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LANDSCAPE VS. LOCAL HABITAT SCALE INFLUENCES TO INSECT COMMUNITIES FROM TALLGRASS PRAIRIE REMNANTS

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Abstract. Habitat loss and fragmentation currently threaten ecosystems worldwide, yet remain difficult to quantify because within-fragment habitat and landscape-scale influences often interact in unique ways. Although individual species respond to fragmentation differently, large-scale conservation planning must unavoidably target multiple species. Although information on a population's response to fragmentation is critical, and measurements of species richness provide useful insights, exclusive reliance on these responses may mask important information about the taxonomic composition of assemblages in response to fragmentation. The North American tallgrass prairie ecosystem is one of the most threatened and fragmented ecosystems in the world, and insects are significant contributors to its biodiversity. In remaining grassland fragments, we evaluated within-fragment influences in conjunction with landscape-scale responses of representative insect communities from four feeding guilds: generalists, specialists, multiple life stage habitat use, and predators. Fragment-specific attributes capable of influencing insect diversity include plant species composition, plant biomass, abundance of blooming flowers, and vertical habitat heterogeneity created by the vegetation. Landscape-scale factors expected to influence patterns of insect species diversity include fragment size and shape as well as the spatial configuration of fragments. Ordination techniques were used to summarize composition of each feeding guild assemblage of each fragment, and structural equation modeling was used to examine the direct and indirect effects of fragmentation with influences from local habitats. Generalists (Orthoptera), mixed-modality feeding that changes with life stage (Lepidoptera), and specialist herbivores (Curculionidae) all responded directly to within-site characterizations of the plant community. Site management from large ungulate grazing or mowing for hay production consistently had an indirect effect on the insect community through influences on plant community composition. The predator assemblage (Coccinellidae) was influenced directly by fragment shape. To maintain insect biodiversity in tallgrass prairie fragments, these results indicate that conservation practices should focus on communities in order to maintain insect biodiversity in tallgrass prairie fragments. Landscape-scale factors must also be considered when making conservation decisions, primarily because predators (top trophic level organisms) are more likely to respond to regional changes.

Key words: *arthropod conservation; Coccinellidae; Curculionidae; fragmentation; insect communities; landscapes; Lepidoptera; LISREL algorithm; Orthoptera; structural equation modeling; tallgrass prairie.*

INTRODUCTION

Habitat loss, fragmentation, and modification are major anthropogenic processes affecting ecosystems at a global level (Saunders et al. 1991, Kruess and Tscharrntke 1994, Forman 1995, Turner et al. 2001). The consequences of fragmentation and community dynamics in response to fragmentation are difficult to assess because of the inherent complexity caused by biotic and abiotic interactions at multiple scales (McGarigal and Cushman 2002). As a result, the effects

of fragmentation are often evaluated using species-specific responses (Kareiva 1987, Robinson et al. 1992, Banks 1999, Bowers and Dooley 1999) at small plot scales, or as a community response quantified using species richness (Panzer and Schwartz 1998, Kruess and Tscharrntke 2000; K. J. L. Stoner and A. Joern, *unpublished manuscript*). Although species responses to fragmentation can be evaluated for individual species at small plot scales, it is increasingly evident that many management and restoration decisions must focus on landscape scales at the community level for practical reasons (U.S. Fish and Wildlife Service 1994, Mazerolle and Villard 1999).

The number of species in an area is indisputably important, but the presence or absence of particular species or overall taxonomic composition of a community can often be an equally important conservation goal. Community species composition may change in accordance with the degree of fragmentation, indepen-

Manuscript received 18 April 2003; revised 3 November 2003; accepted 8 November 2003; final version received 6 January 2004. Corresponding Editor: J. A. Logan.

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dent of the number of species. For example, the amount of edge habitat relative to the amount of fragment interior can influence the density of “invasive” or “edge specialist species” vs. “interior species” (Yahner 1988, Forman 1995).

The effects of fragmentation on communities are difficult to assess as the local habitat within a site may be influenced by geographic attributes of a fragmented landscape (area, shape, spatial arrangement of fragments; Fahrig and Merriam 1985, Fahrig and Palohimo 1988, Robinson et al. 1992, Holt et al. 1995, Leach and Givnish 1996, Van Dorp et al. 1997, Zschokke et al. 2000). In addition, responses to fragmentation at specific trophic levels may impact responses at other levels as biotic interactions are transferred through a food chain. For example, the local habitat for consumers may be altered as the plant species community is affected by fragmentation, perhaps because of altered seed dispersal from patch isolation, disturbance regimes, species–area relations, and land management practices. This interaction of landscape-scale factors and local habitat dynamics presents a significant challenge for determining which factors influence changes in the resident consumer community (Mazerolle and Villard 1999), with important implications for conservation planning. In particular, a large number of possible direct and indirect effects must be uncovered as a basis for understanding the underlying dynamics between landscape-scale factors and local attributes.

Insect communities

Insects dominate terrestrial ecosystems worldwide (Pyle 1981, Fisher 1998), such that their diversity and abundance makes them an ideal model for investigating habitat fragmentation and modification (Kremen et al. 1993, Panzer and Schwartz 1998, Allan et al. 2003, Collinge et al. 2003), and thus they are often used as indicators of fragment restoration success (Burger et al. 2003). Habitat fragmentation is known to affect arthropods differently depending upon the feeding guild they are associated with and whether they specialize on few host species or can utilize many food sources (Jonsen and Fahrig 1997, Golden and Crist 1999, Kruess and Tschardtke 2000, Davies et al. 2001). Generalist feeding species are more likely to find sufficient resources within a fragment compared to specialists and are also more likely to utilize corridors that could provide nourishment and additional habitat (Forman 1995, Haddad 1999, Collinge 2000). Changes in local habitat and food sources are then expected to have a greater impact on generalist feeders compared to landscape-scale factors. Local food sources often have a strong, direct impact on herbivores in fragmented studies compared with regional, geographical factors (Kruess and Tschardtke 1994, Kindvall 1996, Dubbert et al. 1998, Panzer and Schwartz 1998, Collinge et al. 2003). Specialists may need to move between fragments to acquire specific resources, and could be sig-

nificantly affected by landscape-scale factors that inhibit dispersal. In a simulation exercise, With and Crist (1995) found that specialists were less likely than generalists to aggregate at resources and continue random searching. Trophic level also plays a role as somewhat different quantitative responses can be expected. Predators may respond to landscape-scale factors based on the “trophic level susceptibility to fragmentation” hypothesis (Kruess and Tschardtke 1994; K. J. L. Stoner and A. Joern, *unpublished manuscript*). This hypothesis suggests that as local extinction occurs in a fragment, re-establishment of prey populations is a prerequisite for the re-establishment of predator populations, making predators more susceptible to fragmentation. Recolonization and establishment will depend heavily on regional factors such as fragment area, amount of edge, and isolation of a fragment from other populations (Kareiva 1987, Kruess and Tschardtke 1994, With and Crist 1995). Interestingly, while landscape context can often be a significant predictor of the presence and abundance for vertebrate species, this is less so for invertebrates (Maserolle and Villard 1999); local patch characteristics had large influences in most cases.

We examined responses of four representative insect feeding guilds to fragmentation in remnant grassland patches in tallgrass prairie habitat (Table 1). The North American tallgrass prairie is currently one of the most threatened ecosystems in the world (Packard and Mutel 1997); the eastern third of the Great Plains was historically comprised of extensive, continuous tallgrass prairie, but has been reduced to ~1% of former land cover (Samson and Knopf 1994). Arthropods are important to grassland communities, contributing significantly to their biodiversity (Arenz and Joern 1996, Kaufman et al. 1998, Panzer and Schwartz 1998).

The Orthoptera (grasshoppers, katydids, and crickets) are generally oligophagous to polyphagous with a small number of species that are host specialists (Joern 1979, Bernays and Chapman 1994), but as a group typically select a wide range of food resources (grasses, forbs, and litter) and can consume large quantities of leaf material. Dispersal is somewhat limited and long-range movement may not occur if feeding and mating needs are met within a small area (Capinera and Sechrist 1982, Joern 1983, Johnson et al. 1986, Narisu et al. 1999). We expected that the generalist feeding Orthoptera community would respond directly to plant community changes and amount of food available, and indirectly to regional factors of area, shape, and neighboring fragments as these regional factors influenced the local plant community (Fig. 1A). Management practices would also directly influence the plant community and thus indirectly the Orthoptera.

Ladybird beetles (Coccinellidae) prey primarily on aphids (Borror et al. 1989) and respond directly to fragment isolation in experiments (Kareiva 1987, Banks 1999). These predators represent an upper trophic level

TABLE 1. Species included in community composition analysis.

Lepidoptera	Orthoptera
<i>Acontia aprica</i>	<i>Arphia conspersa</i>
<i>Ancyloxypha numitor</i>	<i>Arphia</i> sp.
<i>Artogeia rapae</i>	<i>Chorthippus curtipennis</i>
<i>Atryone logan logan</i>	<i>Conocephalus</i> sp.
<i>Basilarchia archippus archippus</i>	<i>Dichromorpha viridis</i>
<i>Caenurgina erechtea</i>	<i>Hesperotettix speciosus</i>
<i>Celastrina argiolus ladon</i>	<i>Hippiscus ocelote</i>
<i>Cercyonis pegala</i>	<i>Hypochlora alba</i>
<i>Charidryas gorgone carlota</i>	<i>Melanoplus bivittatus</i>
<i>Charidryas nycteis nycteis</i>	<i>Melanoplus differentialis</i>
<i>Colias eurytheme</i>	<i>Melanoplus femurrubrum</i>
<i>Colias philodice philodice</i>	<i>Mermiria bivittata</i>
<i>Cyenia tenera</i>	<i>Neoconocephalus ensiger</i>
<i>Danaus plexippus</i>	<i>Neomembius variegatus</i>
<i>Estigmene acrea</i>	<i>Oecanthus</i> sp.
<i>Everes comyntas comyntas</i>	<i>Orphylella speciosa</i>
<i>Haematopsis grataria</i>	<i>Phoetaliotes nebrascensis</i>
<i>Haploa reversa</i>	<i>Scudderella texensis</i>
<i>Hemiargus isola alce</i>	<i>Syrbula admirabilis</i>
<i>Junonia coenia</i>	Curculionidae
<i>Libytheana bachmanii bachmanii</i>	<i>Anthonomus molochinus</i>
<i>Megisto cymela cymela</i>	<i>Aphrastus taeniatus</i>
<i>Ostrinia nubilaslus</i>	<i>Apion melanarium</i>
<i>Papilio polyxenes asterius</i>	<i>Ceutorhynchus</i> sp.
<i>Phoebis sennae eubule</i>	<i>Epicaerus imbricatus</i>
<i>Pholisora catullus</i>	<i>Geraeus baridinae</i>
<i>Phyciodes tharos tharos</i>	<i>Haplorthynchites aeneus</i>
<i>Polites coras</i>	<i>Pantamorus tessellatus</i>
<i>Polites themistocles</i>	<i>Pseudobaris farcta</i>
<i>Pontia protodice</i>	<i>Sitona cylindricolis</i>
<i>Pterourus glaucus glaucus</i>	<i>Smicronyx lineolatus</i>
<i>Pyrgus communis</i>	Coccinellidae
<i>Pyrissitia lisa lisa</i>	<i>Hyperaspis undulata</i>
<i>Schinia jaguarina</i>	<i>Coccinella septempunctata</i>
<i>Speyeria cybele cybele</i>	<i>Coleomegilla maculata</i>
<i>Speyeria idalia</i>	<i>Hippodamia convergens</i>
<i>Strymon melinus</i>	<i>Hippodamia parenthesis</i>
<i>Vanessa atalanta rubria</i>	<i>Hyperaspis bigeminata</i>
<i>Vanessa cardui</i>	<i>Pseudoscymnus tsugae</i>
	<i>Scymnus</i> sp.

and are predicted to respond directly to landscape level factors (Fig. 1B). The resident aphid community would also influence the ladybird beetles; we have no direct measurement of the aphid community in this study, but they are often common in both grasslands and neighboring crops. We predicted that ladybird beetles, as a representative insect predator community, would be influenced directly by regional factors of area, shape, and neighboring fragments (Fig. 1B). Because of the great reliance of the host specialist prey, ladybird beetles would also be influenced directly by the local plant community, which we predicted would be influenced by management and regional factors.

Lepidoptera are conspicuous and taxonomically well known insects, which makes them ideal for a community study of fragmentation. This group represents a feeding guild that is influenced by both the adult nectar sources of food and larval host plants (Grossmueller and Lederhouse 1987, Collinge et al. 2003). Lepidoptera have dispersal capabilities that could allow

them to readily move between fragments to assess resources, therefore eliminating the regional effects of fragmentation. Despite their relatively high dispersal capability, individual Lepidoptera species are affected by area, edge, and spatial arrangement of fragments (Fahrig and Paloheimo 1987, 1988, Brommer and Fred 1999, Schultz and Crone 2001). For example, results of available studies indicated that 60–97% of species examined remain in their natal patch (Thomas and Hanski 1997, Hanski 1999), and many species disperse no more than a few kilometers (Hanski and Kuussaari 1995, Hanski 1999, Haddad 1999). Because Lepidoptera belong to different feeding guilds in nymphal and adult life stages, they could be affected by many interacting factors at both the landscape scale (fragment area, juxtaposition of fragments) and the local scale (blooming flower community and larval plant species abundances) as predicted in Fig. 1C.

Curculionidae (weevils) are typically specialist feeders that often select one family, genus, or even species

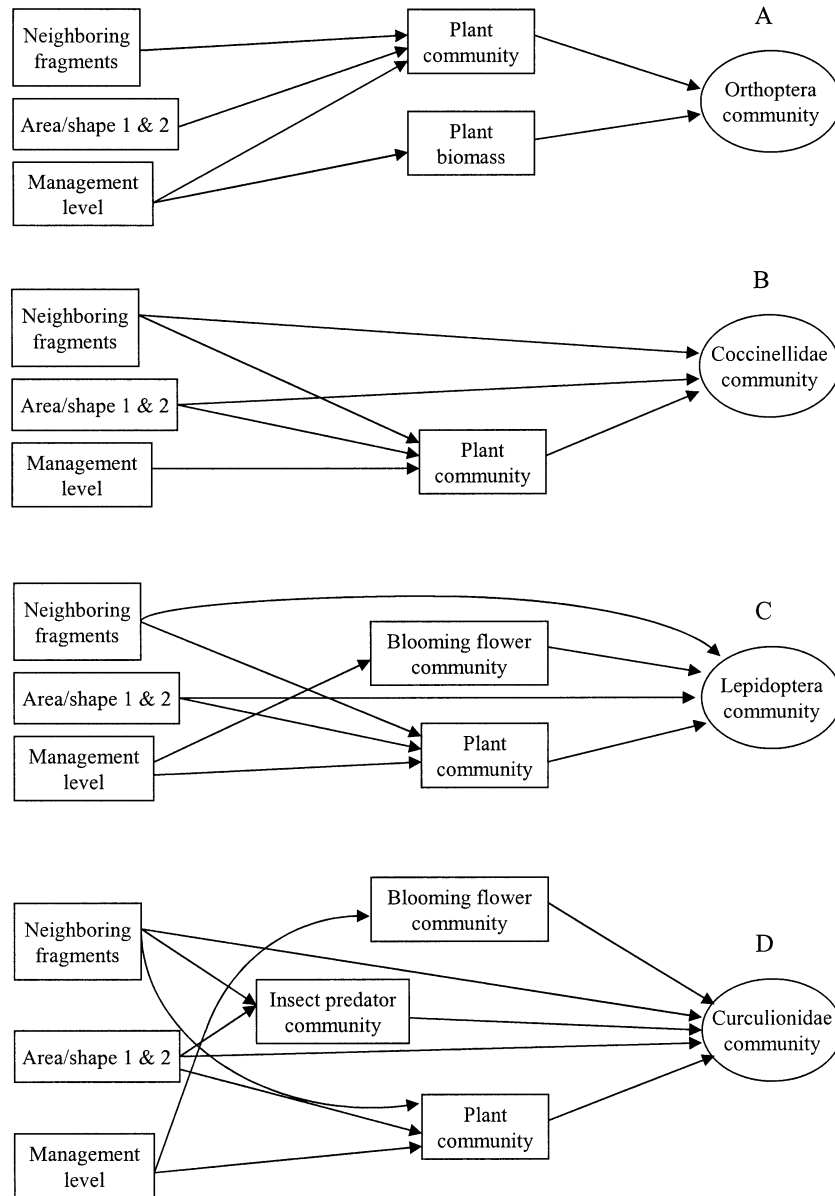


FIG. 1. Initial hypotheses of “causal relationships” for each insect consumer group. The variable “area/shape 1 & 2” represents both principal component scores for area and shape. “Blooming flower community” represents both blooming flower density and diversity. “Management level” indicates hay, moderate grazing, or intense grazing. “Neighboring fragments” is the result of the proximity analysis. “Plant” and all “insect communities” (e.g., “Orthoptera community,” “Coccinellidae community,” etc.) are ordination scores. Each path diagram has representative fit statistics in Table 2.

of vascular plant. Different species often specialize on different parts of plants (e.g., roots, stems, or seeds; Morris 1991). Most weevil species have the potential to fly (fully developed wings), but rarely do so except in extremely hot weather (Borror et al. 1989, Morris 1991). They are more likely to escape predators by dropping to the ground than by flight (Borror et al. 1989). Limited dispersal tendencies coupled with food source specialization are characteristics that suggest Curculionidae may be less tolerant of fragmented systems as specific resources become rare and more iso-

lated. Kruess and Tschardtke (1994) found significant decreases in density of several curculionid species in response to habitat isolation. As specialists, this group may be responding directly to changes in the blooming flower community, predators, local plant community, proximity of neighboring fragments, area, and shape, with many interacting indirect influences (Fig. 1D).

Currently, insect diversity in regional tallgrass remnant prairie in an agricultural landscape such as eastern Nebraska, USA, depends primarily on two remaining types of habitat: grassland grazed by cattle and horses,

and prairie managed for hay production through mowing. These two management practices produce different disturbance regimes, and both were sampled in this study. Sites included in this study rarely, if ever, employed fire for management. We examined regional effects of fragmentation on the composition of insect species assemblies, including area, shape, and spatial relationship of fragments, and then evaluated how these factors contributed to explaining insect species assemblies compared with contributions from local biotic characteristics of each individual fragment. Local factors in this study include plant species composition, plant biomass, abundance and diversity of blooming flowers, and vertical habitat heterogeneity created by the vegetation. The response of these communities is evaluated for changes in the context of tallgrass prairie fragmentation consisting of both regional geographic and local biotic factors.

METHODS AND MATERIALS

We used ordination techniques coupled with structural equation modeling to examine the direct and indirect effects of fragmentation and local habitat attributes on species assemblages of these four insect groups in eastern Nebraska, USA. Ordination succinctly summarizes community data in which sites with similar species compositions are closely situated within n -dimensional ordination space (Beals 1973, Pielou 1984, Quinn and Walgenbach 1990, ter Braak 1995, Wardle et al. 1999). A community score is then calculated for each fragment based on its location in ordination space. This score can then be used as a response variable to determine which environmental variables are important to changes in species composition between sites.

Structural equation modeling, a general form of path analysis, is a powerful method of extracting direct and indirect effects (Johnson et al. 1991, Shipley 1999). Structural equation modeling supports rigorous hypothesis testing as complex relationships are established a priori between variables using a series of regression equations. One may incorporate both regional and local factors in a comprehensive assessment with this approach. The entire hypothesized model can be analyzed simultaneously using computer algorithms such as LISREL (Johnson et al. 1991, Jöreskog and Sörbom 1996, Grace and Pugsek 1998, Shipley 1999), and results are easily visualized using a path diagram.

Native vegetation of eastern Nebraska was historically comprised of extensive, continuous tallgrass prairie (Johnsgard 2001), a situation that no longer exists. Most remaining tallgrass grassland is currently reduced to remnant fragments, largely due to varying degrees of human impact. Grassland fragments from eastern Nebraska, mostly within Lancaster County (Lancaster County, Nebraska; northeast corner of rectangular county, 41°2'42" N, 96°27'50" W, southwest corner, 40°31'25" N, 96°54'44" N) were used in this study. In

this region, native prairie that has not been impacted in some way by intensive row crop agriculture is rare. Prairie fragments were selected based on a survey of native prairie sites conducted by the Lancaster County Ecological Advisory Committee in 1985. Thirty-six sites varying in size from 0.10 ha to 242.8 ha were included in this study; 19 were managed for hay production and 17 were grazed primarily by cattle. In Lancaster County, it is common practice for hay fields to be mowed annually in early August (B. E. Anderson, *personal communication*). For inclusion in this study, we required that fragments be isolated and contain significant amounts of native vegetation. All sites also included non-native plant species and some degree of human impact. Sites were considered isolated if they were separated from other prairie habitat by a road, agriculture, or a continuous line of trees. Sites supporting intensive row crop agriculture were not studied as they contain limited numbers of host plants and pesticides are widely and often heavily used at these sites.

Regional factors

Fragment area, shape, and spatial juxtaposition of fragments can disrupt dispersal, affect colonization and extinction rates and alter the community composition within remaining fragments (Forman 1995, With and Crist 1995, Banks 1998). The area and perimeter of each fragment were estimated with ENVI 3.4 software based on GPS coordinates of each corner (Research Systems, Boulder, Colorado, USA). Shape was characterized using a perimeter to area ratio of each fragment (Helzer and Jelinski 1999). Since the shape index is a ratio, the area and shape variables are highly correlated. Structural equation modeling using LISREL software allows relationships between independent variables to be specified, although collinearity may have serious impacts on stability of correlation coefficients (Maruyama 1998). We eliminated collinearity with principal components analysis applied to area and shape (perimeter/area ratio); the first two principal components scores were used to create new indices (Scheiner and Gurevitch 2001). The principal component scores, named "area/shape 1" and "area/shape 2," were used in analyses that follow.

Although each fragment may be isolated from other fragments, some insects may move between grassland fragments, requiring that spatial relationships be evaluated. Large fragments that support large populations with high species diversity within dispersal distance may strongly impact the insect community present in an isolated fragment (Simberloff and Abele 1976, Shmida and Wilson 1985, Rosenzweig 1995, With and King 1999). To evaluate the possible impact of neighboring fragments within the matrix of a fragmented landscape, a principal components analysis was applied to two Landsat Thematic Mapper scenes (path 28, row 32) from 4 April and 26 August 1991. The resulting 30-m resolution image (G. Henebry, *unpublished man-*

uscript) was displayed as red, green, and blue pixels, which are the sixth, first, and third principal components. This image was used to identify neighboring grassland fragments within an 8-km radius of each of the 36 sampled fragments. This distance was selected based on estimates of butterfly dispersal (Hanski and Kuussaari 1995). The area of each of these neighboring fragments and distance to the sampled fragment was determined. The distance was measured from the neighboring patch edge to the approximate location of sampling within the remnant. A proximity analysis was performed to obtain an index of the abundance and proximity of neighboring fragments (Gustafson and Parker 1992). This index is the sum of all fragment areas of the neighboring fragments divided by the distance to the sampled fragment. High values indicate greater connectivity.

Local factors

Habitat attributes of each fragment were characterized in several ways to assess the influence of local (within-fragment) biotic relationships. The plant community was characterized by counting the number of plant species in a 0.25-m² rectangular frame at 30 locations in each fragment. Sampling locations were at six randomly predetermined intervals along five transects centrally located in each fragment. Sampling was completed over a period of 21 days in June 2001. The forb blooming flower community, plant biomass, and habitat structure were all measured in 17 days from the end of July to the beginning of August 2001 on the same day insects were collected, and before mowing commenced. Each of these local factors (forb blooming flower community, plant biomass, and habitat structure) were measured at predetermined random distances along each of the five insect sweep transects. Blooming flower diversity and density were measured by counting the number of blooming plants (forbs with at least one open bloom) within 10, 4 × 4-m plots. Ten plant biomass samples clipped in 1.0 × 0.10-m strips were randomly collected, dried, and weighed for each fragment. Habitat structure was measured as the variability in vegetation canopy height (or vertical heterogeneity). A meter stick was placed into the vegetation perpendicular to the ground and the height of all vegetation touching the meter stick was recorded at 10 randomly selected points. The diversity of canopy heights (using a Shannon index) was employed as a measure of vertical structural heterogeneity.

Survey techniques

Orthoptera (families Acrididae, Gryllidae, and Tetrigoniidae), Coccinellidae, and Curculionidae were collected using a sweep net. Sweep net sampling is an efficient way to achieve estimates of relative abundance of foliage dwelling arthropods (Evans et al. 1983), and is useful for conservation managers because of its relative ease of use. Before beginning sampling, a species

accumulation curve was constructed. The sampling effort required for a reliable estimate of species richness with five transects was 125 sweeps (*data not shown*). In our analysis, five transects of 150 sweeps were made at each site. Insects were frozen and later identified to genus and species. Lepidoptera were censused using Pollard visual transects 150 m long in which all species seen 5 m on either side of the transect were recorded (Pollard and Yates 1993). Five sites were smaller than the transect area, so these areas were considered to be exhaustively sampled. Insects were collected and censused only on sunny days between 1000 and 1600 hours if the vegetation was dry and the wind speed was >15 mph (>24 km/h).

Ordination

Principal components analysis (PCA) is a basic eigenanalysis ordination technique that maximizes the variance explained by each successive orthogonal axis (McCune and Mefford 1999). Prior to ordination using PC-ORD, an outlier analysis was performed as extreme values can have a profound influence on multivariate analysis that leads to extreme non-normality. Sites with values more than two standard deviations away from the mean were considered outliers and removed from further analysis. Different sites for each group of insects were outliers. We used principal components analysis to extract axes that summarized the taxonomic composition of each representative insect community and plant community for each site. Site scores of the first PCA axis summarized multivariate community composition of insect assemblages as a single value that was then treated as a response variable in structural equation modeling. Using ordination to summarize different community assemblages by site is a powerful way to extract which environmental variables influence the changes seen in the assemblage composition. The first three PCA axes were examined as response variables in structural equation models to determine how regional landscape factors, local factors, and management practices interact to explain the resulting insect species composition. Species composition of the plant community was also summarized using principal components analysis and the first axis scores were used to represent the variable "plant community composition" in the structural equation modeling analysis.

Structural equation modeling

Structural equation modeling (SEM) is a hypothesis-testing approach to traditional multivariate analysis. An initial model represented visually as a path diagram was formulated for each insect group based on putative causal relationships based on a priori relationships expected from literature reports (Fig. 1). In the process of SEM, initial model hypotheses should include all expected possible relationships. Anticipating that the initial model hypothesis, which included all possible relationships (Mitchell 2001), would not generate the

TABLE 2. LISREL fit statistics for each hypothesis.

Hypothesis	Chi-square		RMSEA		RMR	CFI	ECVI	CAIC
	X^2	P	RMSEA	P				
Initial								
Coccinellidae	1.84	0.17469	0.165	0.19	0.027	0.98	1.35	92.08
Curculionidae	21.38	0.01862	0.192	0.03	0.094	0.8	2.37	142.1
Lepidoptera	18.61	0.00094	0.338	0.0017	0.11	0.77	1.64	131.36
Orthoptera	9.94	0.12707	0.143	0.16	0.12	0.93	1.25	122.31
Alternative								
Curculionidae	0.79	0.67407	0.000	0.7	0.045	1.00	0.55	31.23
Lepidoptera	0.01	0.93261	0.000	0.94	0.0022	1.00	0.56	75.72
Orthoptera	0.22	0.63759	0.000	0.65	0.017	1.00	0.32	58.74

Notes: Boldface type indicates a good fit. A nonsignificant low X^2 with an associated high P value indicates a close fit between the hypothesized model and a perfect fit. Key to abbreviations: RMSEA, root mean square error of approximation (RMSEA <0.05 with $P > 0.50$ indicates a good fit); RMR, standardized root mean square residual (the mean of all standardized residual values; RMR <0.05 indicates a good fit); CFI, comparative fit index (accounts for sample size; a CFI value close to 1.0 is acceptable); ECVI, expected cross-validation index; CAIC, information criterion index (consistent version). CAIC and ECVI are used to compare models with similar fits with smaller values indicating greater potential for replication and a parsimonious model (indicated particularly with CAIC).

best explanation of the data many alternate hypotheses were also formulated (Wootton 1994). These alternative models are revisions of the initial hypothesis, as they were also grounded in theory, but contained select variables with relationships consistent with the predictions made for each insect group. Individual paths were added or removed to generate a model with the best fit, making it valuable for prediction purposes in insect conservation. All variables were transformed to have a normal distribution using z scores and log transformation prior to analysis. Maximum-likelihood estimation of parameters on covariance matrices were used in LISREL.

Multiple goodness of fit statistics are available using LISREL programming. Selection of a best fit model can be greatly refined by using multiple fit statistics that analyze different aspects of the model, such as sample size and parsimony. Because our data included relatively few samples (36 sites), fit statistics were selected that included sample size to determine which model has the best fit (Table 2). The foremost test of fit is the chi-square. A nonsignificant chi-square value with an associated high P value is desired, as this indicates close agreement between the hypothesized model and a perfect fit (Bryne 1998). The root mean square error of approximation (RMSEA) is currently recognized as an important goodness-of-fit statistic in model selection (Bryne 1998). This statistic is sensitive to the number of parameters selected in the model. Values <0.08 represent an acceptable fit and values <0.05 indicate a good fit (Bryne 1998). A test for the closeness of fit of the RMSEA is also included; P values >0.50 are suggested targets (Jöreskog and Sörbom 1996). Other fit statistics are included in model selection (Table 2).

After selecting a model, the direct and indirect effects were evaluated. LISREL provides a standardized solution of direct and indirect effects where variables were rescaled to have a variance of 1 and all variables were then given a value between 0 and 1. This allows comparison of the relative strength of each effect (Johnson et al. 1991). The correlation coefficient was also examined for each of the relationships specified in the model for amount of variance explained.

RESULTS

LISREL analysis for each insect consumer group yielded significant yet different combinations of environmental variables that predicted changes in community composition. For each consumer group, the initial model hypothesis contained all relationships and variables measured that were predicted from the literature (Fig. 1). Alternate model hypotheses were generated for each consumer group that contained a subset of variables, more consistent with specific predictions for each group. For herbivorous taxa, generalist feeders, life-stage dependent mixed-modality feeders, and feeding specialists were best explained by an accepted alternate model that identified strong direct and indirect relationships. For each group, the first PCA scores were used in path diagrams. The second and third PCA scores did not correlate with any environmental variables. Characteristics of the plant community and management were consistently seen in resulting modified path models. The variables "neighboring fragments," "area/shape 1," "area/shape 2," and "plant biomass" were not retained in any accepted alternate model. Shape, characterized as perimeter/area ratio, was the only variable that significantly correlated with the predator community (represented as the first PCA axis

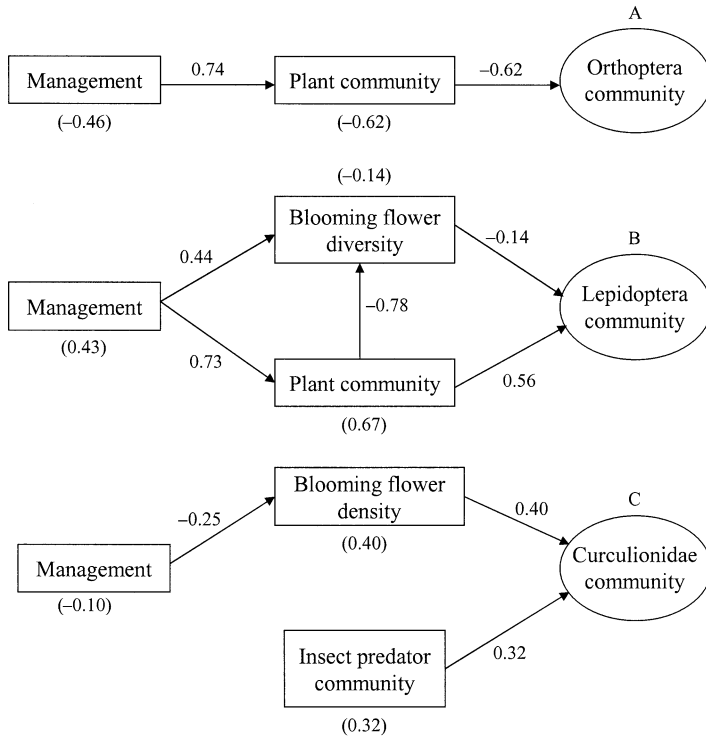


FIG. 2. Numbers associated with each path arrow are the standardized direct effects of each variable. Numbers in parentheses below the variables are the total standardized effects (total of direct and indirect) of each variable on the insect community. (A) Grasshopper community path diagram. Plant community composition explains 38.4% of the variation of the grasshopper community composition ($P < 0.0001$). Management level indicates hay, moderate grazing, or intense grazing. (B) Lepidoptera community path diagram. Plant community composition and blooming flower diversity explain 40% of the variation seen in the lepidoptera community ($P = 0.0002$). Plant community composition and management level explain 29.6% of the variation in blooming flower diversity ($P = 0.0031$). Management level explains 54% of the variation in plant community composition ($P < 0.0001$). (C) Weevil community path diagram. Blooming flower density and predator community composition explain 24.1% ($P = 0.0158$) of the variation in weevil community composition. Management level explains 8.1% ($P = 0.0923$) of the variation in blooming flower density.

scores). The plant community composition analysis extracted 27.02% of the variance in the first axis.

Orthoptera

The Orthoptera PCA analysis extracted 15.54, 11.41, and 11.25% of the variance in the first three axes, respectively, for a cumulative total of 38.20% of variance explained. Although the initial structural equation modeling (SEM) model hypothesis of Orthoptera produced a nonsignificant chi-square (at the 0.05 level), it was rejected based on root mean square error of approximation (RMSEA) and standardized root mean square residual (Table 2). The alternative model for Orthoptera fit all criteria and had much lower values for both the ECVI (expected cross-validation index) and CAIC (consistent information criterion index) comparison indices when compared to the initial hypothesis (Fig. 2A, Table 2). The standardized solution of the direct and total effects for the alternative model indicated that plant community composition is strongly correlated with Orthoptera community composition. Management had a strong direct effect on the plant community, and a corresponding indirect effect on the Orthoptera community composition (Fig. 2A). Conclusions were reinforced with stepwise regression analyses where plant community composition was the only variable retained in the model of Orthoptera community composition ($\alpha = 0.05$).

Sites scores appeared to segregate according to management which is logical, as the plant community composition was the primary environmental factor chang-

ing along axis 1. The tettigoniids *Conocephalus* spp. and *Neoconocephalus ensiger* and the acridids *Hesperotettix speciosus* and *Dichromorpha viridis* were all highly correlated with axis 1 ($R = 0.70$, $R = 0.67$, $R = 0.54$, $R = 0.43$), respectively (Fig. 3A).

Coccinellidae

The Coccinellidae PCA analysis extracted 26.34, 20.96, and 16.15% of the variance in the first three PC axes, respectively, for a cumulative total of 63.45% variance of Coccinellidae community explained by the analysis. The initial LISREL model was rejected by RMSEA and associated P value (Table 2). No alternative model had an acceptable fit, nor did stepwise regression retain any variables included in the initial model hypothesis ($\alpha = 0.05$; *results not shown*). Other studies have shown that regional effects such as area and shape have significant impacts on predators. Moreover, introduced coccinellid species for biocontrol of aphids (Hodek 1973) are rapidly moving across the United States. The natural history, biogeography, and fragmentation experiments focused on this beetle family prompted additional simple regression analysis to see if there were correlations between the original variables of perimeter (often created by row crops) to area ratio (shape) and area, each analyzed in a simple regression. Coccinellid community scores were significantly correlated with shape ($R = 0.36$, $P = 0.038$; Fig. 4), but with much unexplained variation. Additional analyses using site scores from axis 1 as the

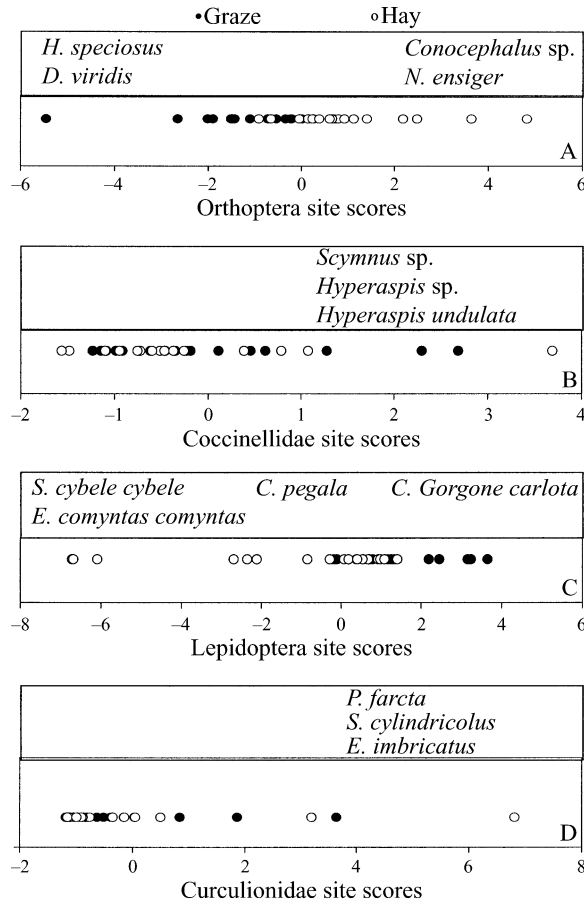


FIG. 3. Axis 1 ordination site scores for each feeding guild. Solid circles are grazed sites; open circles are sites managed for hay production. Species that have high correlations with axis 1 are shown above the site scores. They are positioned where they are approximately located in ordination space. Inference can then be made regarding where they are located along axis 1 and which environmental variable is correlated with axis 1.

coccinellid response variable revealed no significant relationships.

Site scores for specific species displayed no obvious aggregation by management (Fig. 3B). Three species showed high correlation with axis 1: *Scymnus* sp. ($R = 0.74$), *Hyperaspis* sp. ($R = 0.77$), and *Hyperaspis undulata* ($R = 0.72$) and all were located in the center right of the ordination diagram (Fig. 3B).

Lepidoptera

In the principal components analysis for Lepidoptera, 13.3, 10.77, and 9.51% of the variation was extracted for axis 1, 2, and 3, respectively, with a cumulative total of 33.60%. The initial Lepidoptera model hypothesis was rejected using SEM (Table 2). The path diagram for the alternative model hypothesis suggested that Lepidoptera community composition was strongly and directly correlated with plant community

composition and somewhat correlated with blooming flower diversity (Fig. 2B). Plant community composition had an additional indirect effect through its influence on the blooming flower diversity. In addition, management had an indirect effect on Lepidoptera through its large effect on plant community composition and small effect on blooming flower diversity. These results were consistent with stepwise multiple regression, where the variable "plant species community composition" was retained in the Lepidoptera community model ($\alpha = 0.05$).

Visual inspection of the graph of sites organized by Lepidoptera scores in ordination space indicated that grazed sites tended to cluster toward the right of the diagram and hayed sites were on the left (Fig. 3C). Distributions of four species were highly correlated with axis 1. The great spangled fritillary (*Speyeria cybele cybele*) ($R = 0.51$) and the eastern tailed blue (*Everes comyntas comyntas*) ($R = 0.88$) are found on the left side of the ordination diagram, the wood nymph (*Cercyonis pegala*) ($R = 0.70$) is centrally located on the ordination graph and gorgone checkerspot (*Charidryas gorgone carlota*) ($R = 0.50$) is found on the far right side of the diagram.

Curculionidae

The Curculionidae PCA analysis extracted 26.18%, 18.35%, and 13.94% of the variation for axis 1, 2, and 3, respectively, with a cumulative total of 58.5% of the variance explained. The initial curculionid model was rejected based on all fit statistics (Table 2). The alternate model hypothesis indicated that blooming flower density and the insect predator community had a strong direct influence on the curculionid community structure. Management had a smaller indirect effect on Curculionidae through grazing effects on the blooming flower density (Fig. 2C). These results were reinforced with stepwise regression ($\alpha = 0.05$) where blooming flower density and insect predator community were re-

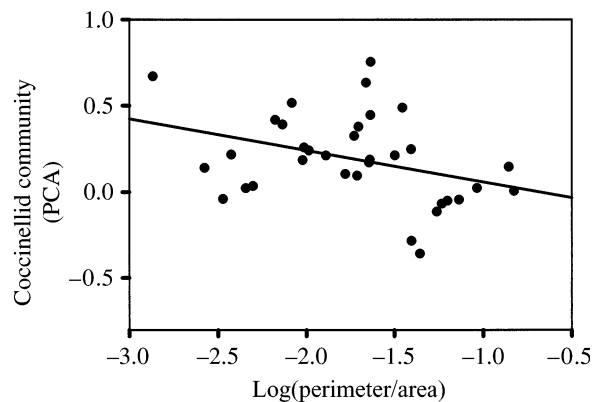


FIG. 4. The Coccinellidae community is significantly correlated (using principal components analysis) with the perimeter/area ratio ($R^2 = 0.127$, $P = 0.038$).

tained in the model and explained the most variation of weevils ($R = 0.49$, $P = 0.0158$).

The ordination plot of sites based on Curculionidae community species composition does not reveal clear clumping associated with management (Fig. 3D). *Epicareus imbricatus* ($R = 0.81$), *Pseudobaris farcta* ($R = 0.84$), and *Sitona cylindricolis* ($R = 0.80$) tended to group on the left side of the ordination diagram (Fig. 3D).

DISCUSSION

Habitat fragmentation presents a challenge for developing conservation measures to preserve biodiversity worldwide. The effects of fragmentation are difficult to assess as landscape-scale factors such as fragment area, isolation, and juxtaposition of fragments interact with aspects of the fragment habitat creating a complex interaction of direct and indirect effects that potentially influence fragment residents in a scale-dependent fashion. This complexity, coupled with challenges associated with large-scale experimental manipulations, has limited many fragmentation studies to focus on one or few species. Although individual species do respond to fragmentation differently, constrained by their specific natural history (Harris 1988, Yahner 1988, Forman 1995) and scale at which they utilize the environment (Wiens 1976), conservation planning now often targets multiple-species conservation needs (Blockstein 1988, U.S. Fish and Wildlife Service 1994). Community responses indexed as species richness to fragmentation provide important insights, but this approach masks important information about the taxonomic composition of assemblages, which may be as or more important. Moreover, conservation decisions require that one recognize and quantify direct and indirect effects as the manipulation of one critical aspect may trigger undesirable responses due to unknown indirect effects.

Summarizing insect community composition using ordination techniques and using structural equation modeling (SEM) proved to be useful in detecting which variable had the most significant direct and indirect effects on insect communities of tallgrass prairie fragments in this study. Plant community composition, blooming flower diversity, and density characterized local habitats and had strong direct influences on generalist, specialist, and insect herbivores that shift feeding modalities throughout their life cycle. This relationship between herbivorous insects and patterns of vegetation serving as habitat and food is well established (Southwood 1977, Kemp et al. 1990, Bernays and Chapman 1994, Panzer and Schwartz 1998, Collinge et al. 2003). Our study suggests that for foliar insect feeding guilds in remaining tallgrass prairie fragments, changes in local habitat may supercede landscape factors as important influences on insect guilds, at least at the scale we examined the problem.

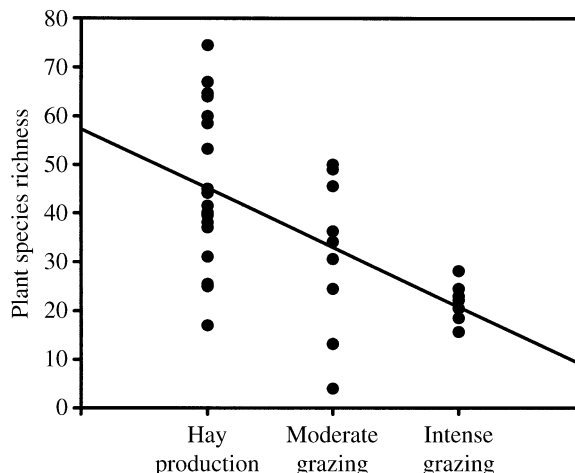


FIG. 5. Plant species richness is significantly negatively correlated with increasing management intensity ($R^2 = 0.344$, $P = 0.0002$). Management was reclassified into three categories based on the percentage of bare ground: hay production, moderate grazing, and intense grazing. Plant species richness was estimated using a rarefaction technique, Chao 2 (Colwell and Coddington 1994).

Management had a dramatic influence on the local plant community, thus consistently having an indirect effect on insect community composition. Grazing by large herbivores has many effects on vegetation and is known to affect insect communities (Quinn and Walgenbach 1990, Onsager 2000). Bison grazing in tallgrass prairie has been shown to increase plant species diversity, increase spatial heterogeneity of vegetation, and affect multiple ecosystem processes through grazing and other behaviors (Hartnett et al. 1996, Knapp et al. 1999). Cattle grazing also has varied effects, with the potential to increase structural heterogeneity, plant diversity, and production at moderate grazing intensity (Collins 1987, Dyer et al. 1993, Lauenroth et al. 1994, Cid and Brizuela 1998, Knapp et al. 1999). In eastern Nebraska, USA, common ragweed (*Ambrosia artemisiifolia*), western ironweed (*Vernonia baldwinii*), snow-on-the-mountain (*Euphorbia marginata*), buffalo bur (*Solanum rostratum*), and sunflower (*Helianthus annuus*) are more likely to be found in heavily grazed areas (Stubbendieck et al. 1995; K. J. L. Stoner and A. Joern, *personal observations*). Hayed areas are dominated by native grasses and forbs such as heath aster (*Aster ericoides*), goldenrod (*Solidago missouriensis*), and leadplant (*Amorpha canescens*) (K. J. L. Stoner and A. Joern, *personal observations*). There is a significant decline in plant species richness as grazing intensity increases in the sites examined here (Fig. 5).

Plant species composition did not respond to any landscape-scale influences as originally predicted. Plants were expected to respond to fragment size and fragment isolation, based on the assumption that both colonization from neighboring "source" fragments and local extinction are important. Plant species in tallgrass

prairie fragments may be temporarily removed through herbivory or mowing, but could remain in the fragment as a seed bank or through asexual reproduction. Holt et al. (1995) found that patch size and level of isolation did not influence secondary succession in old field habitats, suggesting that abandoned agricultural fields contain a sufficient seed bank to repopulate a fragment.

Generalist and specialist feeders

Consistent with our predictions, the Orthoptera community responded directly and strongly to changes in the plant species community. We also found that the plant species community was influenced strongly by management, and less by regional aspects such as area reduction, edge, and proximity of neighboring fragments as predicted. Management practices acted indirectly on Orthoptera community composition (Fig. 2A). We predicted that curculionid species, representing specialists, would respond to local biotic changes within a fragment and to regional aspects of fragment area, shape, and isolation. Curculionidae responded with approximately equivalent strength to both the blooming flower density and insect predator community. Management contributed a smaller indirect effect by influencing the blooming flower density (Fig. 2C).

A generalist may have sufficient resources to support a population in fragments of reduced size even though the diversity of resources would be less, although a specialist feeder using fewer host plants may not have appropriate resources in the same fragment. Generalist feeders may not require conservation efforts at a landscape scale, as long as sufficient resources are readily available in close proximity. Generalists can utilize a variety of habitat types and may readily use corridors and move between fragments, so a landscape may have much greater connectivity to a generalist. Habitat generalists may "aggregate" at higher levels of fragmentation in the landscape (where a lower percent of the landscape is habitat) compared with specialists (With and Crist 1995). Because isolation levels influence colonization and establishment of both food plants and the insect specialist populations, food specialists were expected to respond to regional effects of fragmentation. This effect was not seen, suggesting that these species may perceive the landscapes at a much smaller scale than considered here, such that the habitat is not fragmented from their perspective. For example, specialists chosen in this study may utilize vegetation found in corridors (ditches) that connect larger habitat patches, or habitat fragments may be situated well within dispersal distances. Consistent with this view, Jonsen and Fahrig (1997) found that isolation had no effect on specialist plant-hoppers at the landscape scale.

Lepidoptera

Lepidoptera change feeding modalities from most specialist feeding larvae to generalist nectar and pollen feeders as adults. We predicted that Lepidoptera species

would respond to both adult and larval food sources as well as regional factors of area and neighboring fragments. Only local effects of plant community composition and blooming flower diversity predicted Lepidoptera community species composition. This relationship showed both a large direct and a smaller indirect effect. Management was also included in the best-fit model as it indirectly influenced the Lepidoptera community composition by influencing the plant species community and blooming flower diversity. The total effect management had on the Lepidoptera community was stronger than the blooming flower density (Fig. 2B).

Butterfly species are influenced by regional aspects of fragment area and isolation levels (Brommer and Fred 1999). However, studies show that butterflies utilize corridors between patches of habitat, but when patches are in close proximity (within 64 m), butterflies do not necessarily utilize corridors and can simply move between patches (Haddad 1999) suggesting that, at this distance, the butterflies could detect neighboring patches. Baguette and Neve (1994) found that butterfly species are likely to readily move between patches in a highly fragmented system. Collinge et al. (2003) found that local habitat characteristics explained patterns of butterfly diversity rather than the juxtaposition of fragments in an urban landscape, and edge-mediated movement behavior can increase residence time in local habitat patches (Schultz and Crone 2001). In tallgrass prairie remnants in eastern Nebraska, butterflies were not obviously responding to area, edge, or isolation based on our analysis in the sense of large-scale distributional patterns, and local plant communities appeared most important. Behavioral controls on movement often alter individual dispersal near patch boundaries, and individuals may remain in patches more often than expected from random movements (Jones 1977, Kareiva and Shigesada 1983, Kindvall 1996, Fagan et al. 1999, Schultz and Crone 2001). Fragments in this landscape may be within dispersal distances and without dispersal barriers, so Lepidoptera species in this study may not perceive the habitat as fragmented. Areas considered inhospitable to Lepidoptera in agricultural landscapes (row crops) may be sometimes used as habitat, such as the monarch butterfly that will lay eggs on milkweed plants in row crop fields (Sears et al. 2001), but this is probably an unsuitable habitat matrix to most species.

Predators

Predators represented in this study by coccinellids responded only to regional aspects of fragmentation in this analysis. Fragment shape was the most important variable in explaining changes in Coccinellidae community composition. Unexpectedly, management had no influence on coccinellids in this study (Fig. 3B). Many studies have found that top trophic-level species richness, represented by a few taxa or an individual

predator, is influenced directly by regional factors, and regional factors such as fragment area and isolation are more important than regional biotic factors (Kruess and Tschardtke 1994, 2000, Tschardtke et al. 2002). Our results reinforce the trophic susceptibility to fragmentation hypothesis that states species associated with higher trophic levels are more susceptible to fragmentation due to the challenge of recolonization after a local extinction event (K. J. L. Stoner and A. Joern, *unpublished manuscript*).

Direct and indirect effects

Causal mechanisms that link species responses to habitat fragmentation are still poorly understood due to the difficulty in performing large-scale landscape manipulation experiments, and the difficulty of evaluating contributions from direct and indirect effects that can have opposing effects on species responses (Haila 2002, McGarigal and Cushman 2002). Although experimental manipulations best identify causal interactions when hypotheses can be properly framed, this direct approach may not be possible if experiments cannot be performed at the scale needed (e.g., regional landscapes), or if the putative causal relationships are too poorly defined and appropriate hypotheses cannot be devised for rigorous testing. Structural equation modeling helps delineate possible direct and indirect effects (Johnson et al. 1991, Grace and Pugsek 1998) from data that can be readily obtained, and is useful for analyzing the impact of fragmentation. The LISREL algorithm is helpful as it provides extensive quantitative insight to tailor selection of alternative models to the specifications of the study. The resulting best-fit model illustrated as a path diagram suggests individual hypotheses that can be tested experimentally or further investigated with more detailed observations as each arrow or path identifies a putative causal relationship between the insect community and environmental aspects within the context of fragmentation. Although this approach can be criticized because the existence of correlations does not necessarily identify underlying causation, the reverse is also certainly true. Causal relationships have definite and specific correlational relationships that once identified, can lead to further investigation through experimentation, or otherwise provide a general framework for conservation planning (Shipley 1999, 2000).

In conclusion, insect assemblages studied here responded primarily to local habitat changes, influenced by management in a fragmented tallgrass prairie system. Based on these results and many published studies, conservation efforts for many herbivorous insect assemblages should concentrate on managing individual fragments, especially factors affecting the responses of the plant community. At the other end of the continuum, predators in this system responded the landscape-scale factor shape. This reinforces the need to evaluate responses at multiple scales (Milne 1992), even when

examining small animals assumed to respond only to small-scale changes. At present, much additional work remains before we will understand landscape responses in sufficient detail to guide conservation efforts for insect predators.

ACKNOWLEDGMENTS

We thank Brad Danner, Kathleen Keeler, Diana Pilson, and two anonymous reviewers for helpful comments and insights. We also gratefully acknowledge Geoff Henebry for providing the image "Prospecting for Tallgrass Prairie" and additional insight to the complex world of landscape ecology. We also thank Matt Paulsen for help with insect identification. Special thanks to Gerald Kubic, David Barry, James Kumm, Don Crawford, Charles Henkelmann, Wayne Schroeder, Ervin Maahs, Theresa Retzlaff, Owen Hertner, Eleanor Francke, Robert Lemnke, Charles Werchert, Harold Minke, The Audubon Society-Nebraska Chapter at Spring Creek Prairie, Steven Kraus, Henery Luers, David Brhel, Chere Atkins, Lyle Mayer, Ronald Trouba, Calvin Sterns, John Sterns, Larry Dvorak, Don Brubaker, Eldon Kratochvil, Larry England, Jimmy Monnier, Raymond Siekmann, David Predmore, Daryl Mitchell, Harley Batie, Lillie Larsen, John Marshalek, Michael Norman, Terrance Vaverka, and Jake Kare at U.S. Bank Farm Management for use of their land. Financial support was provided by the National Science Foundation grant 0087259, The Nature Conservancy-Nebraska Chapter's J. E. Weaver Competitive Grants Program, and the School of Biological Sciences and Initiative for Ecological and Evolutionary Analysis at the University of Nebraska at Lincoln.

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