac	near1	nearcac	slp	ls1	elev
	sand	silt	clay	near1	arte4	arte2	ls5	ls5	wasp
	sdhard		brgd	prop1	yucc2		ls6a	slp	slp
				yucc2			ls1	elev	
							ls7		
							ls3		
							wasp		
							elev		
							ls8		
S2	sand	sdhard	stvght	yucc2	yucc2	near1	wasp	slp	ls6a
	silt		clay	propcac	cact1		elev	ls4	nasp
	mxvght		mxvght	yucc1			ls4	ls7	wasp
	mvght						ls1	ls6a	elev
							ls2	elev	ls7
								ls8	
								ls6b	ls2
K1	clay	mvght	mvght	corn3	stag4	arom1	elev	ls6b	ls2
	ph	clay		rosa2	rosa2	stag2	wasp	nasp	ls6b
		brgd		rosa1	near1	stag4	ls8		ls5
		mxvght		soft2	soft2	prop13	ls6a		slp
				amor3	stag3	prop1			
				stag3	amor1	soft1			
				stag2	corn3	soft2			
K2	mvght	mvght	—	near13	rosa2	arom1	ls8	elev	ls8
	ph	stvght		rosa1	corn4	amor1	elev	ls6a	
	silt	brgd		rosa2	stag1	near13	ls4	ls4	
	brgd			corn2	amor1	prop1	nasp	ls7	
	stvght			corn4	soft3	soft1	ls6b	ls8	
				stag3	soft1		ls2		
				soft2					
				arom1					
				rosa3					

The four sites are the Pawnee National Grasslands (P), Arikaree (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.

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