

**DISTURBANCE, SPATIAL TURNOVER, AND SPECIES
COEXISTENCE IN GRASSLAND PLANT COMMUNITIES**

By

Erin J. Questad

B.S., The Pennsylvania State University, 1997

Submitted to the graduate program in Ecology and Evolutionary Biology
and to the Graduate Faculty of the University of Kansas
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy.

Chairperson

Committee members

Date defended: _____

The Dissertation Committee for Erin J. Questad certifies
that this is the approved version of the following dissertation:

**DISTURBANCE, SPATIAL TURNOVER, AND SPECIES
COEXISTENCE IN GRASSLAND PLANT COMMUNITIES**

Committee:

Chairperson

Date approved _____

ABSTRACT

Questad, Erin J. (Ph.D.)
Department of Ecology and Evolutionary Biology
University of Kansas

Humans have dramatically altered natural disturbance regimes. We thus need to understand how these alterations affect plant communities and whether natural disturbance regimes can be restored. I explored the effect of disturbance on plant community patterns and species coexistence in grasslands of northeastern Kansas. In the first chapter, I examined the impact of disturbance associated with the five most common grassland management practices on plant community patterns. I measured species richness and differences in community composition among habitat patches at three spatial scales, at two levels of ecological resolution, and at three levels of taxonomic resolution. There were extensive changes to plant community structure associated with grassland management practices, which may be due to reduced environmental heterogeneity, increased dominance by perennial grasses, and/or decreased functional diversity. The second chapter investigates the smaller-scale disturbance associated with prairie vole, *Microtus ochrogaster*, burrows. I found that vole disturbance affected the mean values of nine environmental variables, contributed to environmental heterogeneity, increased local plant species richness, metacommunity evenness, and the presence of fugitive species. Variation in community composition was high among burrows because disturbance shifted the identity of dominant species away from the species dominant in the undisturbed matrix and allowed fugitive species to persist in higher abundances. These patterns are consistent with a successional mosaic and alternative successional trajectories among burrows disturbed at different times. In the third chapter, I used prairie vole burrows as a model system to develop a field experiment testing whether the timing of small-scale disturbances contributes to environmental heterogeneity, and whether the functional complementarity of species in the species pool affects the ability of community composition to reflect heterogeneity through species sorting. Disturbance treatments affected coexistence by creating colonization opportunities and successional niche heterogeneity. The effect of environmental heterogeneity on variation in community composition among habitat patches was the greatest in the presence of a complementary species pool. This interaction between complementarity and heterogeneity demonstrates the importance of trait variation among species for exploiting environmental variation among patches and suggests niche-based coexistence through species sorting. Together, these studies indicate how the negative impacts of human activities on plant communities can be mitigated by improving grassland management practices, restoring small-scale disturbance heterogeneity, and increasing the functional diversity of communities.

ACKNOWLEDGEMENTS

I would not have completed this work without the assistance of several funding sources and many generous people. Funding was provided by the National Science Foundation Graduate Research Fellowship and grant #DEB 01-08302, the U.S. Department of Agriculture grant #USDA-NRICGP (2003-35101-12934), the Kansas Ecological Reserves, University of Kansas (KU) Department of Ecology and Evolutionary Biology, KU Women's Club and Graduate School, and the NASA-MSU program of the U.S. International Association for the Society of Landscape Ecology.

I thank Bryan Foster for being an outstanding advisor and an all-around nice person to work with. He was instrumental in helping me form my research questions, supporting me throughout my work, and teaching me to be a good scientist and collaborator. It has been a real pleasure working with him.

I am also grateful to my committee members and have had unique opportunities to learn from each of them. Kelly Kindscher was an excellent mentor in the field and collaborator on the managed grassland study. Helen Alexander has taught me a great deal, both in and out of the classroom. I am impressed with her deep level of commitment to her students, and thank her for her generosity. John Kelly was kind enough to let me teach Biometry several times, which helped me to become more confident in my abilities to use and teach statistics. This experience was a critical part of my graduate training. I also appreciate Chris Brown for his willingness to participate in my work. I am indebted to all members of my committee for their contributions to my research and education.

The staff of the Kansas Ecological Reserves provided space and support for my research, and met my requests with kindness. I am especially grateful to Bruce Johanning, Dean Kettle, and Galen Pittman. I also thank the numerous land-owners who granted access to their managed grasslands, showed interest in my research, and shared their experiences with me. Craig Freeman and Caleb Morse were also very kind to offer their time and expertise in botanical knowledge. Numerous undergraduate assistants were instrumental to this work, including Karl Anderson, Ronnie Chase, Paul Crangle, Jennifer Dziuvenis, Becca Evanhoe, Stephanie Fritts, Ariana Jones, Brian Lefler, Jason McVay, Erika Nougera, Nathan Olds, Sarah Pittman, Sharon Shmiege, Diane Slocum, Eli Stogsdill, Lynn Swafford, and Andrea Wolf.

Many faculty members at KU have shared their time and expertise with me. I especially thank Norm Slade, Mike Tourtellot, Daphne Fautin, and Craig Martin. Jon Chase of Washington University and several anonymous reviewers contributed helpful comments on manuscripts. I appreciate Alan Knapp and Lissy Coley, former mentors who have been instrumental in my success as a graduate student.

Many graduate students, post-docs, and lab members contributed to the intellectual and material development of this work. I am forever in debt to Todd Aschenbach, Cathy Collins, Tim Dickson, Irene Khavin, and Cheryl Murphy. I thank them for listening to my ideas (good and bad), for engaging in thoughtful conversations, and for making field work in high heat and high humidity fun. There

are so many reasons to thank them that it is impossible to list them all. I also thank Lisa Castle, Sarah Hinman, Greg Houseman, Suneeti Jog, Hillary Loring, Jennifer Moody-Weis, and Matt Ramspott for their help with and insight into my research. I am also grateful for the support of dear friends Becca Rampsott, Kristen Karle, Nina Stewart, and the gorgeous biologist knitters.

My family has been extremely supportive throughout my education. I thank Brian Questad, Meghann Questad, Laura Klein, and Adam Questad for the many ways they encouraged me. I owe a huge debt to my parents, Ken and Fran Questad, who gave me opportunities to learn and whose support has never wavered. I am very thankful for my family, and I would not have completed this degree without them. I am the most grateful for Mario Espinoza, whose thoughtfulness, generosity, and care were the key elements helping me through graduate school. In addition to being supportive, he has challenged me to think deeply and approach life with intention. This journey would have been impossible without him.

TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	vi
LIST OF FIGURES	vii
LIST OF TABLES.....	viii
INTRODUCTION	1
CHAPTER 1.Management disturbance in Kansas grassland communities: patterns of compositional turnover, spatial scale, and taxonomic resolution	3
CHAPTER 2.Vole disturbances and plant diversity in a grassland metacommunity.	42
CHAPTER 3.Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities.....	71
CONCLUSION.....	101
LITERATURE CITED.....	105

LIST OF FIGURES

Fig. 1.1. Map of study area.	35
Fig. 1.2. Detrended correspondence analysis axes 1 and 2.....	36
Fig. 1.3. Compositional variation among sites in each management class.....	38
Fig. 1.4. Species richness for each area sampled by management class.....	40
Fig. 1.5. Spatial turnover for each area sampled by management class.	41
Fig. 2.1. Results of paired t-tests for patch-scale diversity and randomization tests for metacommunity-scale diversity.	70
Fig. 3.1. Experimental plot design.....	96
Fig. 3.2. Interaction plots for patch richness, spatial turnover, and community richness of the complete community (a-c) and added species (d-f).....	98
Fig. 3.3. Interaction plots for the effect of seed addition and resource heterogeneity on spatial turnover.....	100

LIST OF TABLES

Table 1.1. Grassland management classes.....	30
Table 1.2. Number of species recorded in each functional group over all 98 sites. ...	31
Table 1.3. Comparisons of species, functional group, and soil productivity metrics among management classes.	32
Table 1.4. Results of Repeated Measures ANOVA's of within site data.	34
Table 2.1. Group means, one standard error, and results of paired t-tests (df = 30) for resource variables.....	65
Table 2.2. Coefficient of variation (CV) over burrow and matrix plots for 10 resource variables.	66
Table 2.3. Species associated with plot types.	67
Table 2.4. Relative percent cover of species associated with plots.	68
Table 2.5. Relative percent cover of dominant species.	69
Table 3.1. Species in added species pools.	91
Table 3.2. Patch richness, spatial turnover, and community richness for analysis of all species and added species.	93
Table 3.3. The effect of seed addition on the response of spatial turnover to environmental heterogeneity.....	95

INTRODUCTION

Disturbance is an essential component of many natural ecosystems and is also a widespread consequence of human activities. The spatial extent of disturbance events can vary from small, such as soil trampling by animals, to large, such as flooding caused by hurricanes. In addition, the response of ecosystems to disturbance can occur at small scales (e.g., through reduced competition among co-occurring species) or at large scales (e.g., the extirpation of species not adapted to disturbance). This dissertation examines the scale-dependent effects of disturbance on grassland plant communities by addressing small-scale and large-scale sources of disturbance, and examining the scale-dependent community responses to these sources.

The intermediate disturbance hypothesis (IDH) has been invoked to explain the effect of disturbance on local diversity through the creation of niche opportunities and periods of decreased competition that lead to coexistence (Grubb 1977; Connell 1978; Huston 1979; Sousa 1979; Huston 1994; Chesson & Huntly 1997; Platt & Connell 2003); however, evidence supporting this mechanism is equivocal (Mackey & Currie 2000). The IDH can be extended by understanding the effect of disturbance at more than one spatial scale (Shea *et al.* 2004), including scales larger than the disturbance itself. For example, a metacommunity can be a collection of disturbed and undisturbed local communities that are connected by dispersal in a landscape (Leibold *et al.* 2004; Holyoak *et al.* 2005). Measuring variation in community composition among patches (spatial turnover) is one method of evaluating the effects of disturbance on community composition at more than one spatial scale.

Here, I study patterns of spatial turnover and examine the scale-dependent effects of disturbance on grassland plant communities. First, I investigate the relatively large-scale disturbance associated with grassland management in northeastern Kansas. I examine differences among management classes in species richness and spatial turnover measured at three spatial scales, two levels of ecological resolution, and three levels of taxonomic resolution (Chapter 1). Second, I study the smaller-scale disturbance associated with prairie vole, *Microtus ochrogaster*, burrows, its effects on resource heterogeneity, local diversity, spatial turnover, and metacommunity diversity (Chapter 2). Third, I use prairie vole burrows as a model system to develop a field experiment that tests whether disturbance contributes to environmental heterogeneity and influences coexistence through species sorting. Species sorting occurs when species exhibit tradeoffs for environmental factors that are distributed heterogeneously among patches in a habitat, and different species are favored in different patches, leading to spatial turnover of community composition among patches and coexistence at the community scale (Tilman & Pacala 1993; Chase & Leibold 2003). This experiment also investigates the impact of complementarity among species in the species pool on species sorting. Complementarity occurs when species are adapted to different resources, and it can promote coexistence through resource partitioning. I investigate whether complementarity affects the ability of community composition to reflect environmental heterogeneity and whether it contributes to coexistence through species sorting (Chapter 3).

CHAPTER 1.

MANAGEMENT DISTURBANCE IN KANSAS GRASSLAND COMMUNITIES: PATTERNS OF COMPOSITIONAL TURNOVER, SPATIAL SCALE, AND TAXONOMIC RESOLUTION

ABSTRACT

Understanding how land-use influences plant communities requires studying multiple management practices and many aspects of community structure. In addition, investigating community patterns that vary with spatial scale and the level of taxonomic or ecological resolution provides insight into the ecological processes responsible for the patterns. I studied the five most common classes of grassland management in northeastern Kansas. I analyzed plant community data recorded at three spatial scales in 98 managed grassland sites, and examined species richness and patterns of compositional turnover among patches (spatial turnover) at these scales, at two levels of ecological resolution (species and functional group), and at three levels of taxonomic resolution (species, genus, and family). Management practices caused significant changes in plant community diversity, composition, and spatial structure. These changes arose from historical cultivation that had persistent effects on soil and community properties, the replanting of perennial grass species that changed the dominance structure of communities, and the contemporary management disturbance applied to the ecosystem. The response of diversity and spatial turnover to

management depended on the spatial scale and taxonomic or ecological resolution of measurement. Management practices may reduce plant diversity by reducing environmental heterogeneity, increasing dominance by perennial grasses, and decreasing the functional diversity of communities. I suggest two major management changes that may mitigate some of these negative impacts: 1) increasing the use of hay management on native sites, and 2) improving the Conservation Reserve Program by increasing enrollment, adding more native prairie species to seed mixes, and incorporating a periodic mid-summer hay disturbance may enhance biodiversity conservation on these sites.

INTRODUCTION

Disturbance is an important component of many natural ecosystems and is also a widespread consequence of human activities (Vitousek *et al.* 1997; Foster *et al.* 2003). It can have a variety of impacts on ecosystem structure, including removing organisms or reducing their growth rates, altering environmental conditions and resources, and establishing unique habitats. Disturbance can facilitate species coexistence by decreasing the abundance of competitively dominant species and creating niche opportunities for inferior competitors (Grubb 1977; Connell 1978; Huston 1979; Sousa 1979; Huston 1994; Chesson & Huntly 1997; Platt & Connell 2003). In the North American tallgrass prairie ecosystem, fire and bison grazing are key sources of disturbance that have shaped plant and animal communities (Collins *et al.* 1998; Knapp *et al.* 1998; Knapp *et al.* 1999a); however the remaining tallgrass

prairie is less than 18% of its original range (Klopatek *et al.* 1979; Samson & Knopf 1994; Noss *et al.* 1995), and is subject to altered natural disturbance regimes. In addition, these prairie remnants are often managed for cattle or hay production and the areas surrounding them have a variety of agricultural uses, including crop production and grazing or hay production on cool-season grasslands. This landscape is now a mosaic of sites with different management practices employing different disturbance regimes that have had significant impacts on plant species diversity (Jog *et al.* 2006). Thus, it is important to understand how management has altered plant community structure in both remnant prairies and in other extensively managed grasslands in order to inform restoration and adaptive management practices in this landscape (Lindenmayer *et al.* 2007).

In addition to species diversity, disturbance can influence other aspects of plant community structure, such as variation in community composition among habitat patches (spatial turnover). In tallgrass prairies, spatial turnover reflects variation among patches in disturbance intensity, disturbance frequency, and community dominance and is influenced by disturbance from a variety of sources, including fire, ungulate grazing, and small-mammal activity (Collins 1989; Gibson 1989; Collins 1992; Collins & Smith 2006; Veen *et al. in press*). Like disturbance in native prairies, the changes to natural disturbance regimes caused by grassland management practices may alter patterns of spatial turnover.

The effect of disturbance on plant community structure can also vary with spatial scale (Wiens 1989; Levin 1992; Collins & Smith 2006). In the tallgrass prairie

ecosystem, disturbance occurs from multiple sources operating at different spatial scales, from the small scale soil trampling by ungulate hooves to the large scale of managed fires (Collins & Glenn 1991; Collins & Smith 2006). Even the same source of disturbance may have different effects on community composition at different scales. For example, selective foraging decisions by grazers can increase spatial turnover at small scales due to variable grazing intensity among patches (Veen et al. *in press*), whereas grazing can reduce spatial turnover at large scales by affecting patterns of dominance by C₄ grass species (Vinton *et al.* 1993; Adler *et al.* 2001; Collins & Smith 2006). It is likely that the effect of managed disturbance regimes on patterns of spatial turnover may also vary with scale. Hay management may cause similar patterns of spatial turnover at small and large scales because cutting hay applies a uniform disturbance across the community. Replanted grasslands on previously cultivated sites may also have similar small and large scale turnover patterns due to a history of plowing and the uniform planting of perennial grass species.

In addition to spatial scale, patterns of community structure can also vary with the level of ecological or taxonomic resolution considered, which may reveal the effects of different ecological processes that organize community composition. A large body of community assembly theory postulates that patterns of community composition are shaped by both stochastic, historical events that can no longer be observed as well as deterministic processes (Diamond 1975; Temperton *et al.* 2004). Historical contingencies (e.g., priority effects) can lead to high spatial turnover in

species composition among communities, but deterministic processes can maintain species with similar traits among communities (Drake 1991; Fukami *et al.* 2005). Thus, patterns of community composition can vary when measured at different levels of ecological resolution (i.e., species vs. functional groups). It has also been proposed that the ecological processes that drive compositional patterns may differ with taxonomic resolution (e.g., species, genus, family, phyla), and that large scale processes like climate and biogeography will affect higher taxonomic levels and small scale processes like competition for resources will primarily affect species composition (Anderson *et al.* 2005). The result of this effect is that community patterns that are apparent at the species level may be obscured at higher levels of taxonomic resolution; however, this idea has received little attention in grassland ecosystems (but see Fukami *et al.* 2005). In addition, human-induced ecological changes could have greater impacts on community organization than natural ecological processes (Vitousek *et al.* 1997; Foster *et al.* 2003) and their effect on community composition measured at different taxonomic levels deserves further exploration.

Here, I investigate how grassland management practices have affected plant community diversity, composition, and spatial structure in the managed landscape of northeastern Kansas. I studied the five most common classes of grassland management in this region (Table 1): cool-season hay (C-H), cool-season grazed (C-G), warm-season native hay (W-NH), warm-season native grazed (W-NG), and warm-season Conservation Reserve Program (W-CRP). These classes include sites

that have been historically cultivated and replanted with perennial grasses (C-H, C-G, and W-CRP) and native prairie remnants (W-NH and W-NG). Contemporary management practices also vary among sites, including hay production (C-H and W-NH), cattle grazing (C-G and W-NG), and conservation (W-CRP).

In addition to differences in historical and contemporary management practices, there are likely other site features that are associated with management classes. For example, native sites remain intact because their topography made them unsuitable for plowing, and hay-managed sites may be more level than grazed sites to facilitate mowing. Here, I focus on plant community patterns as a function of historical cultivation, contemporary management, and their interaction; but recognize that there may be landscape features that also contribute to community differences among management classes.

I analyzed plant community data recorded at three spatial scales in 98 managed grassland sites, and examined species richness and spatial turnover at these scales and at two levels of ecological resolution (species and functional group) and three levels of taxonomic resolution (species, genus, and family). I thus test for differences in plant community structure as a function of historical and contemporary grassland management practices by examining patterns of 1) species diversity and variation in community composition among sites; 2) species richness and spatial turnover measured at different scales within sites; and 3) species richness and spatial turnover measured at different levels of ecological and taxonomic resolution.

METHODS

Sampling

The study area was an agricultural region that was approximately 1500 km² in size and located at the prairie-forest ecotone of northeastern Kansas in Jefferson, Leavenworth, and Douglas counties (39°N, 95°W; Fig. 1.1). Hay production and cattle grazing account for approximately 45% of the value of agricultural products from these three counties, and grain production (corn, soybeans, and wheat) account for the majority of agricultural products (Kansas Agricultural Statistics Service 2006). Sites with areas greater than or equal to one hectare were identified from a previous study of managed grasslands (Murphy et al. 2006), the Kansas Natural Heritage Program database of tallgrass prairie remnants, digital aerial photography (NRCS 2003), and driving surveys. In order to minimize the influence of substrate variation, sites with silt loam or silty clay loam soils and upland topography were selected for sampling (Dickey *et al.* 1977a; Dickey *et al.* 1977b; Zavesky & Boatright 1977). All sites were privately owned, and land owners were contacted to obtain permission for sampling and to determine the dominant management practice on the site.

Field crews sampled 98 sites in five grassland management classes (Table 1.1), representing the major grassland land-cover in the region: cool-season hay (C-H, 20 sites), cool-season grazed (C-G, 24 sites), warm-season hay (W-NH, 18 sites), warm-season grazed (W-NG, 17 sites), and conservation reserve program (W-CRP, 19 sites). These management classes were based on historical and contemporary land-use. C-H and C-G sites were historically plowed, planted with crops, taken out of

cultivation, and reseeded with exotic cool-season grass species, most commonly *Bromus inermis*, and *Lolium arundinacea* (Kansas Agricultural Statistics Service 2006). Cool-season grasses use the three-carbon (C₃) photosynthetic pathway, grow in the cooler spring and fall months, and reach peak biomass in early summer. W-NH and W-NG sites are never-plowed tallgrass prairies and are dominated by warm-season grasses and native forb species. Warm-season species use the four-carbon (C₄) photosynthetic pathway, grow most actively during the warm, dry summer months, and reach peak biomass during the late summer. Hay management on C-H and W-NH sites involves cutting and baling all plant material from the field during times of peak biomass. These times are typically June for C-H and July for W-NH (C. Freeman, *pers. comm.*). Grazed sites are generally stocked with cattle during the growing season and allowed to rest during the dormant period. W-CRP sites were historically plowed and cultivated for crop production. Landowners receive a federal government subsidy to plant native warm-season grass species (USDA 2007b), and they occasionally burn these sites. No other management occurs on W-CRP sites except in cases of drought when they can be grazed.

All 98 sites were surveyed from 26 May through 28 July 2004. In order to characterize the plant community at various spatial scales in each site, three replicates of nested quadrats were evenly distributed along a 100-m transect located in an upland, interior area. Nested quadrats measured three spatial grains: 1 m² (1 x 1 m), 100 m² (10 x 10 m), and 400 m² (20 x 20 m). All plant species were recorded in each quadrat, and percent cover for each species was visually estimated in the 400-m²

quadrats. To measure the soil quality of each 400-m² quadrat, three 150-mm deep soil samples were collected with a 914-mm tube sampler for pH and nutrient analysis. The three samples were mixed together and air dried at room temperature (22-27°C) to a constant mass. Soils were sifted through a 2-mm sieve to remove roots and plant debris. Samples were sent to the Soil Testing Laboratory at Kansas State University where they were analyzed for total soil nitrogen and carbon (% by mass) using a LECO CN 2000 dry combustion analyzer. Soil pH was measured using a glass electrode pH meter (McLean 1982).

Taxonomic and functional group classification

In order to examine community patterns at different levels of taxonomic resolution, species were placed into genera and families using *The Flora of the Great Plains* (GPFA 1986). To compare patterns at different levels of ecological resolution, each species was placed into a functional group based on its longevity and growth form. Species were divided into four longevity classes (annual, annual/biennial, biennial, and perennial) and ten growth form classes (C₃ grass; C₄ grass; non-grass graminoid; C₃ forb; C₄ forb; shrub; vine; tree; leguminous forbs; and leguminous vines, shrubs, and trees). I classified species based on information in Downton (1975), GPFA (1986), Towne (2002), and USDA (2006). When these sources provided inconclusive information, I consulted with experts on the species in this geographical region to make classifications (K. Kindscher and S. Jog, pers. comm.). Species were placed into functional groups using all combinations of longevity

classes with growth form classes, thus each species was placed into only one functional group.

Data Analysis

To characterize the diversity patterns for each site, I first calculated the relative abundance of each species in a site by adding its percent cover from the three 400-m² quadrats and dividing that sum by the total vegetative cover from the three quadrats. These data were used to calculate site-level species richness (S), species evenness (E), and Simpson's index of species diversity (D') (McCune & Mefford 1999). The relative abundance of each functional group was determined in order to calculate site-level functional group richness (S_{FG}), functional group evenness (E_{FG}), and functional group diversity (D'_{FG}). I calculated site-level metrics of soil quality (soil N, C, and pH) by averaging the three values of each measure from the 400-m² quadrats for each site. In order to examine the heterogeneity of soil conditions, I calculated the coefficient of variation (CV) of soil N and C for each site.

To test the effect of management class on site-level S , E , D' , FR , S_{FG} , E_{FG} , D'_{FG} , soil N, soil C, soil pH, CV N, and CV C, I used two analysis of variance (ANOVA) models in Minitab 14.1. One model was a one-way ANOVA using the five management classes as fixed factors. The other model was a two-way ANOVA omitting the W-CRP sites. The two factors were Historical Disturbance (cultivated or not cultivated) and Contemporary Disturbance (hay or grazing management). By omitting the W-CRP sites from this analysis, I obtained a balanced design and could test for an interaction between Historical and Contemporary Disturbance. For each

model, residuals were tested for normality using a Kolmogorov-Smirnov test ($P > 0.10$) and homogeneity of variance (HOV) was tested with Bartlett's test ($P > 0.10$). If normality or HOV assumptions were not met, I used a Kruskal Wallis test for one-way models and the Scheirer-Ray-Hare extension of the Kruskal-Wallis test for two-way models (Sokal & Rohlf 1995). To further characterize the composition of plant communities in each management class, I performed detrended correspondence analyses (DCA) in PC-ORD 4.14 at two levels of ecological resolution, one using the species relative abundance data and one using the functional group relative abundance data. I used DCA because its rescaling procedure performs better than unconstrained ordination techniques when analyzing large, ecological datasets like this one that are likely to have non-linear distributions (McGarigal et al. 2000). To evaluate the variance explained by ordination axes, I calculated a coefficient of determination for each axis between relative Euclidean distance in the species space to Euclidean distance in the ordination space (McCune & Mefford 1999).

I used the site-level community data and spatial turnover metrics to characterize variation in community composition (compositional variation) among sites in each management class. Spatial turnover metrics measure differences in community composition on a scale of zero (identical communities) to one (completely different communities). I used two turnover metrics to measure the compositional variation among all sites in each management class: 1) Jaccard dissimilarity estimated turnover using species presence-absence data and 2) Bray-Curtis dissimilarity used species relative abundance data. I used PERMDISP to

determine whether community composition was more variable among sites in certain management classes (Anderson et al. 2006). PERMDISP finds the mean deviation of sites from the centroid for each management class and uses permutations to statistically evaluate differences in mean deviation from the centroid among classes. This permutational approach does not require some of the assumptions of classic multivariate and parametric statistical analyses, and was developed for use with multivariate community datasets like this one. I ran two PERMDISP analyses with 999 permutations, one using Jaccard dissimilarity to measure compositional variation and one using Bray-Curtis dissimilarity.

To test whether plant diversity patterns vary with spatial scale and taxonomic or ecological resolution, the following diversity metrics were calculated for each quadrat: species richness (S_S), generic richness (S_G), family richness (S_F), and functional group richness (S_{FG}). I calculated the mean of each of these values over the three replicate quadrats of a given size in each site, resulting in three values of each metric for each site representing the mean for 1-m², 100-m², and 400-m² quadrat sizes. In order to test whether spatial turnover varied with spatial scale and taxonomic or ecological resolution, I calculated spatial turnover (Sorenson's dissimilarity index) of species (T_S), genera (T_G), families (T_F), and functional groups (T_{FG}) among all possible pairs of quadrats of each size in a site and found the mean spatial turnover for each quadrat size in each site.

To test whether the effect of management on community patterns was scale-dependent, I used a repeated-measures ANOVA in SPSS 14.0. The repeated measure

was sampling area (1-m², 100-m², and 400-m²) and management class was a fixed factor with five levels. A significant interaction term indicated the effect of management on the dependent variable varied among sampling areas. I ran separate ANOVA's for S_S , S_G , S_F , S_{FG} , T_S , T_G , T_F , and T_{FG} . I log-transformed richness measures to allow for a more direct comparison of the effects of management among areas of different sizes (Rosenzweig 1996). I tested the residuals for normality using the Kolomogorov-Smirnov test ($P > 0.1$) and the variance-covariance matrix for circularity with Mauchly's W ($P < 0.05$). If the variance-covariance matrix did not meet the assumption of circularity, I adjusted the degrees of freedom for F-tests based on the Huynh-Feldt Epsilon. I qualitatively compared the results of these ANOVA's to examine the effects of taxonomic and ecological resolution. In particular, I was interested in whether significant effects occurred at some levels of resolution and not at others.

RESULTS

Site-level patterns

Over all sites, 390 species in 224 genera, 66 families, and 20 functional groups were observed (Table 1.2). Most species were perennial (32%) and annual (17%) forbs. Site-level (across the three 400-m² plots) S ranged from 7 to 108 species. Warm-season native sites had the greatest values of species and functional group metrics analyzed at the site level (Table 1.3). Cool-season sites had the lowest S , E , D' , and S_{FG} ; W-CRP sites had intermediate values for these metrics. The historical x

contemporary disturbance interaction was significant for values of S and E_{FG} (Table 1.3), which occurred because grazed sites had lower values than hayed sites among warm-season grasslands, but grazed sites had values greater than or equivalent to hayed sites among cool-season grasslands. Warm-season native sites had the greatest soil N and C (Table 1.3). Grazed sites had greater N and C than hayed sites. W-CRP sites had the lowest N and C and the highest pH, and W-NH sites had the lowest pH. There was no effect of management class, historical disturbance, contemporary disturbance, or the historical x contemporary disturbance interaction on soil heterogeneity variables, CV N and CV C ($P > 0.20$).

DCA of both species and functional groups provided clear separation of warm-season and cool-season sites on the first axis, which was highly influenced by dominant perennial grass species (Fig. 1.2). W-CRP sites were more closely associated with native sites, and were the farthest sites from cool-season sites on the first axis. W-NH and W-NG sites separated on the second species axis, with W-CRP sites more closely associated with W-NG (Fig. 1.2a and 1.2b). Grazed and hayed cool-season sites did not separate on this axis, and W-NH and W-NG sites did not separate on the second axis when functional groups were analyzed (Fig. 1.2c and 1.2d). There were significant differences in compositional variation (mean deviation from centroid) among management classes using species presence-absence ($F_{\text{PERMDISP}} = 23.77$, $P < 0.001$) and species relative abundance ($F_{\text{PERMDISP}} = 7.06$, $P < 0.001$) data, showing that the degree of variation in community composition among sites was related to management class. Using presence-absence data, compositional variation

was higher among cool-season and W-CRP sites and lower among warm-season sites (Fig. 1.3a). Using relative abundance data, compositional variation was higher among grazed (C-G and W-NG) and W-NH sites and lower among C-H and W-CRP sites (Fig. 1.3b).

Spatial scale and taxonomic/ecological resolution

Warm-season sites had the greatest values for all richness measures [species richness (S_S), generic richness (S_G), family richness (S_F), and functional group richness (S_{FG})] at the three spatial scales sampled (Fig. 1.4). W-NH sites had greater S_S , S_G , and S_F than W-NG sites, but had similar S_{FG} . The scale x management interaction was significant for S_S , S_G , S_F , S_{FG} , spatial turnover of species (T_S), and spatial turnover of genera (T_G ; Table 1.4, Figs. 1.4 and 1.5). There was a greater difference in S_S , S_G , S_F , and S_{FG} among management categories at small scales compared to large scales. T_S and T_G of warm-season sites was higher than other management categories at the 1-m² scale and was lower or equivalent at the 400-m² scale (Fig. 1.5). In particular, W-NG sites had high T_S and T_G at the 1-m² scale, and W-NH sites had low T_S and T_G at the 400-m² scale. This interaction did not occur for spatial turnover of families (T_F) or functional groups (T_{FG}), and there was no main effect of area on T_{FG} . In general, cool-season and W-CRP sites had T_F and T_{FG} greater than or equivalent to warm-season sites at all spatial scales.

DISCUSSION

I found significant differences in plant community diversity, composition, and spatial structure among management regimes. These differences were associated with historical cultivation that had persistent effects on ecosystem properties, the replanting of perennial grass species that changed the dominance structure of communities, and the contemporary management disturbance applied to the ecosystem. There was an influence of contemporary management disturbance on values of site richness and functional group evenness among native sites, but not among historically cultivated cool-season sites. In addition the differences in richness and spatial turnover among management classes depended on the spatial scale and taxonomic or ecological resolution of measurement. Management practices may influence community patterns by reducing environmental heterogeneity, increasing dominance by perennial grasses, and decreasing the functional diversity of communities.

Historical and contemporary disturbance

Sites that were historically cultivated and replanted with grass species had much lower diversity than native sites. These cultivated sites also had lower functional group diversity, lower soil quality, and a distinct community composition. The patterns of species richness and functional group evenness among contemporary management regimes differed between cool-season and warm-season sites. Among warm-season sites, grazed sites had lower species richness and the evenness of functional groups when compared to hay management, but this pattern did not occur

among cool-season sites. These results suggest that in this cultivated landscape, the large-scale historical conversion of prairie to cool-season grasslands likely has a greater impact on plant diversity than localized contemporary management practices.

Soils on cultivated sites have been severely impacted by repeated plowing, erosion, and fertilizer use. These practices have likely had long-term impacts, including the reduced soil N and C and increased pH found in this study, which may be a result of topsoil erosion, extensive cultivation, and removal of biomass that reduces nutrient inputs from decomposition (Knops & Tilman 2000; Foster *et al.* 2003; Murphy *et al.* 2006). This nutrient limitation could create harsh environments in which only a few species can persist, thus limiting plant diversity (Huston 1994). Diversity may be further limited by extensive habitat fragmentation that prevents native species from recolonizing a site once it is removed from cultivation and replanted with perennial grasses (MacArthur & Wilson 1967; Cook *et al.* 2005).

There was a trend among cool-season sites for greater species richness and functional group evenness with grazing management, compared with hay management, which could be a result of nutrient cycling and disturbance effects that differ among these management practices. Homogeneous fertilization and mowing on hay sites may promote dominance by cool-season grass species (Murphy 2004), whereas grazing may produce more heterogeneous patterns of disturbance and nutrient additions from dung and urine (Mcnaughton 1979; Day & Detling 1990; Vandvik & Birks 2002a, b) that could cause more variable dominance patterns. Thus,

competitive exclusion may contribute to lower diversity and functional group evenness on hay sites, and grazing management may reduce this effect.

Contemporary management of warm-season native grasslands exhibited opposite patterns: hayed sites had greater species richness and functional group evenness than grazed sites. The lower diversity in grazed sites could be due to soil erosion that occurs from grazing (or over-grazing) on these sites. Erosion may also be a result of the steeper slopes present on native grazed sites, a site characteristic that is associated with this management practice (E.J. Questad, unpublished data). In addition, lower diversity could result from the elimination of species that cannot tolerate cattle grazing but are adapted to hay disturbance. Bison grazing can promote the growth of specific functional groups that are adapted to this type of disturbance (Towne et al. 2005), thus increasing the dominance of these groups and reducing functional group evenness of the community; but I did not find differences in functional group composition between W-NH and W-NG sites using multivariate ordination, suggesting that cattle grazing may not have this effect on the functional groups I analyzed.

It is possible that cattle grazing management in this region may not have the same impact on plant diversity as bison grazing (Towne et al. 2005). Bison preferentially graze *Andropogon gerardii* and other dominant C₄ grasses, which decreases dominance and competitive exclusion and increases diversity compared to ungrazed prairie (Knapp et al. 1999a; Towne et al. 2005). Cattle grazing can have similar impacts on plant community diversity when cattle are stocked equally to

bison; however, the management decisions associated with cattle grazing (e.g., stocking rates, herbicide use, etc.) may cause plant community changes that differ from bison (Towne et al. 2005). Stocking rates of cattle may be higher than naturally occurring bison populations, which could lead to soil erosion and high rates of disturbance that negatively affect plant communities. Herbicide application for unpalatable species may also reduce diversity on these sites.

Site composition

In addition to differences in measures of diversity, I also found significant differences in species and functional group composition among management classes, indicated by the separation of sites on multivariate axes (Fig. 1.2). I found that cool-season sites (C-H and C-G) separated from warm-season sites (W-NH, W-NG, and W-CRP) on the first axis, which revealed the effect of the dominant grass species on community composition. In this case, W-CRP sites were more similar to native warm-season sites even though W-CRP sites have experienced the most cultivation, showing that some aspects of native community structure can be restored through simple seed additions of native warm-season grasses. The effect of dominant species on composition was maintained when functional groups were used in the ordination. In contrast, sites undergoing hay and grazing management had distinct compositions among warm-season sites for the species ordination, but not for the functional group ordination, suggesting that compositional differences among these sites occur at the species level.

The variation in community composition among sites also differed among management class. Using presence-absence data, I found greater compositional variation among cultivated sites compared to native prairies. These results differ from studies of serpentine plant communities in the California Floristic Province (Harrison & Inouye 2002) and tallgrass prairies in the state of Iowa (Wilsey *et al.* 2005), which found high compositional variation (beta richness) among remnant native communities. The area of the California Floristic Province is 293,804 km² (Conservation International 2007) and the state of Iowa is 144,701 km² (U.S. Census Bureau 2008), compared with 1,500 km² in my study. Thus, the contrasting results are likely due to the smaller geographic extent and the deliberate selection of sites with similar substrate and climatic conditions in my study (Condit *et al.* 2002).

The observed patterns of high compositional variation among cultivated sites could occur in response to several factors. First, most native prairie remnants are intact because their topography made them difficult to plow, leading to similar topographical features among these sites that could contribute to their compositional similarity. Second, cultivated sites have fewer species and are dominated by planted grass species. Even small differences in the identity of less common species could have large impacts on compositional variation in these low-diversity sites because they account for a greater proportion of the total number of species. Third, compositional variation may be a result of differences in management practices among landowners. For example, the rate of fertilizer application, herbicide use,

stocking density of cattle, or timing of hay harvest may vary more among land owners of cool-season grasslands than native warm-season sites.

In contrast to the presence-absence patterns, relative abundance patterns showed that native warm-season sites and grazed sites had greater compositional variation than cool-season hay or W-CRP sites. This result may demonstrate the influence of contemporary management practices on dominance patterns. For example, cool-season hay sites are managed with uniform fertilizer application and mowing, which likely creates high levels of dominance by cool-season grass species, leading to greater compositional similarity among sites. W-CRP sites are planted with warm-season grass species and receive little additional management, a practice that promotes warm-season grass dominance (Knapp et al. 1998). In contrast, grazing management may be more variable due to different stocking densities or grazing may favor opportunistic species that vary among sites, thus creating greater variation in composition. Native warm-season sites have greater species evenness and lower dominance, which may cause the relative abundances of species to vary among sites. Thus, reducing dominance by perennial grass species may be one aspect of adaptive management that is important for restoring natural community structure within sites and at the landscape scale.

Spatial scale and taxonomic/ecological resolution

The scale-dependence of community patterns can also help reveal the processes that cause these patterns (Wiens 1989; Levin 1992; Scheiner *et al.* 2000). One aspect of determining scale-dependence is testing whether the relationship

between a causal factor, such as management class, and a response variable, such as species richness or spatial turnover in species composition, is rank-invariant (Scheiner et al. 2000). Rank-invariance occurs when causal factors have the same effect across the observed scales, and rank-variance indicates that the effect of the causal factor depends on the scale observed. Here, I found rank-invariance for all measures of richness among management classes (i.e., warm-season hay sites had the greatest richness at all scales, followed by warm-season grazed, etc.). In contrast, I found rank-variance for measures of spatial turnover (T_S and T_G), where warm-season sites had higher turnover than other management classes at small scales and lower or equivalent turnover at large scales.

These scale-dependent patterns could have several explanations. High turnover at small scales may arise due to a reduction in dominance caused by disturbance (Veen et al. *in press*), fine-scale species sorting across environmental heterogeneity (Tilman & Pacala 1993; Questad & Foster *in press*; Chapter 3), stochastic events (Vandvik & Birks 2002a), or historical contingencies that lead to priority effects and alternative community states (Drake 1991). Cultivation may have reduced the ability of these processes to influence turnover by eliminating natural patterns of environmental heterogeneity and increasing dominance by planted perennial grasses. This replanting also reduces the trait variation among species in the species pool by introducing many seeds from one functional group. Trait variation can be important for allowing different species to exploit different environmental conditions throughout the ecosystem (species sorting) and can significantly affect

spatial turnover (Questad & Foster *in press*; Chapter 3); therefore, changes in dominance patterns caused by cultivation may influence turnover directly and indirectly through a reduced capacity for species sorting. A reduction in turnover at larger scales in warm-season sites may be due to incorporating more of the same habitat types in sampling quadrats (Rosenzweig 1996), such as including both grazed and ungrazed patches in all samples (Vinton *et al.* 1993; Adler *et al.* 2001; Collins & Smith 2006).

These patterns could also arise if different niche dimensions structured communities at different scales. This idea is consistent with the results at different levels of taxonomic and ecological resolution. I found the differences in spatial turnover among management classes to be scale-dependent for species and genera, but not for families or functional groups, suggesting that scale-dependent processes are not as important for structuring coarser levels of taxonomic and ecological resolution. It is possible that community structure at these coarser levels is most influence by dominant perennial grass species. The species and genera of these dominant individuals may vary among 1-m² plots, but their family and functional groups are the same. Thus, it is possible that niche differentiation structures small-scale species and generic composition, but larger-scale phenomena (e.g., environmental gradients, management disturbance) influence families and functional groups. I also found greater overall spatial variation in cool-season and W-CRP sites for both family and functional group composition, but no area x management

interaction, suggesting that large-scale management practices had an overriding influence on patterns of family and functional group structure at all scales.

Finally, it is also possible that scale-dependent patterns of spatial turnover could be associated with the species diversity or number of individuals present on a site, and native sites with higher diversity (and possibly more individuals) may exhibit scale-dependent patterns that species-poor sites do not. The absence of scale-dependence when analyzing turnover of families and functional groups is also consistent with this idea, where reducing the number of taxonomic groups compared across plots also reduced scale-dependent patterns.

Management Implications

Distinct and significant differences in community structure occurred among management classes. Although this study is based on observational data, the extensive survey of 98 privately-owned sites provides insight into the impacts of management decisions on biodiversity in this region. Conserving the remaining tallgrass prairie remnants will have the greatest impact on preserving native species diversity and populations of conservative plant species (Jog et al. 2006). I propose several additional changes to management practices that may increase biodiversity in grassland communities, but acknowledge that they should receive further examination before they are implemented. These recommendation include: 1) increasing the use of hay management on native prairie remnants, and 2) improving the Conservation Reserve Program by increasing enrollment, adding more native prairie species to seed

mixes, and incorporating a periodic mid-summer hay disturbance may enhance biodiversity conservation on these sites.

The community differences among W-NH and W-NG sites suggest that contemporary management disturbance can play a role in maintaining diversity in native prairies, and that hay management in particular may be an important tool for prairie plant conservation. I propose that mid-season hay management may approximate the prehistoric fire disturbance to which these native tallgrass communities have adapted. The majority of widespread fires ignited by lightning likely occurred during July-October as a result of vegetation flammability and weather conditions (Bragg 1982; Higgins 1984; Howe 1994a). Currently, burning management in prairies occurs early in the growing season (March-May), during periods with higher rainfall, in order to prevent uncontrollable fires. Burning in the early season reduces shrub invasion, but reduces diversity by increasing the dominance of warm-season grass species that exclude cool-season grasses and forbs from the community (Howe 1994a; Collins *et al.* 1998; Knapp *et al.* 1998). Late-season fire disturbance has been shown to reduce dominance and increase species diversity compared to cool-season fires and has been suggested to mimic prehistoric fires that were ignited by lightning (Howe 1994a, b). I suggest that mid-season hay management, which occurs in mid-July, may promote greater species coexistence by approximating late-season fire. In addition, other studies have suggested that mowing and grazing can cause similar increases to plant diversity by reducing competitive dominance (Collins *et al.* 1998; Knapp *et al.* 1999a; Knapp *et al.* 1999b). Mowing

may also be a lower intensity disturbance that benefits species of conservation concern (Knapp *et al.* 1999b; Leach *et al.* 1999), such as Mead's milkweed, a federally endangered plant species (Jog *et al.* 2006). Thus, implementing hay management may enhance community composition on grazed sites; and reducing stocking densities and resting sites in order to reduce erosion, temporarily switching sites to hay management, or rotating hay management through portions of a site should be explored.

The management of W-CRP sites could also be adapted to increase plant diversity. The W-CRP communities in this study have undergone the most intense cultivation; however, when compared to cool-season sites they have greater diversity, floristic quality, and support more conservative prairie species (Jog *et al.* 2006). Thus, the Conservation Reserve Program (CRP) serves an important role in this region, not only for its main purposes of conserving wildlife and soil properties (Natural Resources Conservation Service 2000), but also for conserving plant biodiversity.

I suggest three changes to CRP management to explore in the context of biodiversity conservation. First, increasing enrollment in the CRP will increase the area of favorable native plant habitat and could reduce habitat fragmentation if sites are strategically placed in the landscape. Recent increases in the price of corn and potential government subsidies for corn-based ethanol production may soon reduce the number of sites enrolled in the CRP, and could be detrimental to soil and biodiversity conservation in this region. Second, the CRP could be enhanced by

adding more native prairie species to seed mixes, including forbs and native cool-season grasses. Third, incorporating a periodic mid-summer hay disturbance may enhance native species diversity on CRP sites. This type of disturbance could also serve the purpose of biomass collection for cellulosic energy production (Tilman *et al.* 2006; USDA 2007a). However, removing vegetation from CRP sites would reduce litter decomposition and may cause an undesirable reduction in soil nutrients (Knops & Tilman 2000; Murphy *et al.* 2006), particularly carbon, which could reduce the soil carbon sequestered by this type of management. I suggest that these changes could restore components of native plant community structure, but further work is needed to evaluate these recommendations in other contexts.

Conclusion

This study provides new insights into the effect of management practices on community patterns throughout this landscape. Management practices may influence community patterns by reducing environmental heterogeneity, increasing dominance by perennial grasses, and decreasing the functional diversity of communities. There are also site features associated with management practices that may influence plant community structure. I suggest improving the Conservation Reserve Program and increasing hay management on native sites in order to mitigate the impacts of management on biodiversity. This study is a starting point for understanding private management in this region, and future experiments are needed to adequately test the utility of changing disturbance and management regimes in order to restore biodiversity and ecosystem function in this landscape.

Table 1.1. Grassland management classes. Management classes (C-H, C-G, W-NH, W-NG, and W-CRP) are based on whether the site has been cultivated, and whether it is currently grazed, hay-managed, or enrolled in the conservation reserve program (CRP).

		Historical Disturbance	
		<i>Cultivated</i>	<i>Native</i>
Contemporary Management	<i>Hay</i>	Cool-season Hay (C-H)	Warm-season Hay (W-NH)
	<i>Grazing</i>	Cool-season Grazed (C-G)	Warm-season Grazed (W-NG)
	<i>CRP</i>	Conservation Reserve Program (W-CRP)	

Table 1.2. Number of species recorded in each functional group over all 98 sites.

Functional Group	Number of Species
Perennial forb	124
Annual forb	66
Tree	29
Perennial non-grass graminoid	26
Perennial legume	22
Perennial C ₃ grass	21
Perennial C ₄ grass	21
Biennial forb	14
Annual C ₄ grass	12
Shrub	12
Perennial vine	12
Annual/biennial forb	9
Annual legume	4
Annual C ₄ forb	4
Annual C ₃ grass	3
Annual vine	3
Perennial leguminous vine, shrub, and tree	3
Annual leguminous vine	2
Annual/biennial legume	2
Annual non-grass graminoid	1

Table 1.3. Comparisons of species, functional group, and soil productivity metrics among management classes. Mean \pm two standard errors are reported for each management class. Letters indicate significantly different groups based on Tukey post-hoc tests of one-way ANOVA's ($P < 0.05$). Significant sources of variation from one-way ANOVA's are reported for the effect of management category on S and soil C; and from Kruskal Wallis tests for the effect of management on E , D' , S_{FG} , E_{FG} , D'_{FG} , soil N, and soil pH. Historical and contemporary disturbance were tested with a two-way factorial ANOVA for S , E_{FG} , soil N, and soil C; and the Sheirer-Ray-Hare extension of the Kruskal Wallis for E , D' , S_{FG} , D'_{FG} , and soil pH.

Response variable	C-G	C-H	W-NG	W-NH	W-CRP	Significant sources of variation†
<i>S</i>	33.9 ± 5.9 ^A	26.0 ± 4.9 ^A	77.6 ± 6.2 ^B	88.1 ± 5.9 ^B	46.0 ± 6.1 ^C	M ^{***} , H ^{***} , H x C ^{**}
<i>E</i>	0.36 ± 0.05 ^A	0.26 ± 0.05 ^B	0.59 ± 0.02 ^C	0.58 ± 0.03 ^C	0.48 ± 0.03 ^D	M ^{***} , H ^{***}
<i>D'</i>	0.52 ± 0.09 ^A	0.36 ± 0.09 ^B	0.83 ± 0.02 ^C	0.83 ± 0.03 ^C	0.71 ± 0.05 ^C	M ^{***} , H ^{***}
<i>S</i> _{FG}	10.8 ± 1.4 ^{AB}	9.0 ± 1.3 ^A	13.6 ± 0.9 ^C	12.6 ± 0.8 ^{BC}	12.8 ± 1.2 ^{BC}	M ^{***} , H ^{***}
<i>E</i> _{FG}	0.25 ± 0.05 ^A	0.18 ± 0.06 ^A	0.39 ± 0.05 ^B	0.46 ± 0.06 ^B	0.19 ± 0.05 ^A	M ^{***} , H ^{***} , H x C [*]
<i>D'</i> _{FG}	0.27 ± 0.07 ^A	0.18 ± 0.08 ^A	0.46 ± 0.08 ^B	0.53 ± 0.08 ^B	0.20 ± 0.07 ^A	M ^{***} , H ^{***}
Soil N	0.24 ± 0.02 ^A	0.20 ± 0.02 ^B	0.26 ± 0.02 ^A	0.25 ± 0.02 ^A	0.16 ± 0.01 ^C	M ^{***} , H ^{**} , C ^{**}
Soil C	2.59 ± 0.21 ^A	2.33 ± 0.20 ^A	3.07 ± 0.22 ^B	3.02 ± 0.20 ^B	1.81 ± 0.12 ^C	M ^{***} , H ^{***}
Soil pH	5.71 ± 0.18 ^A	5.72 ± 0.11 ^A	5.60 ± 0.14 ^{AB}	5.35 ± 0.11 ^B	5.86 ± 0.18 ^{AB}	M ^{***} , H ^{**}

† One-way ANOVA: M= effect of management class; Two-way ANOVA: H = effect of historical disturbance, C = effect of contemporary disturbance, H x C = interaction of historical and contemporary disturbance; *P<0.05, **P<0.01, ***P<0.001.

Table 1.4. Results of Repeated Measures ANOVA's of within site data. Variables were measured at three replicates of three areas in each site. The repeated measure is the mean measurement over the replicates for each area. The among site variable is management class. *P<0.05, **P<0.01, ***P<0.001

Dependent Variable	Management	Area	Management x Area Sampled
Species Richness (S_S)	58.6***	1479.8***	4.9***
Genus Richness (S_G)	49.8***	1472.42***	7.3***
Family Richness (S_F)	32.7***	893.42***	7.6***
Functional Group Richness (S_{FG})	21.3***	642.5***	13.9***
Species Turnover (T_S)	3.874**	70.105***	6.204***
Genus Turnover (T_G)	7.905***	82.638***	4.476***
Family Turnover (T_F)	4.964**	34.641***	1.102
Functional Group Turnover (T_{FG})	17.470***	0.029	1.149

Fig. 1.1. Map of study area. Legend and scale correspond to detailed map, which shows the location of the majority of study sites coded by management category.

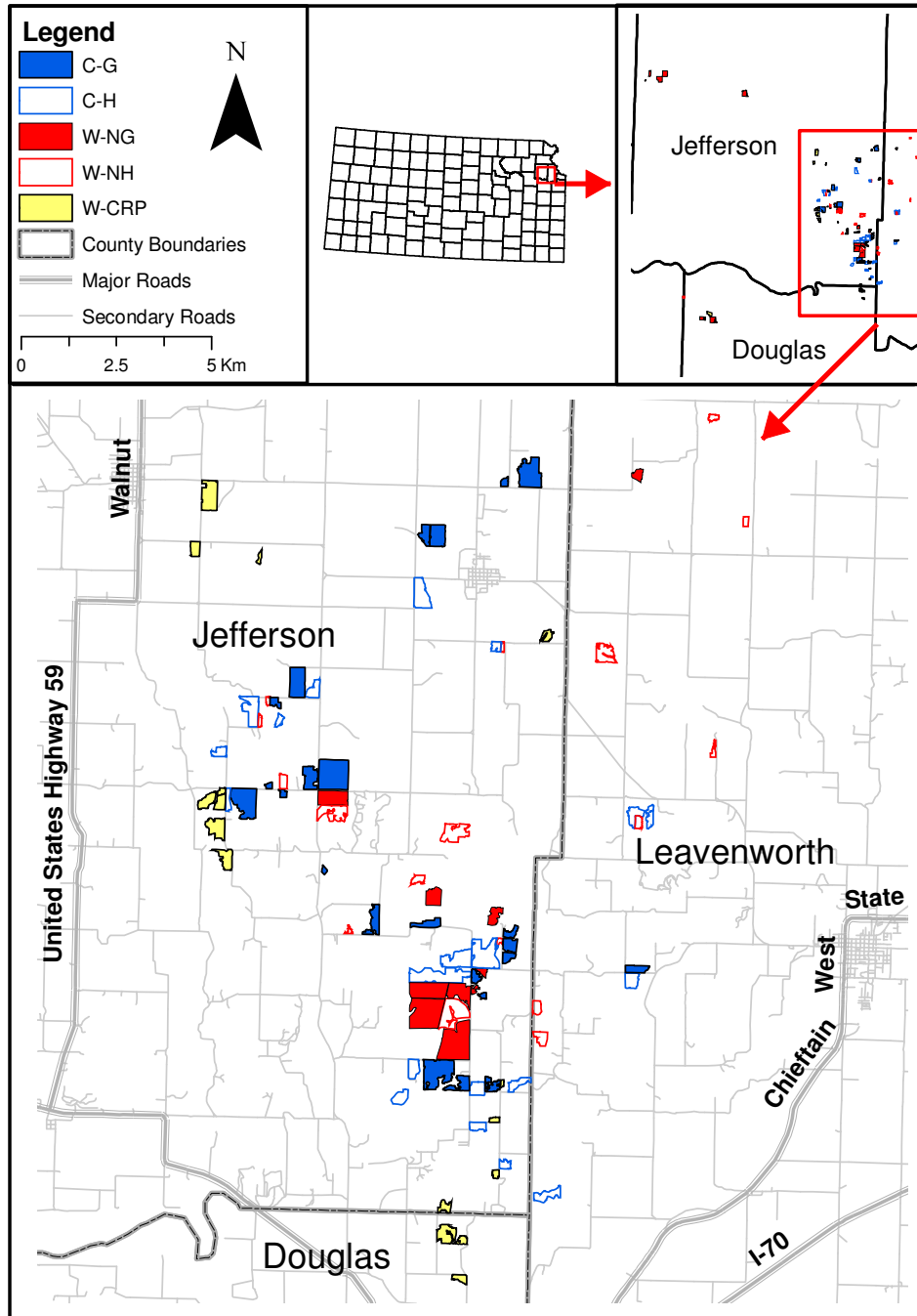
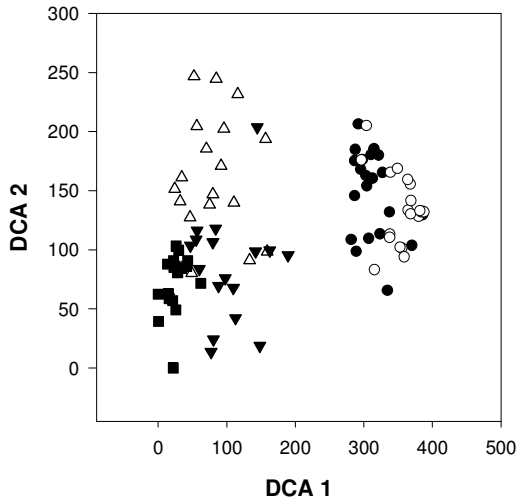
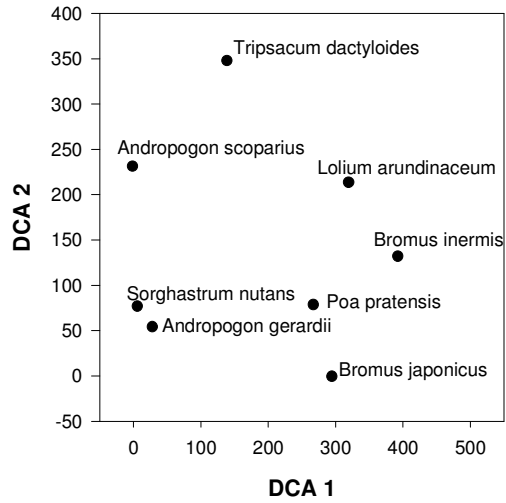


Fig. 1.2. Detrended correspondence analysis axes 1 and 2. Sites are coded by management class. A) Species ordination: the first axis explained 60.8 percent of the variation in site composition, and the second axis explained an additional 5.9 percent. B) Dominant species with > 50% cover. C) Functional group ordination: the first axis explained 93.1 percent of the variation in site composition, and the second axis explained an additional 1.4 percent. D) Dominant functional groups with > 10% cover.

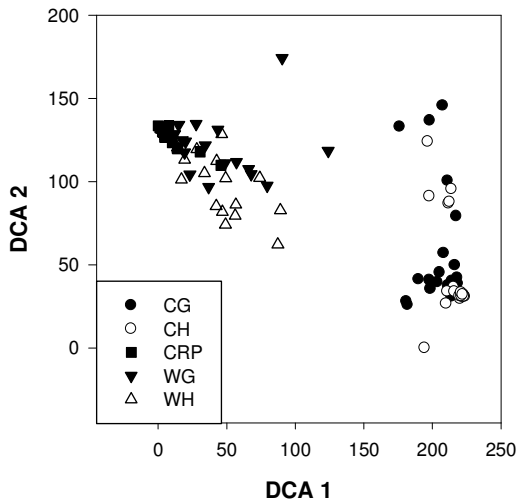
A) Sites based on species



B) Dominant species



C) Sites based on functional groups



D) Dominant functional groups

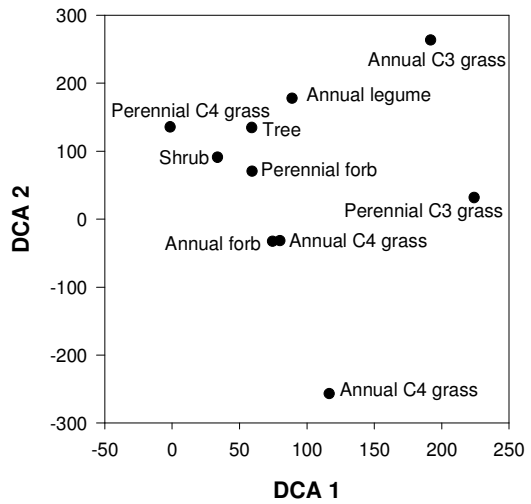
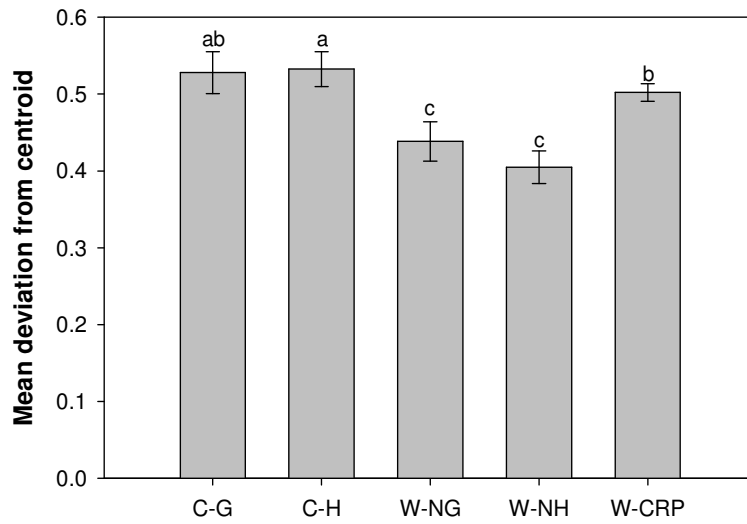


Fig. 1.3. Compositional variation among sites in each management class.

Compositional variation was calculated as the mean deviation from the group centroid of sites in each management class using, A) presence-absence data (Jaccard dissimilarity index) and B) relative abundance data (Bray-Curtis dissimilarity index). Letters represent significant differences among groups ($P < 0.05$). Error bars are two standard errors. Using the Jaccard index, variation was high among cool-season and W-CRP sites and low among native sites. Using the Bray-Curtis index, variation was high among grazed sites and W-NH and low among C-H and W-CRP sites.

A) Jaccard



B) Bray-Curtis

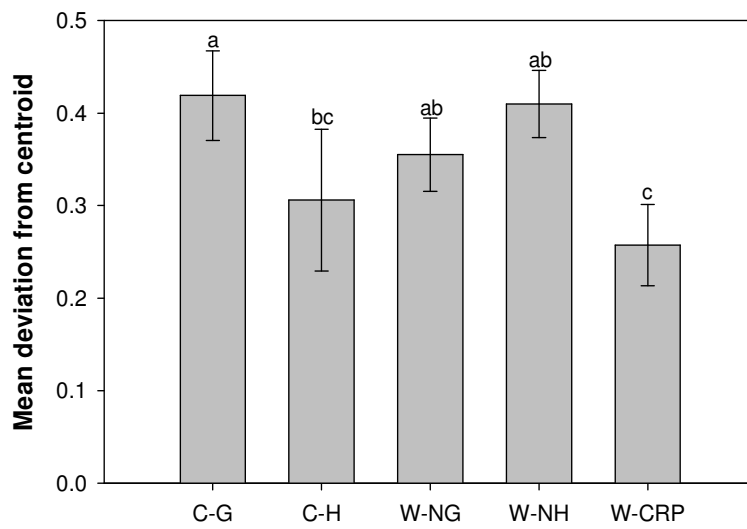


Fig. 1.4. Species richness for each area sampled by management class. Symbols represent mean log richness \pm 2SE plotted against log area.

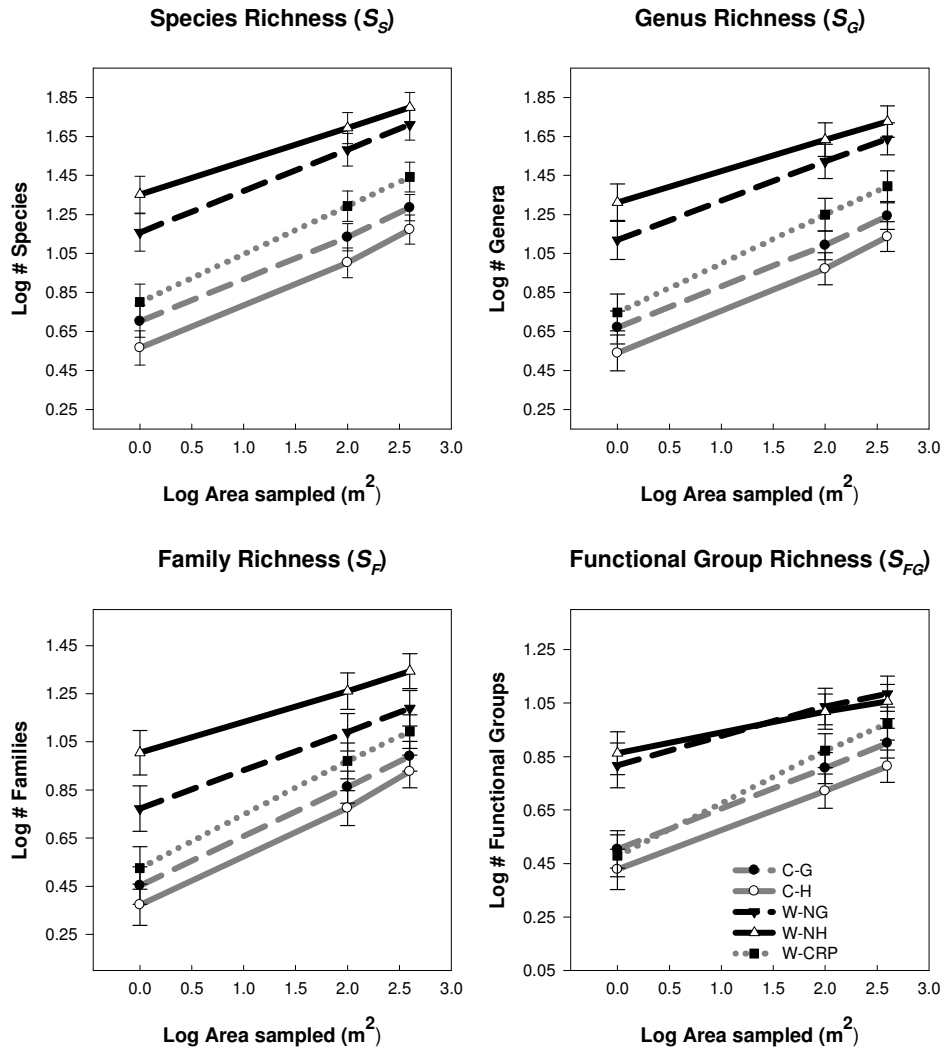
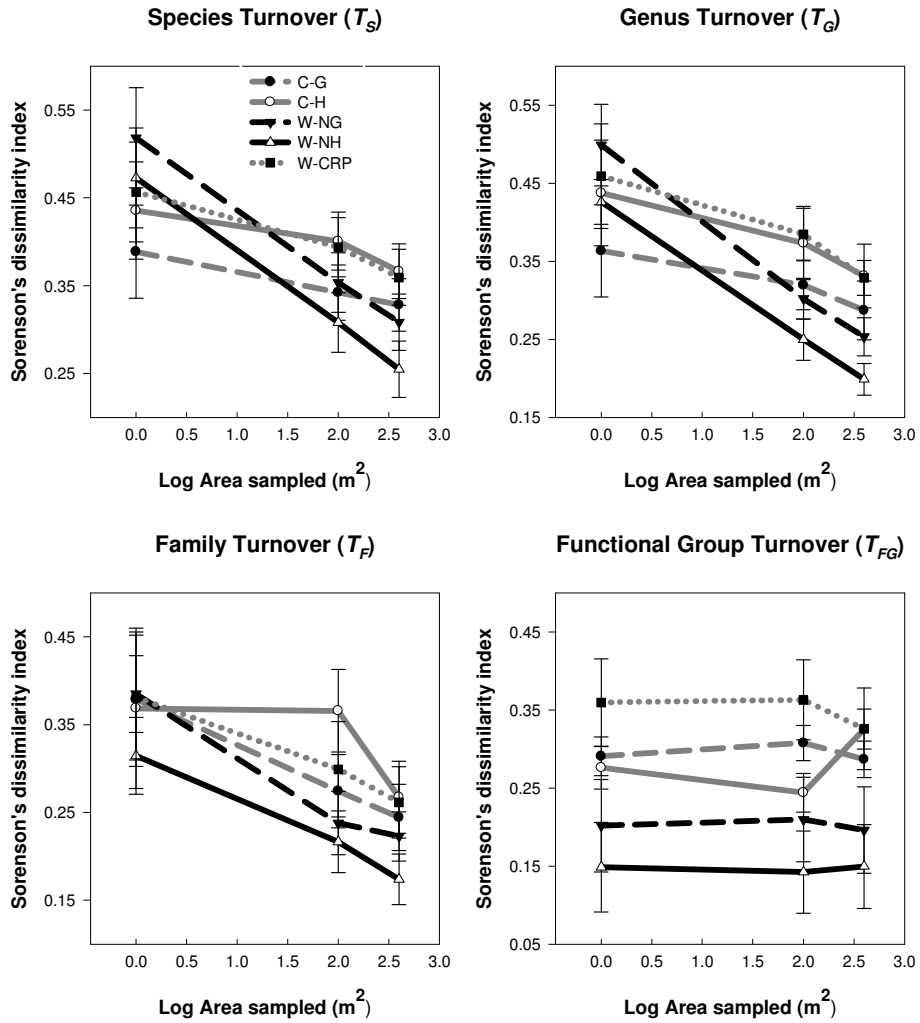


Fig. 1.5. Spatial turnover for each area sampled by management class. Symbols represent mean turnover \pm 2SE plotted against log area.



CHAPTER 2.

VOLE DISTURBANCES AND PLANT DIVERSITY IN A GRASSLAND

METACOMMUNITY

ABSTRACT

I studied the disturbance associated with prairie vole burrows and its effects on grassland plant diversity at the patch (1 m²) and metacommunity (> 5 ha) scales. I expected vole burrows to increase patch-scale plant species diversity by locally reducing competition for resources or creating niche opportunities that increase the presence of fugitive species. At the metacommunity scale, I expected burrows to increase resource heterogeneity and have a community composition distinct from the matrix. I measured resource variables and plant community composition in 30 paired plots representing disturbed burrows and undisturbed matrix patches in a cool-season grassland. Vole disturbance affected the mean values of nine resource variables measured and contributed more to resource heterogeneity in the metacommunity than matrix plots. Disturbance increased local plant species richness, metacommunity evenness, and the presence and abundance of fugitive species. To learn more about the contribution of burrow and matrix habitats to metacommunity diversity, I compared community similarity among burrow and matrix plots. Using Sorenson's similarity index, which considers only presence-absence data, I found no difference in community similarity among burrows and matrix plots. Using a proportional similarity index, which considers both presence-absence and relative abundance data,

I found low community similarity among burrows. Burrows appeared to shift the identity of dominant species away from the species dominant in the matrix. They also allowed subordinate species to persist in higher abundances. The patterns I observed are consistent with several diversity-maintaining mechanisms, including a successional mosaic and alternative successional trajectories. I also found evidence that prairie voles may be ecosystem engineers.

INTRODUCTION

Disturbance may affect the diversity and composition of ecological communities by creating niche or colonization opportunities, reducing competition, and shifting back the stage of succession (Connell 1978; Huston 1979; Sousa 1979; Huston 1994; Chesson & Huntly 1997; Platt & Connell 2003). Even small disturbances can affect habitat heterogeneity and plant community dynamics across a continuum of spatial scales. Two scales frequently studied in plant communities are 1) the local scale of plant assemblages, hereafter called a patch, which is characterized by alpha diversity and 2) the metacommunity scale, a collection of patches that are potentially connected by dispersal in a landscape. The metacommunity scale can be characterized by beta diversity, or the dissimilarity of community composition among patches. Studying the scale-dependent impacts of disturbance on plant communities may reveal complex ecological dynamics.

Soil disturbance and herbivory (Huntly & Inouye 1988; Gibson 1989; Hobbs & Huenneke 1992; Reichman & Seabloom 2002b; Seabloom & Richards 2003) as

well as granivory (Howe & Brown 2001; Howe *et al.* 2002) by mammals are forms of disturbance that shape grassland plant communities, especially in the absence of other types of disturbance. Territoriality and feeding preference can produce spatial patterns of disturbance that can affect metacommunity diversity (Seabloom & Richards 2003). Another pattern caused by disturbance is a successional mosaic, a collection of patches at various stages along the same successional trajectory (Chesson & Huntly 1997). Variation among these patches can result in compositional dissimilarity among patches in a metacommunity. Disturbances can also contribute to patch and metacommunity diversity by allowing fugitive species to persist among disturbed patches (Platt 1975; Platt & Connell 2003; Seabloom & Richards 2003). Fugitive species are unable to persist in the later-successional matrix due to biotic or abiotic constraints (Hutchinson 1951). In the mid-successional grasslands that I studied in Kansas, fugitive species are characterized as annuals or short-lived perennials that are excluded by later-successional dominant species in undisturbed matrix patches.

Disturbances can contribute to resource heterogeneity by altering patch resource levels in contrast to the surrounding undisturbed matrix habitat (Huston 1994). When a disturbance kills organisms or reduces their growth rates, resources may become available, contributing a distinct resource environment to the metacommunity. At a given point in time, resources may vary more across the metacommunity among disturbed than undisturbed patches due to their various successional stages.

Ecosystem engineers are organisms that cause large changes to resources and ecosystem properties, often through disturbance (Reichman & Seabloom 2002a, b). These alterations to the ecosystem can have cascading influences on many types of organisms, including the engineering organism itself. I studied a potential ecosystem engineer, the prairie vole, *Microtus ochrogaster* (Wagner, 1842), and the effects of its burrowing disturbance on plant community and ecosystem patterns in a cool-season grassland in NE Kansas. Prairie voles are the most abundant microtine rodent in Kansas (Bee et al. 1981). Humans have destroyed much of *M. ochrogaster*'s original tallgrass prairie habitat, but have created cool-season grasslands that are ubiquitous in the regional landscape (Jog et al. 2006) and are highly favorable habitats for prairie voles (Getz 1985; Getz *et al.* 2001). It is important to study the consequences of vole activity in these grasslands in order to understand the impact of this large-scale land conversion on ecological interactions.

I examined the effect of prairie vole burrows on plant diversity at two spatial scales: 1) *the patch* is the spatial scale at which plants locally interact (1 m²) and is represented by plant assemblages on disturbed burrows and in relatively undisturbed matrix habitat; 2) *the metacommunity* is a larger region in which dispersal among patches occurs (> 5 ha) and is represented by a field that includes many disturbed burrows and matrix patches. Matrix habitats are areas that have not been disturbed recently, and are characterized by a taller canopy and mid-successional cool-season grassland communities. In the grassland metacommunity I studied, discrete disturbed patches existed within a continuous matrix habitat.

I expected vole burrows to increase patch-scale plant species diversity by locally reducing competition for resources or creating niche opportunities that increase the presence of fugitive species. At the metacommunity scale, I expected the altered resource environment on burrows to support a community composition distinct from the matrix. To learn more about the contribution of burrow and matrix habitats to metacommunity diversity, I compared community similarity, a measure of beta diversity, among burrow and matrix patches. A successional mosaic among burrows would lead to lower similarity among burrows than among matrix patches. If only a few, well-dispersed fugitive plant species are adapted to burrowing disturbance, I expected greater similarity among burrow patches than among matrix patches. If a successional mosaic existed, I expected the drawdown of resources to vary among burrows, thus increasing the spatial heterogeneity of resources in the metacommunity. At the ecosystem level, I expected reduced plant uptake and increased mineralization on burrows to increase the mean level of available resources. I discuss the effects of burrows on resources in the context of ecosystem engineering.

METHODS

Prairie vole natural history

Prairie voles occur in sparsely vegetated grassland habitats, making them different from other species of *Microtus* that require dense vegetation (Getz 1985). They eat aboveground vegetation, seeds, and roots of grasses and forbs (Getz 1985). Prairie voles nest communally in subterranean burrows with an average of five

individuals per nest (Getz et al. 1992). Burrows, created for both nesting and escape from predators, are occupied an average of 51 days (Mankin & Getz 1994) and have a mean aboveground area of 5.7 m² (E.J. Questad, unpublished data). Prairie voles move aboveground in grasslands through a series of surface runways which are pathways where detritus and vegetation are cleared from the ground (Getz 1985). The combination of herbivory, granivory, soil disturbance, and runway maintenance creates a complex interaction between prairie voles and their grassland plant habitats.

Study site

I studied a site at the Nelson Environmental Studies Area (NESA), part of the University of Kansas Field Station and Ecological Reserves (KSR). NESA is located at the prairie-forest ecotone of northeastern Kansas in Jefferson County (39°03'N, 95°12'W), 10 km north of the city of Lawrence. The study site was approximately 6 ha of mid-successional grassland, dominated by the cool-season perennial grasses smooth brome, *Bromus inermis* Leyss.; Kentucky bluegrass, *Poa pratensis* L.; and tall fescue, *Schedonorus phoenix* (Scop.) Holub. These grasses are exotic species planted for cattle pasture and hay production, their dominance is maintained by periodic mowing or grazing, and they have become widely naturalized in the region. These species are now an important component of the local flora, and my study site is representative of the dominant current land cover in the regional landscape (Jog *et al.* 2006; Chapter 1).

Most of the site has 3-7% slopes and Pawnee clay loam soils (Dickey *et al.* 1977a). The site was taken out of agricultural production in the mid-1970's and has

not been managed since 1998 when it was mowed (Dean Kettle, KSR director, in litt., September 2004). The primary sources of disturbance during the study period were herbivory and granivory by small mammals, herbivory by white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780), and burrows created by prairie voles.

Study design

In April 2003, I located vole burrows by visually surveying parallel transects throughout the site. Burrows were characterized as areas with soil disturbance, clipped vegetation, and more than one underground entrance. Early spring is the best time to survey for burrows because the canopy is low and vegetation on burrows is often dark green, which is suggested to be a result of enhanced soil fertility and plant productivity associated with burrows (Davis & Kalisz 1992; Kalisz & Davis 1992). I marked all visible burrows (N = 90) in their centers with identifying pin flags and recorded their geographic location with a Garmin GPS 76 (accuracy < 5 m).

Of the 90 burrows, 30 were randomly selected for observation. I located a paired matrix plot for each selected burrow plot by choosing a random compass direction and placing an identifying pin flag 5 m from the center of the burrow in the compass direction. If a matrix plot was less than 5 m from another burrow, I chose a new random compass point and placed a flag 5 m in that direction. Matrix plots represented the intact grassland. Due to the prevalence of runways in the field, some matrix plots included vole runways.

Data collection

I identified plant species from 11 to 14 June 2003 in 1-m² quadrats placed on the center of each plot, and visually estimated percent cover of all species, bare ground, and litter.

To examine the impact of vole disturbances on light availability and heterogeneity, I measured photosynthetically active radiation (PAR) on a subset of 16 burrow and 16 matrix plots. The data were collected on 9 June 2003, using a PAR ceptometer (Decagon Devices; Pullman, WA, USA). I recorded four pairs of PAR measurements in each plot in approximately the N, S, E, and W directions. For each pair, one measurement was taken approximately 1 m above the canopy and one was taken below the live canopy placing the ceptometer on top of the dead litter. The ceptometer internally calculated leaf area index (LAI) for each pair of PAR measurements. I used the four pairs to calculate mean LAI for each plot, and report mean LAI as an index of light penetration in the plot.

Soil data were collected from representative areas of each plot, avoiding vole runways and underground tunnels. Soil moisture (% volumetric) was collected on 10 June 2003, using time domain reflectometry (TDR). Four 0.1-m deep soil cores were collected from all plots on 2 and 3 July 2003, using a 914-mm tube sampler. Two cores were combined in a mesh soil bag and air dried at room temperature (22-27°C) to a constant weight. The dry soils were mixed, large plant debris was removed by sifting soils through a 2-mm sieve, and remaining roots and plant material were removed with tweezers. These soils were sent to the Ecosystems Analysis Lab at the

University of Nebraska Lincoln School of Biological Sciences (EAL) where they were analyzed for %N and %C using a Costech Analytical ECS 4010. The remaining two soil cores from each plot were combined and dried to a constant weight at 90°C. These soils were weighed and bulk density (g/m^3) was calculated.

I collected aboveground biomass, a surrogate measure for primary productivity, by clipping a 1-m by 0.08-m strip in the center of each quadrat. Biomass was collected on 19, 20, and 23 June 2003 and 3 July 2003. It was sorted to species and litter, dried to a constant weight at 74°C, and weighed. After weighing, all species from each quadrat were combined, ground in a Wiley Mill, and sent to the EAL for %N and %C analysis.

Data analysis

Because spatial patterns of disturbance have been shown to affect plant diversity, I analyzed the spatial distribution of the 90 burrows with nearest-neighbor analysis in ArcGIS and calculated a Z-score to determine whether burrows were clustered, dispersed, or randomly distributed in space.

To determine whether mean values of resource measurements differed between plot types, I compared measurements of biomass, nutrients, and soil resources between 30 pairs of burrow and matrix plots using paired t-tests. When necessary, data were log-transformed to meet assumptions of normality.

I calculated the coefficient of variation (CV) over 30 burrow plots and 30 matrix plots for nine of these resource measures to examine differences in resource heterogeneity among plot types. I used 16 plots from each group to calculate the CV

for LAI. I resampled the data 1,000 times, randomizing plots among groups, in order to statistically compare the difference in the CV between burrow and matrix plots.

For all plots, I calculated species richness (S), Simpson's index of species diversity ($1/D$), Simpson's measure of evenness ($E_{1/D}$), and the relative abundance of each species. I compared the patch-level community response to burrowing by using paired t-tests to examine mean differences between burrow and matrix plots of total S , annual and perennial species richness, the proportion of annual species, annual and perennial relative percent cover, $E_{1/D}$, and $1/D$. An arc-sin square root transformation was used to obtain a normal distribution for perennial relative percent cover. A Mann-Whitney U test was used to test differences in the proportion of perennial species, which could not be transformed to a normal distribution.

To determine which of nine resource variables were correlated with each other and with species diversity metrics (S , $E_{1/D}$, and $1/D$), I calculated Pearson product moment correlation coefficients. In order to test whether burrowing influences patch species diversity indirectly through a combination of these nine resource variables, I used best subsets multiple regression to find the resource variables that best predicted S , $E_{1/D}$, and $1/D$.

In order to characterize the metacommunity impact of burrow and matrix habitat types, I pooled community data over the 30 burrow plots and 30 matrix plots to calculate S , $E_{1/D}$, and $1/D$ over each plot type. I resampled the data 1,000 times, randomizing plots among groups, in order to statistically compare the difference in these community metrics between burrow and matrix plots. Because some diversity

statistics can be biased for certain data (Magurran 2004), I tested several other statistics in this manner: Shannon diversity (H), evenness derived from H (E), and two additional transformations of Simpson's diversity, $1-D$ and $-\ln(D)$.

I further analyzed metacommunity patterns by using community similarity indices to describe community similarity among burrows and among matrix plots. I calculated community similarity over all possible pairs of burrow plots and all pairs of matrix plots using two similarity indices (Pielou 1977). Sorenson's index (S_1), was based on presence-absence data only. Proportional similarity (S_2) was based on quantitative relative abundance values for each species. I calculated the difference between mean burrow similarity and mean matrix similarity (D_S) for both similarity indices:

$$(1) \quad D_S = S_{matrix} - S_{burrow}$$

A similarity value of $S = 0$ indicates that two communities have completely different compositions, whereas a value of $S = 1$ indicates that two communities have identical compositions. A positive value of D_S demonstrates that matrix plots are more similar to each other than burrow plots. A negative value of D_S shows that burrow plots are more similar to each other than matrix plots. I resampled the data 1,000 times, randomizing plots among groups, in order to statistically compare D_S for S_1 and S_2 . Because some similarity indices can be biased for certain data (Magurran 2004), I tested several indices in the same manner: Whittaker's measure of beta diversity, Jaccard's similarity index, and β_{sim} (Lennon *et al.* 2001; Magurran 2004). I also used the EstimateS software (Colwell 2005) to calculate the Chao-Sorenson

abundance-based estimated similarity index, which is not biased by species that are unseen during sampling (Chao et al. 2005).

I used Fisher's Exact test of two-by-two contingency tables to determine the association of individual species with burrow or matrix plots (Sokal & Rohlf 1995). Only species that were present on more than five burrow or matrix patches were included, allowing analysis of 21 species.

RESULTS

The 90 burrows were not significantly clustered or dispersed; they were randomly distributed in two-dimensional space (Z-score = 1.59, $P > 0.10$). The average nearest-neighbor distance between burrows was 9.2 m (95% CI: 8.4 m, 10.0 m).

Soil and canopy resources

Soils from burrows had lower bulk density, higher total carbon and nitrogen content, and lower C:N than those from matrix plots (Table 2.1). Burrow soils were marginally drier than matrix soils ($P = 0.051$; Table 2.1). Burrows had more visible bare ground (Table 1), lower grass biomass, and lower litter accumulation (Table 2.1). Total live biomass and forb biomass were not different between plot types (Table 2.1). Plant tissue from burrows had higher nitrogen and lower C:N than that from matrix plots (Table 2.1). There was no difference in light penetration (mean LAI) between plot types ($t = -0.69$, $P > 0.25$).

The CV was significantly greater among burrows for soil bulk density, total live biomass, litter biomass, leaf tissue N, and light penetration. It was greater among matrix plots for bare ground (Table 2.2). Several resource variables were correlated with one another, including soil N and plant tissue N ($r = 0.269$, $P < 0.05$), and soil N and soil C ($r = 0.924$, $P < 0.005$). Soil C was not correlated with plant tissue C ($P > 0.90$).

Plant community

Across all sampling locations, a total of 59 species were recorded. Fifteen species (25%) were found only on burrows, nine species (15%) were found only in matrix plots, and 35 species (59%) were found on both plot types.

At the patch scale, Simpson's diversity ($1/D$) was significantly greater on than off burrows (Fig. 2.1c). This effect was entirely due to differences in species richness (S) because community evenness ($E_{1/D}$) did not differ significantly (Fig. 2.1a, b). Annual species richness ($t = 5.34$, $P < 0.001$), perennial species richness ($t = 2.27$, $P = 0.031$), and the proportion of annual species ($t = 3.40$, $P = 0.002$) were greater on burrows. The proportion of perennial species was greater on control plots ($W = 764.0$, $P = 0.026$). Neither annual nor perennial relative percent cover differed among plot types ($P > 0.30$).

S was correlated with leaf tissue nitrogen ($r = 0.307$, $P < 0.05$) and bare ground ($r = 0.380$, $P \leq 0.005$). $E_{1/D}$ was correlated with leaf tissue nitrogen ($r = -0.174$, $P < 0.05$), soil carbon ($r = -0.372$, $P \leq 0.005$), and soil nitrogen ($r = -0.319$, $P < 0.05$). $1/D$ was correlated with soil carbon ($r = -0.344$, $P < 0.05$). Bare ground was the

only significant predictor of S ($S = 11.8 + 0.0861 * \text{Bare Ground}$; $R^2_{\text{adj}} = 12.9$). Soil carbon was the best predictor of $E_{I/D}$ ($E_{I/D} = 0.535 - 0.112 * \text{Soil Carbon}$; $R^2_{\text{adj}} = 12.4$) and I/D ($I/D = 6.79 - 1.43 * \text{Soil Carbon}$; $R^2_{\text{adj}} = 9.6$). All regression coefficients were not equal to zero ($P < 0.05$).

The pooled data for all plots within a group showed that burrows had 50 species compared with 44 species on matrix plots; this difference was not significant (Fig. 2.1a). $E_{I/D}$ and I/D were significantly greater over all burrows than over all matrix plots (Fig. 2.1b, c). H , E , $I-D$, and $-\ln(D)$ showed qualitatively similar significant differences.

The difference in Sorenson's similarity index between burrow and matrix patches (D_{S1}) was negative, but not significantly negative ($D_{S1} = -0.048$, $P > 0.10$), demonstrating that, based on species presence-absence only, community similarity did not differ significantly among burrow plots and matrix plots. This result was qualitatively similar for all other presence-absence indices tested. In contrast, D_{S2} was significantly positive ($D_{S2} = 0.14$, $P < 0.001$) and mean Chao-Sorenson abundance-based estimated similarity was 0.607 and 0.725 for burrow and matrix plots, respectively, showing that, based on species relative abundance data, communities were less similar among burrow plots than among matrix plots.

Scientific and common names of species significantly associated with burrow and matrix plots are listed in Table 2.3; I will refer to them by their genus names hereafter. Of the five species significantly associated with burrows, four were annual or short-lived perennial forbs (Table 2.3). These species were *Acalypha*, *Chamaesyce*,

Pseudognaphalium, and *Oxalis*. The fifth species, *Tridens*, is a perennial grass. The relative cover of *Chamaesyce* was greater on burrows (Table 2.4). Only one species, *Ambrosia*, was associated with matrix plots (Table 2.3). Its relative cover was greater on matrix plots than burrow plots (Table 2.4), and it is an annual forb.

The identity of dominant species varied more among burrows than matrix plots (Table 2.5). There were three species with > 50% relative cover on burrow plots, and only one, *Bromus inermis*, on matrix plots (Table 2.5). Ten species had between 30% and 50% relative cover on burrow plots, compared to seven species on matrix plots (Table 2.5).

DISCUSSION

The effects of prairie vole burrowing disturbances on plant community patterns varied with spatial scale. At the patch scale, disturbance was associated with greater species richness. At the metacommunity scale, disturbance was related to the distribution of fugitive species, total species evenness, and resource heterogeneity. Based on my results, I present several possible ecological processes that may be occurring in this grassland and discuss whether prairie voles may be ecosystem engineers.

Patch-scale diversity

Vole burrows appear to increase species diversity on disturbed patches, which may be a result of reduced plant competition or increased niche opportunities associated with disturbance. Prairie vole burrows had greater species richness and

diversity than matrix patches, with no difference in species evenness, suggesting that disturbance at the patch scale has a greater effect on the number of species present and not the distribution of species' relative abundances. The increase in species richness on burrows is at least partially due to the presence of fugitive species, which persist where competition is reduced.

Metacommunity patterns

My study suggests that plant community patterns differ among burrow and matrix patches in the metacommunity. Most of the species associated with burrows are fugitive species that exist in low abundance in the non-disturbed matrix (Table 2.3). *Chamaesyce*, a species associated with burrows, is an annual that germinates in the spring and summer and undergoes seed dormancy at the end of the growing season (Baskin & Baskin 1998). In contrast, *Ambrosia*, the species associated with matrix plots, is a spring-germinating annual and undergoes seed dormancy in late spring or early summer (Baskin & Baskin 1998). In at least one study, disturbance in the fall increased populations of *Ambrosia*, but disturbance in early summer did not (Squiers 1989). I suggest that the timing of disturbance affects the species present in the grassland I studied. If voles create most of their burrows in the spring and early summer when soils are most friable, the plants associated with burrows will be species that germinate in the spring and summer. The soils in my study area have relatively high clay contents, and freeze-thaw cycles throughout the winter likely create small soil cracks in the grassland matrix that favor species like *Ambrosia* that germinate in the winter and early spring. The association of certain fugitive species

with burrows and one with matrix patches suggests that different types of disturbance may support alternative communities.

Competition-colonization tradeoffs may also help maintain fugitive species on burrows. Fugitive species are poor competitors and good dispersers. They are able to persist on burrows where disturbance decreases the competitive ability of dominant species. Mammal disturbances were clustered in California grasslands, thereby facilitating the movement of species among disturbed patches (Fehmi & Bartolome 2002; Seabloom & Richards 2003). In my study burrows were randomly distributed in space, suggesting that colonization by fugitive species is not due to the spatial clustering of disturbances, but is more likely associated with the dispersal ability of these species both in space and through the seedbank.

Mass effects may maintain populations of fugitive species in the matrix. A mass effect occurs when a species can persist through source-sink relationships among patches. For example, a fugitive species is adapted to disturbance and is quickly excluded by better competitors in the matrix. It could, however, maintain a high abundance on burrows and persist in the matrix through dispersal from burrow populations. The high abundance of fugitive species, such as *Chamaesyce*, on burrows may act as source populations that maintain these species in the matrix through mass effects.

Burrows also significantly altered relative abundance patterns in the metacommunity. Proportional community similarity over all burrows was lower than over matrix patches and species evenness was greater. Matrix patches are likely

similar to one another due to the dominance of *Bromus inermis*. The identity of the dominant species was much more variable on burrows (Table 2.5), causing low proportional similarity. When pooled across all burrow patches, this irregular dominance pattern leads to greater overall evenness in the community, suggesting that disturbance either reduces competition with *Bromus inermis* or creates other niche opportunities for subordinate species. The abundance-based patterns I observed are consistent with two potential processes occurring in the metacommunity: 1) asynchrony of successional pathways among burrows (successional mosaic) and 2) alternative successional trajectories among burrows.

1) Asynchronously disturbed burrows may create a successional mosaic of patches at various stages of succession (Tilman 1983; Huntly & Inouye 1988; Chesson & Huntly 1997), which is consistent with the observed pattern of greater beta diversity on burrows and the dominance of a greater number of species on burrows compared to matrix plots. The variation in dominant species may represent various stages of the same successional trajectory. Succession without additional disturbance would eventually result in dominance by *Bromus inermis* over all burrows and a reduction in metacommunity evenness.

2) These results are also consistent with priority effects that create alternative successional trajectories depending on which species are the original colonists of disturbed patches. Burrows appear to be created whenever the soil is friable (Jameson 1947), leading to burrowing in spring, early summer, and early fall. As burrows are created throughout time, the underlying resources, the available species pool, and the

seed dormancy and germination requirements of plant species affect which species can successfully colonize the disturbed patch. Successional trajectories on burrows may differ due to priority effects caused by the persistent impacts of different initial colonists, leading to the observed pattern of divergent communities on burrows but not on matrix patches.

Soil and canopy resources

Vole disturbances were associated with changes in soil bulk density, moisture, and nutrient quality. Bulk density on burrows was lower than that on matrix plots, consistent with a study of gopher burrows (Canals et al. 2003). The decrease in bulk density is likely a result of soil mixing and aeration that occurs during burrowing. Soil moisture was lower on burrows, which is consistent with a study of mole mounds in old fields (Bradshaw & Goldberg 1989). The abundance of bare ground on burrows may result in increased soil temperatures that could lead to greater water evaporation.

I also found higher total soil C and N content on burrows, suggesting that disturbance strongly alters soil nutrient pools. These results are in contrast to studies that found lower C and N on mounds and burrows (Bradshaw & Goldberg 1989; Canals *et al.* 2003). Changes in total soil N could occur through effects of disturbance on organic or inorganic forms of N (e.g., NO_3 , NH_4 , or Urea). I suspect that the greater total N observed on burrows largely reflects increased inorganic N, the form useable by plants. Inorganic N could increase by faster decomposition rates, slower uptake rates, or increased inputs via excretion. Urea, deposited by voles in urine used to mark social territory, is 45% N by weight and is converted to NH_4 , which is

available to plants (Kalisz and Davis 1992). Several other lines of evidence suggest that vole disturbances increased soil inorganic N: 1) vegetation was noticeably greener on burrows than on matrix plots early in the season, indicating greater canopy uptake of N; 2) leaf N content was greater on burrows, also suggesting greater canopy uptake of N; 3) leaf N was correlated with soil N; and 4) a pilot study using ion exchange membranes suggested that burrows had greater supply rates of available nitrogen compared to matrix plots (E. J. Questad, unpublished data). By increasing available N pools, voles can increase the levels of N available for plant uptake, reduce or alter competition among plants, and allow fugitive species with high resource requirements to persist.

I found higher N, but not C, in aboveground biomass samples from burrows, similar to a study of prairie voles in Kentucky (Kalisz and Davis 1992). In contrast to N, leaf C was not correlated with soil C, suggesting that increased carbon pools in the soil are not coupled to plant tissue C, and that voles may affect carbon and nitrogen cycles differently. I hypothesize that prairie voles have a greater influence on the rate of carbon inputs relative to mineralization. Burrows have lower litter accumulation, suggesting that voles speed the decomposition of plant material, thereby increasing nutrients in the soil (Buyanovsky et al. 1987). Disturbance may increase carbon mineralization, but the low moisture environment could reduce this effect and contribute to the total increase in soil carbon (Buyanovsky et al. 1987). It is also possible that soil conditions on burrows do not favor microbial populations (Lupwayi et al. 2004), which would normally respire soil carbon into the atmosphere.

The amount of aboveground vegetation often determines light levels beneath the canopy. I did not find an effect of disturbance on mean light levels, but I did find a large difference in the amount of bare ground. At the patch scale, bare ground was the only significant predictor of species richness. High light levels may be necessary for some seed germination (Bazzaz 1996), but physical germination space (i.e., bare ground) could be the dominant way that prairie voles influence seed germination (Platt 1975; Grubb 1977; Inouye *et al.* 1987; Glenn-Lewin *et al.* 1990). Bare ground was the only soil resource measured that varied more among matrix plots than burrows, suggesting that germination space is not only less abundant on average, but is also less predictable in the matrix grassland. Grass was the most abundant functional group in this community and its biomass was lower on burrows, suggesting that voles may reduce the abundance of competitively dominant species (Fehmi & Bartolome 2002), which may also favor germination and growth of subordinate species.

Herbivory can result in more intense or more variable light penetration through the canopy (Tilman 1983; Huntly & Inouye 1988). I found that light levels, measured as mean LAI, varied more among burrows than among matrix plots. This variation could be due to burrowing activity, herbivory, or a successional mosaic, and may be associated with the time since burrows were formed. Four other resource measurements varied more among burrows: soil bulk density, leaf N, live biomass, and litter biomass. This greater variation implies that metaecosystem functioning

(Loreau et al. 2003, 2005) may be altered due to the presence of burrows, and that resources available to plants are distributed more heterogeneously among burrows.

Prairie voles as ecosystem engineers

Studies of pocket gophers suggest that they are ecosystem engineers and cultivate species they prefer to eat (Huntly & Inouye 1988; Reichman & Seabloom 2002b). In general, prairie voles exhibit little species preference, eating species in proportion to their abundance in the community (Pascarella & Gaines 1991). Of the six species that were associated with burrow or matrix plots in my study, four were included in two feeding studies reported in the literature: voles did not prefer or avoid *Chamaesyce*, *Oxalis*, or *Tridens*; and they avoided *Ambrosia* (Menhusen 1963; Pascarella & Gaines 1991). Studies of meadow voles suggest that they prefer to eat large-seeded species (Howe & Brown 2001). The burrows I studied had a higher occurrence of small-seeded species (Table 2.3). If prairie voles also prefer large-seeded species or have no preference, caching seeds (Jameson 1947) is not likely to cause increases in the presence and abundance of these plants. Instead, increased colonization (Platt 1975; Huntly & Inouye 1988) or release from competition are more likely mechanisms that allow these fugitive species to be locally abundant.

Voles do not appear to engineer the species available on their burrows, but my study and that of Kalisz and Davis (1992) suggest that they may engineer the local nutrient quality of their forage. Forage quality has been shown to have a positive effect on prairie vole habitat selection (Lin et al. 2006) and population densities (Cole & Batzli 1978; Getz *et al.* 2001). I observed higher nitrogen and lower C:N in

aboveground biomass collected from burrows, which indicates higher nutritional quality of vegetation on burrows than vegetation five meters from burrows. I suggest that voles may engineer optimal foraging conditions close to their protection from predators.

Conclusion

By measuring the impacts of prairie voles on plant community patterns at two spatial scales, I am able to suggest several possible mechanisms responsible for the effect of disturbance on diversity in this metacommunity. The presence of voles in this ecosystem is associated with the persistence of fugitive species, a shift in dominant species, and increased resource heterogeneity, all of which lead to greater metacommunity diversity.

Table 2.1. Group means, one standard error, and results of paired t-tests (df = 30) for resource variables. *P < 0.05, **P < 0.005

Resource	Burrow mean	Matrix mean	t
Soil bulk density (g/m ³)	480 ± 10	540 ± 10	-4.72**
Soil moisture (% vol. moisture)	35.44 ± 0.49	36.15 ± 0.52	-1.69
Soil carbon (% by mass)	2.19 ± 0.05	2.07 ± 0.05	2.69*
Soil nitrogen (% by mass)	0.20 ± 0.004	0.18 ± 0.003	4.39**
Soil C:N	10.85 ± 0.07	11.33 ± 0.11	-4.24**
Bare ground (% cover)	22.50 ± 2.52	2.49 ± 0.58	7.67**
Total live biomass (g)	16.42 ± 2.13	17.19 ± 1.04	-1.40
Grass biomass (g)	9.47 ± 1.16	10.96 ± 0.63	-2.32*
Forb biomass (g)	6.94 ± 1.86	6.23 ± 1.15	-0.31
Litter biomass (g)	12.69 ± 1.65	17.91 ± 1.41	-3.25**
Leaf tissue carbon (% by mass)	43.73 ± 0.18	43.76 ± 0.16	-0.14
Leaf tissue nitrogen (% by mass)	2.04 ± 0.11	1.26 ± 0.03	7.26**
Leaf tissue C:N	23.05 ± 1.14	35.24 ± 0.82	-8.53**

Table 2.2. Coefficient of variation (CV) over burrow and matrix plots for 10 resource variables. Asterisks indicate significantly greater CV's based on a two-tailed test and resampling data 1,000 times. *P < 0.05, **P < 0.005

Resource	Burrow CV	Matrix CV
Soil bulk density (g/m ³)	13.30**	5.42
Soil moisture (% volumetric moisture)	7.62	7.83
Soil carbon (% by mass)	12.61	13.24
Soil nitrogen (% by mass)	12.03	10.14
Bare ground (% cover)	61.25	127.28**
Total live biomass	70.93*	33.14
Litter biomass	71.33**	43.01
Leaf tissue carbon (% by mass)	2.29	1.97
Leaf tissue nitrogen (% by mass)	28.44*	12.80
Light penetration (LAI)	63.26**	28.15

Table 2.3. Species associated with plot types. Significant results of Fisher's Exact Test for 21 species. *P < 0.05, **P < 0.005, +P < sequential Bonferroni P-value for 21 tests

Species	Common name	Growth habit	Number of burrow plots	Number of matrix plots
Burrow species				
<i>Acalypha virginica</i> L.	Virginia copperleaf	Annual forb	20*	10
<i>Chamaesyce maculata</i> (L.) Small	Spotted spurge	Annual forb	24**	12
<i>Pseudognaphalium obtusifolium</i> (L.) Hilliard and Burt	Fragrant cudweed	Annual/ biennial forb	11 ⁺	1
<i>Oxalis stricta</i> L.	Yellow wood sorrel	Short-lived perennial forb	27 ⁺	15
<i>Tridens flavus</i> (L.) A.S. Hitchc.	Purpletop	Perennial grass	13*	5
Matrix species				
<i>Ambrosia artemisiifolia</i> L.	Common ragweed	Annual forb	23	29*

Table 2.4. Relative percent cover of species associated with plots. Group means, one standard error, and results of paired t-tests. Paired plots on which the species of interest was present on both the matrix and burrow plot were used for analysis.

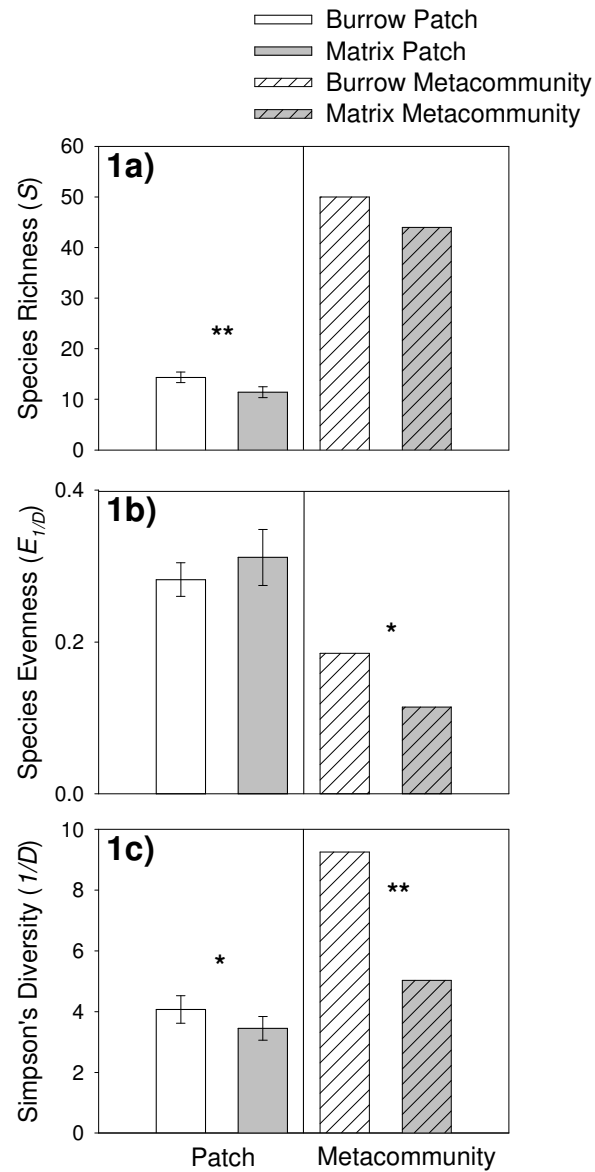
Pseudognaphalium was excluded due to lack of replication. *P < 0.05, **P < 0.005

Species	% Cover on burrow plots	% Cover on matrix plots	t	df
<i>Acalypha virginica</i>	3.59 ± 1.88	0.69 ± 0.14	1.54	10
<i>Chamaesyce maculata</i>	0.16 ± 0.05	0.04 ± 0.01	2.57*	10
<i>Oxalis stricta</i>	0.71 ± 0.39	0.04 ± 0.01	1.70	15
<i>Tridens flavus</i>	10.60 ± 4.24	7.63 ± 3.67	1.70	5
<i>Ambrosia artemesiifolia</i>	2.87 ± 1.10	8.67 ± 1.92	-2.62*	22

Table 2.5. Relative percent cover of dominant species. Dominant species are listed in two classes (> 50% relative cover and 30%-50% relative cover) followed by the number of burrow and matrix plots containing the species at that cover value.

Species	Common name	Burrow Plots	Matrix Plots
RELATIVE COVER > 50%			
<i>Poa pratensis</i> L.	Kentucky bluegrass	2	0
<i>Solidago canadensis</i> L.	Canada goldenrod	2	0
<i>Sporobolus compositus</i> (Poir.) Merr.	Dropseed	1	0
<i>Bromus inermis</i> Leyss.	Smooth brome	0	9
RELATIVE COVER 30% - 50%			
<i>Bromus inermis</i> Leyss.	Smooth brome	10	11
<i>Poa pratensis</i> L.	Kentucky bluegrass	4	1
<i>Apocynum cannabinum</i> L.	Hemp dogbane	3	1
<i>Solidago canadensis</i> L.	Canada goldenrod	3	5
<i>Sporobolus compositus</i> (Poir.) Merr.	Dropseed	3	2
<i>Carex sp.</i> L.	Sedge	1	0
<i>Carduus nutans</i> L.	Musk thistle	1	0
<i>Cornus drummondii</i> C.A. Mey.	Roughleaf dogwood	1	0
<i>Schedonorus phoenix</i> (Scop.) Holub	Tall fescue	1	0
<i>Brickellia eupatorioides</i> (L.) Shinnars	False boneset	1	0
<i>Asclepias verticillata</i> L.	Whorled milkweed	0	3
<i>Toxicodendron radicans</i> (L.) Kuntze	Poison ivy	0	1

Fig. 2.1. Results of paired t-tests for patch-scale diversity and randomization tests for metacommunity-scale diversity. * $P < 0.05$, ** $P < 0.001$



CHAPTER 3.

COEXISTENCE THROUGH SPATIO-TEMPORAL HETEROGENEITY AND SPECIES SORTING IN GRASSLAND PLANT COMMUNITIES

ABSTRACT

The effect of spatial heterogeneity on species coexistence relies on the degree of niche heterogeneity in the habitat and the ability of species to exploit the available niche opportunities. I studied species coexistence in a perennial grassland, and tested whether small-scale disturbances create environmental heterogeneity that affects coexistence and whether the functional diversity of species in the species pool affects the ability of community composition to reflect heterogeneity through species sorting. I manipulated the spatio-temporal heterogeneity of disturbance and the functional diversity of species added as seed and measured their impact on the spatial turnover of species composition. Disturbance increased environmental heterogeneity and spatial turnover, and the effect of heterogeneity on turnover was greatest in the presence of a functionally diverse species pool, showing the importance of trait variation among species for exploiting environmental heterogeneity, and suggesting that coexistence occurred due to species sorting among heterogeneous niches.

INTRODUCTION

Coexistence theory predicts that spatial heterogeneity of environmental factors that affect fitness, such as resources and abiotic conditions, will promote coexistence through species-environment sorting (Tilman & Pacala 1993; Reynolds *et al.* 2007). When species exhibit tradeoffs for environmental factors that are distributed heterogeneously among patches in a habitat, different species will be favored in different patches, leading to spatial turnover of community composition and coexistence at the community scale (Tilman & Pacala 1993; Huston 1994; Chase & Leibold 2003). The importance of environmental heterogeneity for regulating plant species coexistence and diversity has been evaluated experimentally by varying nutrients, soil physical characteristics, and light levels in spatially heterogeneous, versus homogeneous, patterns (Vivian-Smith 1997; Collins & Wein 1998; Stevens & Carson 2002; Baer *et al.* 2004; Wijesinghe *et al.* 2005; Reynolds *et al.* 2007); however, these studies had mixed results and most showed no effect of heterogeneity on diversity (but see Vivian-Smith 1997). One reason why experimental heterogeneity may not have increased diversity in these studies could be that the manipulated heterogeneity was not extensive enough to increase sorting opportunities. Another explanation for this result is that dominant grasses or other clonal species may be able to integrate their resource use across patch types, thus using homogeneous and heterogeneous habitats similarly and excluding other species from the community (Baer *et al.* 2004; Reynolds *et al.* 2007). A third explanation is

that the community response to heterogeneity may have been limited by dispersal from the available species pool (Vivian-Smith 1997; Reynolds *et al.* 2007).

In fact, a number of studies show that plant species richness can often be more limited by species pools and dispersal constraints than by niche availability (e.g., Tilman 1997; Zobel *et al.* 2000; Foster & Dickson 2004), leaving many communities undersaturated with species and with potentially underexploited niche heterogeneity. Thus, plant community diversity may be influenced not only by spatial environmental heterogeneity (spatial niche dimensionality), but also by the availability of species that are able to exploit the existing heterogeneity (species pool dimensionality). In order for community composition to reflect heterogeneity by species sorting among patches, the species pool must not only contain a sufficient number of species and propagules, it must also contain species with the functional traits necessary to exploit the various niche opportunities available throughout the habitat. I hypothesize that species diversity will be greatest in communities with the most environmental heterogeneity, minimal dispersal limitation, and a functionally diverse species pool. I predict that experimental enhancement of spatial niche dimensionality and species pool dimensionality will increase species sorting, spatial turnover of species composition, and coexistence at the community scale.

In this study I experimentally evaluate the interplay of spatial niche dimensionality and species pool dimensionality in regulating grassland plant diversity. Unlike previous studies that used fertilizer application to manipulate the heterogeneity of soil nutrients, I investigate the importance of small-scale

disturbances for creating spatio-temporal heterogeneity in grasslands. In contrast to nutrient enhancement, disturbance can create successional niche opportunities that favor the growth of competitively inferior species through the increased availability of establishment microsites, areas with reduced competition where seeds can germinate and grow (Grubb 1977; Zobel *et al.* 2000), and altered ratios of resources important for plant growth (e.g., soil nutrients and light levels; Grubb 1977; Tilman & Pacala 1993; Tilman 1994; Chesson & Huntly 1997; Pacala & Rees 1998; Amarasekare 2003; Chase & Leibold 2003). Disturbance is critical for maintaining species coexistence in non-equilibrium ecosystems like grasslands (Grubb 1977; Hobbs & Hueneke 1992; Howe 1994a; Tilman 1994; Collins *et al.* 1998; Pacala & Rees 1998) where spatio-temporal variation in disturbance patterns can create successional niche heterogeneity that is important for plant species coexistence at the community scale (Tilman & Pacala 1993; Chesson & Huntly 1997).

Small mammals often create heterogeneous, small-scale disturbance patterns in grasslands that have persistent effects on plant community composition (Hobbs & Mooney 1985, 1995; Seabloom & Richards 2003). In cool-season grasslands of northeastern Kansas where I conducted my dissertation research, prairie voles, *Microtus ochrogaster* (Wagner, 1842), can be extremely abundant, and their burrows increase plant diversity throughout the community (Questad & Foster 2007; Chapter 2), providing an ideal system for testing the effect of disturbance heterogeneity on plant diversity. Prairie vole burrowing activity enhances spatial environmental heterogeneity by creating disturbed patches with environmental conditions that

contrast strongly with the undisturbed grass-dominated matrix (Kalisz & Davis 1992; Questad & Foster 2007; Chapter 2). In addition, resources and abiotic conditions important for plant growth vary more among burrows than among undisturbed matrix areas, creating an additional source of heterogeneity which may be due to differences in the size, intensity, and timing of the disturbances. Here, I experimentally disturbed 1-m² patches within 4-m by 4-m communities. I created disturbed patches seasonally and inter-annually to increase spatio-temporal heterogeneity by mimicking the formation of burrows through time.

In addition to these disturbance manipulations, I used seed addition treatments to test the effect of species pool dimensionality on diversity and its interaction with disturbance heterogeneity. Most previous seed addition experiments, designed to examine the role of dispersal limitation on plant diversity, compared plots without seeds added to plots enriched with a mixture of many species from many functional groups (e.g., Tilman 1997; Zobel *et al.* 2000; Foster & Dickson 2004; Gross *et al.* 2005). By using only one seed mixture, these studies cannot distinguish the relative importance of enhancing the number of species available to the community versus enhancing the diversity of functional traits. It has been demonstrated that functional complementarity, or adaptations to different resources, among species is important for coexistence in niche-structured communities (Tilman 1997; Fargione *et al.* 2003). I hypothesize that as the degree of functional complementarity in the available species pool increases, there will be an increased capacity for niche partitioning and coexistence, especially in the presence of environmental heterogeneity. I tested the

importance of species pool complementarity by comparing plots with no seeds added to plots enriched with either 13 species with redundant functional traits or 13 species with diverse functional traits. These two seed addition treatments allowed us to determine the importance of species pool complementarity while keeping the number of species and propagule pressure constant.

If both spatial niche dimensionality and species pool dimensionality influence species coexistence, I make the following predictions: 1) communities with the greatest heterogeneity will have the greatest diversity; 2) increasing species pool complementarity will increase diversity, as species with different traits exploit patches with different environmental conditions; and 3) communities with the greatest amount of environmental heterogeneity and a species pool with the greatest functional complementarity will have the greatest capacity for coexistence through species sorting, which will lead to high spatial turnover in community composition among patches.

METHODS

The study site was in the Nelson Environmental Studies Area (NESA), part of the University of Kansas Field Station and Ecological Reserves. NESA is located at the prairie-forest ecotone of northeastern Kansas in Jefferson County (39°03'N, 95°12'W), 10 km north of the city of Lawrence. The site was mid-successional grassland, dominated by the cool-season perennial grasses smooth brome (*Bromus*

inermis Leyss.), tall fescue (*Schedonorus phoenix* (Scop.) Holub), and Kentucky bluegrass (*Poa pratensis* L.).

In April 2005 I established 72 4-m by 4-m plots in six randomized blocks. Each plot was separated by a 1-m buffer, and blocks were separated by a 2-m buffer. I employed a factorial combination of four disturbance treatments with three seed addition treatments, replicated six times. Within each 4-m by 4-m plot, I randomly located eight 1-m² patches in a grid (Fig. 3.1). I defined a community as a plot containing multiple 1-m² patches, and a patch as a contiguous area in which the impact of disturbance (or no disturbance) on the locally-residing individuals was uniform (Petraitis *et al.* 1989).

The disturbance treatments were four manipulated levels of spatio-temporal patch heterogeneity applied at the scale of the 1-m² patches: 1) no disturbance (ND), 2) spring disturbance (SD), 3) fall disturbance (FD), and 4) spring/fall disturbance (SFD). All patches were left undisturbed in ND treatments (Fig. 3.1). In the SD, FD, and SFD treatments, four of the 1-m² patches were disturbed and four were left undisturbed (Fig. 3.1). I disturbed two of these patches in 2005, and two in 2006 to create inter-annual variability. To create seasonal variability, SD and FD treatments had two patches per year disturbed during the same season, and SFD treatments had one patch per year disturbed in spring and one in fall.

Disturbed patches approximated the soil disturbance associated with prairie vole burrows and were created with a combination of herbicide application and rototilling. First, I sprayed a 2% solution of Roundup Pro (41% glyphosate as an

isopropylamine salt) with a backpack sprayer at a rate of approximately 0.4 L/m² and used a plywood frame to prevent overspray into undisturbed areas. After waiting at least 14 days, I then used a rear-tine roto-tiller to disturb the top 150 mm of soil, which is the depth of most vole burrowing disturbance (Davis & Kalisz 1992). I selected the time of disturbance application to coincide with times of vole burrowing activity (Jameson 1947). Spring patches were roto-tilled on 17 May 2005 and 22 May 2006. Fall patches were roto-tilled on 18, 19, and 24 October 2005 and 20 October 2006. All areas outside the eight patches were left undisturbed in all plots.

The seed addition treatments were considered either functionally complementary or redundant based on several classes of traits that affect a species' resource use (Naeem & Wright 2003): regeneration strategy (annual, biennial, perennial), life form (grass, forb, legume), and family (Grime 2001). The functionally redundant species pool was made up of 13 perennial grass species. The functionally diverse pool contained 13 species with a variety of life-history traits (Table 3.1). The mean seed size (t-test, $t_{21} = 1.13$, $P = 0.273$) and the variance in seed size (F-test, $F_{12, 12} = 0.48$, $P = 0.222$) among species were equivalent between pools to minimize colonization or competition differences due to seed size (Rees *et al.* 2001). Seeds were added four times to seed addition plots, once in late May and once in late October in 2005 and 2006. Each time they were added at a rate of 75 seeds/species/m². The resident species pool treatment had no species added. Two of the added species, *Andropogon virginicus* L. and *Tridens flavus* (L.) Hitchc., were

present in at least one resident pool treatment plot in the first year of the study, suggesting that these two species were also resident species.

From 18 June 2007 to 2 July 2007, I visually estimated the percent cover of all plant species, bare ground, and litter in each plot and in a 0.5-m by 0.5-m quadrat placed in the center of each of the eight patches. I calculated community richness as the number of species present in each 4-m by 4-m plot; patch richness as the mean number of species in the eight 0.5-m by 0.5-m quadrats; and spatial turnover as community richness minus patch richness (Lande 1996). I used this additive measure of spatial turnover instead of a community dissimilarity metric in order to directly compare the contributions of patch richness and spatial turnover to community richness. I calculated these three diversity measures for the complete community of resident and added species. I also tested the effect of the treatments on the establishment of the species I directly manipulated, and I calculated patch richness, spatial turnover, and community richness in the same way for added species only.

In order to measure whether the treatments affected the heterogeneity of environmental variables important for plant growth, I calculated the coefficient of variation (CV) of bare ground and litter cover among the eight patches in each plot. I also measured light penetrating through the canopy as below canopy photosynthetically active radiation (PAR)/above canopy PAR. I took 16 measurements in a 4-m by 4-m grid in each plot using an Accupar LP 80 (Decagon Devices; Pullman, WA, USA). Measurements were taken on clear days (31 May and

4-6 June 2007) within two hours of solar noon. I calculated the CV of light penetration among the 16 measurements.

I used factorial analysis of variance (ANOVA) to test the effect of disturbance (four levels), seed addition (three levels), the disturbance x seed addition interaction, and a random blocking factor on the measures of patch richness, spatial turnover, community richness, and the three environmental heterogeneity variables. In order to test whether seasonal disturbance treatments affected diversity measures, I removed the ND plots and reran the ANOVA's. If I found a significant main effect or interaction, I used Tukey simultaneous tests to determine significant differences in group means ($P < 0.05$). When necessary, data were square root-transformed to meet the assumption of homogeneity of variance (HOV). I calculated Pearson product moment correlation coefficients to determine whether spatial turnover was associated with environmental heterogeneity variables. I used a general linear model to test whether seed addition treatments affected the relationship between environmental heterogeneity variables and spatial turnover. If species sorting occurred I expected the complementary species pool to increase the slope of the relationship between spatial turnover and environmental heterogeneity by providing species with trait variation to sort among heterogeneous resources. I performed a separate test for each environmental heterogeneity variable (bare ground, litter, and light penetration) using seed addition as a fixed factor, the CV of the environmental variable as a covariate, and including the seed addition x CV interaction. I used Minitab version 14.1 for all analyses (Minitab, Inc.; State College, PA).

RESULTS

Effect of treatments on environmental heterogeneity

Disturbance increased the CV of litter and light ($P < 0.001$), but not the CV of bare ground ($P > 0.15$). There was no effect of seed addition or the disturbance x seed addition interaction on any environmental heterogeneity variable ($P > 0.1$).

Effect of treatments on the complete community – resident and added species

I found significant increases of patch richness, spatial turnover, and community richness in response to disturbance and seed addition (Table 3.2a). There was a significant disturbance x seed addition interaction for spatial turnover and community richness, but not patch richness, in the model including ND plots. This interaction occurred because seed addition increased spatial turnover and community richness in the presence of disturbance, but had no effect in the absence of disturbance (Fig. 3.2a-c). When the ND plots were removed from analysis, the interaction term remained significant only for spatial turnover (Table 3.2b). Post-hoc tests from the model with ND plots removed revealed that the complementary species pool increased spatial turnover over the resident pool at all disturbance levels (SD, FD, and SFD), but the redundant pool only increased spatial turnover over the resident pool for two of three (FD and SFD) disturbance levels (Fig. 3.2b), showing that the effect of disturbance on spatial turnover was consistently greatest when seeds of complementary species were added. There was also a trend toward greatest spatial turnover in the treatment combination of SFD with the complementary species pool,

which represented a combination of the greatest level of disturbance heterogeneity and greatest functional diversity of the species pool (Fig. 3.2b).

In contrast to spatial turnover, community and patch richness were influenced only by seed addition, and not disturbance treatment, when ND plots were removed (Table 3.2b). Post-hoc tests of the model excluding ND plots showed that the complementary seed addition treatment, but not the redundant treatment, increased patch richness over the resident pool (Fig. 3.2a; $P < 0.05$). Both seed addition treatments increased community richness over the resident pool, and the complementary treatment caused the greatest increase (Fig. 3.2c; $P < 0.05$).

Effect of treatments on added species

In the model including ND plots, patch richness, spatial turnover, and community richness of added species increased with disturbance and seed addition, with a significant disturbance x seed addition interaction for all three diversity measures (Table 3.2a). This interaction occurred because both seed addition treatments increased diversity over the resident pool in the presence of disturbance, but only the complementary treatment increased diversity in the absence of disturbance (Fig. 3.2d-f). When the ND plots were removed, the interaction remained significant for spatial turnover and community richness (Table 3.2b). Although both seed addition treatments increased spatial turnover and community richness over the resident pool, the combination of the complementary species pool treatment with the SD and SFD treatments maintained the highest spatial turnover and community richness, which represented the effect of the greatest functional diversity of the

species pool combined with two levels of disturbance heterogeneity (Fig. 3.2e and 3.2f).

In contrast to spatial turnover and community richness, patch richness was only influenced by seed addition, and not disturbance, when ND plots were removed (Table 3.2b). Post-hoc tests of the model excluding ND plots showed that both seed addition treatments increased patch richness over the resident pool, and the complementary treatment caused the greatest increase (Fig. 3.2d; $P < 0.05$).

Relationship between environmental heterogeneity and spatial turnover

Spatial turnover was significantly ($\alpha = 0.05$) correlated with CV of litter ($r^2 = 0.30$, $P < 0.001$) and CV of light penetration ($r^2 = 0.42$, $P < 0.001$). There was a trend toward a relationship between spatial turnover and the CV of bare ground, although it was not significant ($r^2 = 0.05$, $P = 0.06$). There was a significant seed addition x CV interaction term for litter (Table 3.3, Fig. 3.3), showing that seed addition affected the response of spatial turnover to litter heterogeneity. There was evidence of a similar effect of seed addition on the response of spatial turnover to light heterogeneity, but the interaction term was not statistically significant (Fig. 3.3; $P = 0.059$). This interaction between seed addition and environmental heterogeneity variables occurred because the seed addition treatments increased the effect of environmental heterogeneity on spatial turnover. There was a trend toward the greatest effect of environmental heterogeneity on spatial turnover, indicated by the greatest slope, when seeds of complementary species were added (Fig. 3.3).

DISCUSSION

I found evidence supporting my predictions about the effect of spatial niche dimensionality, species pool dimensionality, and species sorting on coexistence. The disturbance treatments created successional niche heterogeneity that increased diversity. Functional complementarity among added species also increased diversity compared with communities that had functionally redundant species or no species added. The effect of environmental heterogeneity on the spatial turnover of community composition was the greatest in the presence of a complementary species pool, showing the importance of trait variation among species for exploiting variation among patches, and suggesting niche-based coexistence through species sorting.

Niche and dispersal limitation

I found evidence for both niche and dispersal limitation of diversity and that these two constraints on coexistence interact in this system. Disturbance increased all measures of diversity both in the absence and presence of seed addition, showing that the availability of establishment microsites limits colonization and species richness in this grassland. There was an interaction between disturbance and seed addition for several measures of diversity, including richness of the complete community, indicating that the ability of disturbance to influence coexistence is constrained by the available species pool. In general, the magnitude of the interaction was greater for added species compared to the complete community. This result is not surprising since the added species were experimentally manipulated and the complete community contained naturally occurring variation in species composition among

plots; however, it does show that disturbance and an enhanced species pool had a relatively greater effect on colonization and recruitment than on overall community richness. The effect of the interaction was consistently significant for spatial turnover of both the added species and the complete community, suggesting that disturbance created environmental heterogeneity and the community response to this heterogeneity was limited by the available species pool.

In fact, disturbance increased spatial turnover as well as the heterogeneity of litter and light, two factors that can strongly influence plant performance at the establishment stage (Grubb 1977; Foster & Gross 1998; Rees *et al.* 2001). These results suggest that spatial turnover among patches increased when disturbance created successional niche opportunities, which were likely due to the increased availability of establishment microsites that were exploited by competitively inferior species (Grubb 1977; Connell 1978; Huston 1979; Sousa 1979) and an increase in the spatial heterogeneity of environmental conditions important for plant growth. This finding is consistent with my previous study of prairie vole burrows, which found that community composition, litter biomass, and light levels were more variable on burrows than in undisturbed grassland (Questad and Foster 2007; Chapter 2), suggesting that although vole burrows can create dynamic, non-equilibrium environments at small scales, they may create stable coexistence at the community scale by maintaining successional niche opportunities throughout the habitat (Pacala & Rees 1998; Amarasekare 2003; Chase & Leibold 2003; Kneitel & Chase 2004;

Urban 2004; Chase *et al.* 2005; Vandvik & Goldberg 2006; Cadotte 2007; Questad & Foster 2007; Chapter 2).

Complementarity and species sorting

Complementarity of the species pool also influenced spatial turnover, providing support for deterministic species sorting among patches in the community. This result contrasts with a neutral expectation that any observed spatial turnover in species composition should occur independent of differences in competitive traits or demographic rates (Hubbell 2001). In this study I observed that spatial turnover was consistently greater in plots that received seeds from the complementary pool compared to the redundant pool, illustrating the importance of functional trait diversity and trade-offs among species for partitioning environmental differences among patches.

Thus, species sorting appeared to influence coexistence in these communities when disturbance increased niche opportunities *and* when the species pool contained species that could exploit these niches. I found the effect of disturbance on spatial turnover to be consistently greater when the species pool contained complementary species. There was also a trend toward greatest spatial turnover with the most heterogeneous disturbance treatment, but only when the species pool contained complementary species. Furthermore, the addition of complementary species caused litter and light heterogeneity to have the greatest impact on spatial turnover. These results all emphasize that coexistence depended on sufficient trait variation among species in the species pool which allowed them to exploit environmental differences

among patches. I found that both spatial niche dimensionality and species pool dimensionality strongly influenced species sorting and community-scale coexistence in this experiment, and I suggest that these factors may also affect species sorting at larger spatial scales, such as among local communities in a metacommunity (Leibold *et al.* 2004).

In addition to spatial turnover, the complementary seed addition also increased patch richness of the complete community over the resident pool, but the redundant seed addition did not, showing that patch diversity was limited by the functional complementarity of species in the species pool and not just the number of new species. Competition with the dominant perennial grass species may have reduced the establishment of the redundant grass species pool, and the establishment of complementary species may have been facilitated by reduced competition with the dominant species and with each other. These results provide an important extension of previous seed addition studies (e.g., Tilman 1997; Zobel *et al.* 2000; Foster & Dickson 2004) by showing that the effect of an enhanced species pool on local diversity was largely a result of complementarity among species that promoted their coexistence. It is possible that the outcome may have differed if I had tested redundant pools of species other than perennial grasses; however, I chose perennial grasses because they dominate the regional landscape and are maintained through management for cattle production. Thus, in addition to highlighting the importance of complementarity for coexistence, this experiment also shows how a landscape-scale

change to dominance by a single functional group may reduce the ability of the species pool to affect coexistence.

Comparison with other studies

Two other studies have examined the interplay between environmental heterogeneity and species pools. In contrast to my results, Reynolds et al. (2007) found that in a nutrient-poor grassland there was no effect of fertilizer heterogeneity on species richness even in the presence of species added to reduce dispersal limitation. In their study, nitrophilic clonal species appeared to exploit patches of fertilizer, leaving few resources available for other species colonizing from seed (Reynolds *et al.* 2007). It is possible that by manipulating spatio-temporal disturbance patterns, my experiment contained niche opportunities that did not exist in their study, which enhanced the spatial niche dimensionality of communities. My results are similar to a study of microtopographic heterogeneity in wetlands in which three species pools with different numbers of species were added to homogeneous and heterogeneous environments (Vivian-Smith 1997). The wetland study showed that heterogeneity increased diversity, but this increase was greatest when the greatest number of species were added to the heterogeneous habitat. My results suggest that this increase in diversity may have been due to the increased trait diversity in the species pool that allowed species to partition resources among patches, affecting coexistence through species sorting.

Previous studies have also shown that disturbance can decrease turnover in community composition by consistently favoring the same disturbance-adapted

species (Chase 2003; Collins & Smith 2006; Chase 2007; Houseman *et al. in press*). My study provides contrasting evidence, which suggests that the effect of disturbance on turnover in community composition is context-dependent. By creating disturbances at different times, I may have created colonization opportunities for disturbance-adapted species that disperse at different times or that exploit resources seasonally through phenological differences. In addition, it is possible that disturbance can increase spatial turnover when species that take advantage of colonization opportunities are spatially distributed, such as in the seedbank, or when species pool complementarity is high, and species that can exploit colonization opportunities are not dispersal-limited; whereas disturbance may decrease spatial turnover if the species pool does not contain sufficient functional diversity.

Conclusion

By manipulating environmental heterogeneity and species pool complementarity in a spatially explicit experimental framework, I have demonstrated the importance of both spatial niche dimensionality and species pool dimensionality for influencing coexistence through species sorting. My experiment showed that spatio-temporal disturbance patterns increase diversity by creating colonization opportunities and increasing successional niche heterogeneity. Complementarity among species increased the effect of the species pool on diversity, most likely due to decreased competition and the ability of species with different traits to exploit environmental differences among patches. I manipulated resource pulses instead of constant supply rates, which is a departure from the traditional equilibrium

framework used by other studies of environmental heterogeneity in grasslands (Collins & Wein 1998; Stevens & Carson 2002; Baer *et al.* 2004; Wijesinghe *et al.* 2005; Reynolds *et al.* 2007). My study emphasizes that community-scale coexistence in perennial grasslands can be enhanced by small-scale non-equilibrium dynamics and species sorting among heterogeneous niches.

Table 3.1. Species in added species pools. The functionally redundant species pool is equal numbers of seeds of 13 perennial grass species. The functionally complementary species pool is equal numbers of seeds of 13 species in many functional groups. C3 denotes cool-season grass species that use a 3-carbon compound during photosynthesis. C4 denotes warm-season grass species that use a 4-carbon compound. Nomenclature follows GPFA (1986).

Redundant Pool		Complementary Pool	
Scientific name	Functional group	Scientific name	Functional group
<i>Andropogon gerardii</i>	Perennial C4 grass	<i>Andropogon gerardii</i>	Perennial C4 grass
<i>Andropogon virginicus</i>	Perennial C4 grass	<i>Sorghastrum nutans</i>	Perennial C4 grass
<i>Agropyron smithii</i>	Perennial C3 grass	<i>Koeleria pyramidata</i>	Perennial C3 grass
<i>Agrostis hyemalis</i>	Perennial C3 grass	<i>Cassia chamaecrista</i>	Annual forb, Fabaceae
<i>Bouteloua curtipendula</i>	Perennial C4 grass	<i>Helianthus annuus</i>	Annual forb, Asteraceae
<i>Elymus canadensis</i>	Perennial C3 grass	<i>Rudbeckia hirta</i>	Biennial forb, Asteraceae
<i>Elymus virginicus</i>	Perennial C3 grass	<i>Echinacea pallida</i>	Perennial forb, Asteraceae
<i>Koeleria pyramidata</i>	Perennial C3 grass	<i>Ratibida columnifera</i>	Perennial forb, Asteraceae
<i>Panicum virgatum</i>	Perennial C4 grass	<i>Dalea purpurea</i>	Perennial forb, Fabaceae
<i>Schizachyrium scoparium</i>	Perennial C4 grass	<i>Amorpha canescens</i>	Perennial forb, Fabaceae
<i>Sorghastrum nutans</i>	Perennial C4 grass	<i>Monarda fistulosa</i>	Perennial forb, Lamiaceae
<i>Sporobolus cryptandrus</i>	Perennial C4 grass	<i>Salvia azurea</i>	Perennial forb, Lamiaceae
<i>Tridens flavus</i>	Perennial C4 grass	<i>Asclepias tuberosa</i>	Perennial forb, Asclepiadaceae

Table 3.2. Patch richness, spatial turnover, and community richness for analysis of all species and added species. F-statistics reported for A) ANOVA including ND treatment. The model included block as a random variable (df = 5), disturbance (df = 3) and seed addition (df = 2) as fixed variables, disturbance x seed addition (df = 6), and error (df = 55). Added community richness and added spatial turnover were square root-transformed to improve HOV. B) ANOVA excluding ND treatment to test for differences in richness among disturbance treatments. Model terms were block (df = 5), disturbance (df = 2), seed addition (df = 2), disturbance x seed addition (df = 4), and error (df = 40). Added spatial turnover was square root-transformed to improve HOV. *P<0.05, **P<0.01, ***P<0.001

	Disturbance x Seed Addition	Disturbance	Seed Addition	Block
A) ND treatment included				
ALL SPECIES				
<i>Community richness</i>	2.39*	99.14***	25.35***	4.89**
<i>Spatial turnover</i>	3.05*	92.07***	23.76***	3.81**
<i>Patch richness</i>	0.45	43.50***	11.16***	6.01***
ADDED SPECIES				
<i>Community richness</i>	6.92***	58.96***	272.77***	1.51
<i>Spatial turnover</i>	8.32***	48.85***	258.82***	1.12
<i>Patch richness</i>	4.37**	35.59***	161.83***	7.19***
B) ND treatment excluded				
ALL SPECIES				
<i>Community richness</i>	2.05	2.50	29.89***	2.76*
<i>Spatial turnover</i>	2.76*	4.09*	26.69***	2.06
<i>Patch richness</i>	0.33	0.18	11.63***	4.86**
ADDED SPECIES				
<i>Community richness</i>	5.40**	11.74***	517.85***	1.02
<i>Spatial turnover</i>	8.45***	7.46**	505.29***	2.57*
<i>Patch richness</i>	0.34	1.51	148.66***	3.73**

Table 3.3. The effect of seed addition on the response of spatial turnover to environmental heterogeneity. F-statistics reported for ANCOVA. The model included seed addition (df = 2) as a fixed variable, the CV of each environmental variable as a covariate (df = 1), and the seed addition x CV interaction (df = 2). The error term had 66 df. †P=0.059, *P<0.05, ***P<0.001,

Resource Variable	Seed Addition x CV	Seed Addition	CV
<i>Litter</i>	2.96 [†]	0.69	35.13***
<i>Bare ground</i>	0.60	1.39	1.98
<i>Light penetration</i>	3.41*	1.26	59.08***

Fig. 3.1. Experimental plot design. Each plot was a 4-m by 4-m square. Eight 1-m² patches were randomly located in a grid. We administered disturbance to four patches in Spring (dotted squares), Fall (hatched squares), and Spring/Fall disturbance treatments. Two patches received disturbance in 2005 and two in 2006. We left four patches undisturbed in these three treatments and all eight patches undisturbed in the No Disturbance treatment (dashed squares). Areas outside the eight patches were left undisturbed.

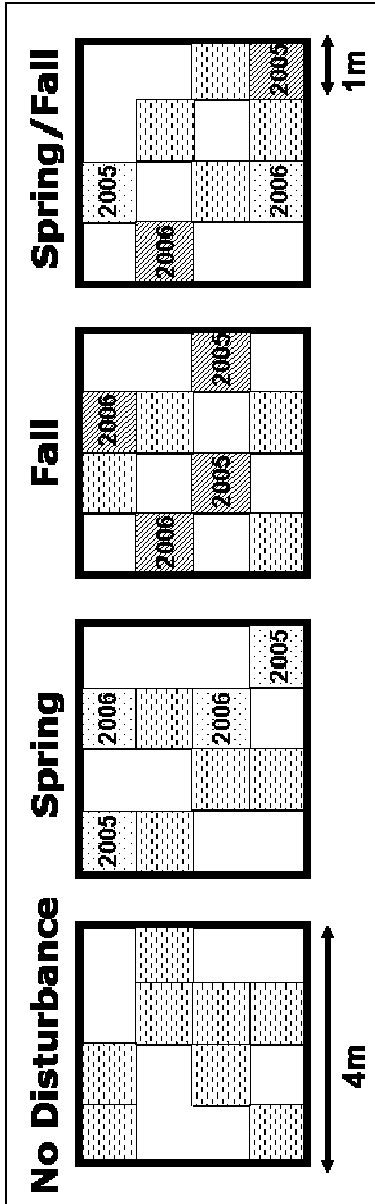


Fig. 3.2. Interaction plots for patch richness, spatial turnover, and community richness of the complete community (a-c) and added species (d-f). Disturbance treatments are on the x-axis. Lines represent seed addition treatments: resident pool (solid lines and circles), redundant pool (dashed lines and triangles), and complementary pool (dotted lines and squares). Symbols represent mean values, error bars are two standard errors. Letters indicate significant differences among means based on Tukey post-hoc tests for significant interaction terms from models with ND treatments removed.

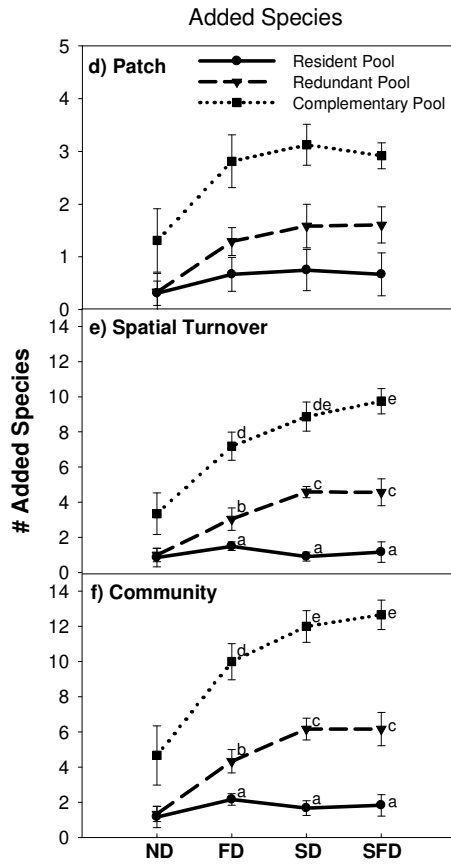
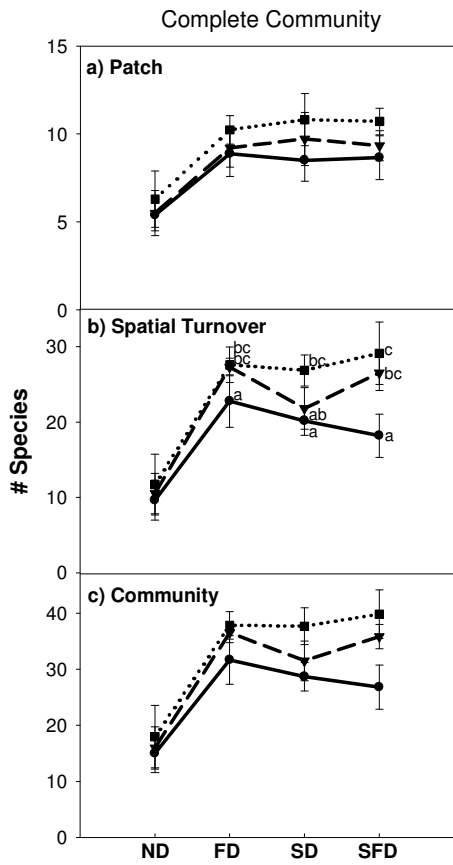
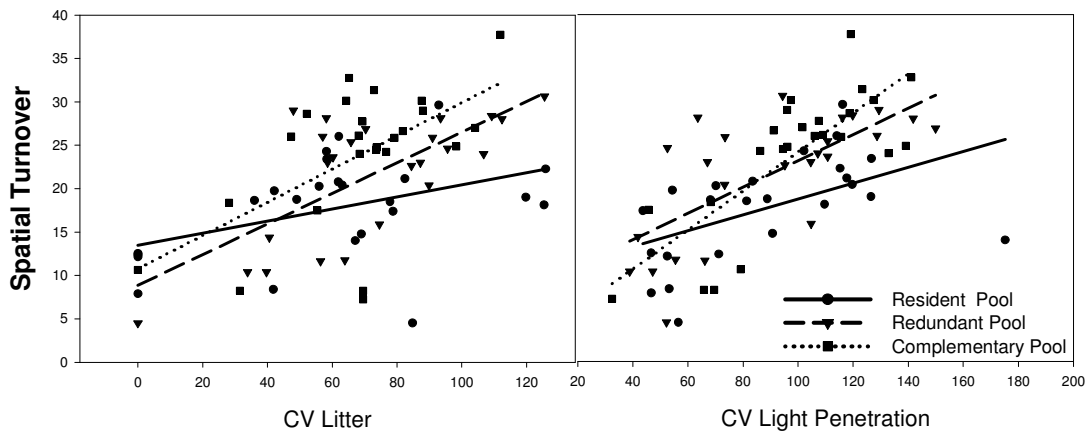


Fig. 3.3. Interaction plots for the effect of seed addition and resource heterogeneity on spatial turnover. Seed addition treatments are resident pool (solid lines and circles), redundant pool (dashed lines and triangles), and complementary pool (dotted lines and squares).



CONCLUSION

Disturbance has had significant impacts on plant community diversity and composition in northeastern Kansas grasslands. Some of these impacts have been negative, such as the degraded soil quality and reduced plant diversity that occurs with grassland management (Chapter 1). Other impacts of disturbance were positive, such as prairie vole burrows that were associated with increased environmental heterogeneity and plant diversity (Chapter 2), and experimental disturbances that increased successional niche opportunities that enhanced species coexistence (Chapter 3). It is also clear that the characteristics of disturbance can determine the plant community response, including the source, size, and intensity of disturbance events.

Grassland management practices have caused extensive and significant changes to plant community diversity, composition, and spatial structure (Chapter 1). These changes arose from historical cultivation that had persistent effects on soil and community properties, the replanting of perennial grass species that changed the dominance structure of communities, and the contemporary grazing and hay management applied to the ecosystem. The influence of contemporary management disturbance on site richness and functional group evenness depended on whether or not a site was historically cultivated. In addition the differences in richness and spatial turnover among management classes depended on the spatial scale and taxonomic or ecological resolution of measurement. Management practices that negatively affected plant diversity may do so by reducing environmental heterogeneity, increasing

dominance by perennial grasses, and decreasing the functional diversity of communities. Improving the CRP program and varying hay and grazing management in a site may help mitigate some of these negative impacts of management.

Prairie vole burrows affected environmental conditions and grassland plant diversity at both the patch (1 m^2) and metacommunity ($> 5 \text{ ha}$) scales (Chapter 2). Vole disturbance affected the mean values of nine resource variables measured, suggesting that disturbance increased niche opportunities. In addition, burrows contributed more to environmental heterogeneity than undisturbed matrix plots. Disturbance increased local plant species richness, metacommunity evenness, and the presence and abundance of fugitive species. Spatial turnover was high among burrows because disturbance shifted the identity of dominant species away from the species dominant in the matrix and allowed fugitive species to persist in higher abundances. These patterns are consistent with several diversity-maintaining mechanisms, including a successional mosaic and alternative successional trajectories among burrows created at different times. Thus, the presence of voles in this ecosystem was associated with the persistence of fugitive species, a shift in dominant species, and increased resource heterogeneity, all of which led to greater metacommunity diversity.

The effect of the timing of disturbance (Chapter 2) and the functional diversity of species in the species pool (Chapter 1) on species coexistence was evaluated further with an experiment that tested whether small-scale disturbances create environmental heterogeneity (niche dimensionality) and whether the trait diversity of

species in the species pool (species pool dimensionality) affects the ability of community composition to reflect heterogeneity through species sorting (Chapter 3). The disturbance treatments affected coexistence by creating colonization opportunities and successional niche heterogeneity. Functional complementarity among species increased the effect of the species pool on diversity compared with communities that had functionally redundant species or no species added, most likely due to decreased competition and the ability of species with different traits to exploit environmental differences among patches. The effect of environmental heterogeneity on the spatial turnover of community composition was the greatest in the presence of a complementary species pool, showing the importance of trait variation among species for exploiting variation among patches, and suggesting niche-based coexistence through species sorting. This experiment demonstrated the importance of both spatial niche dimensionality and species pool dimensionality for influencing coexistence through species sorting and emphasized that community-scale coexistence in perennial grasslands can be enhanced by small-scale disturbance and species sorting among heterogeneous niches.

Together, these studies suggest that the negative impacts of human-induced disturbance on plant communities can be mitigated by adaptive management practices and restoration. Specifically, mid-season hay disturbance may enhance species diversity in managed native prairies, small-scale heterogeneous disturbances can create niche opportunities in cool-season grasslands with high levels of dominance, and functional complementarity among species added as seed can promote the

successful establishment of species in grassland restorations. Thus, aspects of natural community structure may be restored by understanding the impact of disturbance at different spatial scales in plant communities.

LITERATURE CITED

- Adler P.B., Raff D.A. & Lauenroth W.K. (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia (Berl)*, 128, 465-479
- Amarasekare P. (2003) Competitive coexistence in spatially structured environments: A synthesis. *Ecol Lett*, 6, 1109-1122
- Anderson M.J., Connell S.D., Gillanders B.M., Diebel C.E., Blom W.M., Saunders J.E. & Landers T.J. (2005) Relationships between taxonomic resolution and spatial scales of multivariate variation. *J Anim Ecol*, 74, 636-646
- Anderson M.J., Ellingsen K.E. & McArdle B.H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecol Lett*, 9, 683-693
- Baer S.G., Blair J.M., Collins S.L. & Knapp A.K. (2004) Plant community responses to resource availability and heterogeneity during restoration. *Oecologia*, 139, 617-629
- Baskin C.C. & Baskin J.M. (1998) *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego, CA.
- Bazzaz F.A. (1996) *Plants in changing environments: Linking physiological, population, and community ecology*. University of Cambridge Press, Cambridge, UK.
- Bee J.W., Glass G.E., Hoffman R.S. & Patterson R.R. (1981) *Mammals in Kansas*. University of Kansas, Lawrence, KS.
- Bradshaw L. & Goldberg D.E. (1989) Resource levels in undisturbed vegetation and mole mounds in old fields. *Am Midl Nat*, 121, 176-783
- Bragg T.B. (1982) Seasonal-variations in fuel and fuel consumption by fires in a bluestem prairie. *Ecology*, 63, 7-11
- Buyanovsky G.A., Kucera C.L. & Wagner G.H. (1987) Comparative analyses of carbon dynamics in native and cultivated ecosystems. *Ecology*, 68, 2023-2031
- Cadotte M.W. (2007) Competition-colonization tradeoffs and disturbance effects at multiple scales. *Ecology*, 88, 823-829
- Canals R.M., Herman D.J. & Firestone M.K. (2003) How disturbance by fossorial mammals alters n cycling in a California annual grassland. *Ecology*, 84, 875-881
- Chao A., Chazdon R.L., Colwell R.K. & Shen T.-J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol Lett*, 8, 148-159
- Chase J.M. (2003) Community assembly: When should history matter? *Oecologia*, 136, 489-498
- Chase J.M. (2007) Drought mediates the importance of stochastic community assembly. *proceedings of the national Academy of Sciences*, 104, 17430-17434
- Chase J.M., Amarasekare P., Cottenie K., Gonzalez A., Holt R.D., Holyoak M., Hoopes M.F., Leibold M.A., Loreau M., Mouquet N., Shurin J.B. & Tilman D. (2005) Competing theories for competitive metacommunities. In:

- Metacommunities: Spatial dynamics and ecological communities* (eds. Holyoak M, Leibold MA & Holt RD), pp. 335-354. University of Chicago Press, Chicago
- Chase J.M. & Leibold M.A. (2003) *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press, Chicago.
- Chesson P. & Huntly N. (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat*, 150, 519-553
- Cole F.R. & Batzli G.O. (1978) Influence of supplemental feeding on a vole population. *J Mammal*, 59, 809-819
- Collins B. & Wein G. (1998) Soil resource heterogeneity effects on early succession. *Oikos*, 82, 238-245
- Collins S.L. (1989) Experimental analysis of patch dynamics and community heterogeneity in tallgrass prairie. *Vegetatio*, 85, 57-66
- Collins S.L. (1992) Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology*, 73, 2001-2006
- Collins S.L. & Glenn S.M. (1991) Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology (Wash D C)*, 72, 654-664
- Collins S.L., Knapp A.K., Briggs J.M., Blair J.M. & Steinauer E.M. (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280, 745-747
- Collins S.L. & Smith M.D. (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology*, 87, 2058-2067
- Colwell R.K. (2005) Estimates: Statistical estimation of species richness and shared species from samples. URL User's Guide and application published at: <http://purl.oclc.org/estimates>
- Condit R., Pitman N., Leigh E.G., Chave J., Terborgh J., Foster R.B., Nunez P., Aguilar S., Valencia R., Villa G., Muller-Landau H.C., Losos E. & Hubbell S.P. (2002) Beta-diversity in tropical forest trees. *Science*, 295, 666-669
- Connell J.H. (1978) Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, 199, 1302-1310
- Conservation International (2007) Biodiversity hotspots: California floristic province. URL http://www.biodiversityhotspots.org/xp/hotspots/california_floristic/Pages/default.aspx
- Cook W.M., Yao J., Foster B.L., Holt R.D. & Patrick L.B. (2005) Secondary succession in an experimentally fragmented landscape: Community patterns across space and time. *Ecology*, 86, 1267-1279
- Davis W.H. & Kalisz P.J. (1992) Burrow systems of the prairie vole, *Microtus ochrogaster*, in central Kentucky. *J Mammal*, 73, 582-585
- Day T.A. & Detling J.K. (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology*, 71, 180-188

- Diamond J.M. (1975) Assembly of species communities. In: *Ecology and evolution of communities* (eds. Cody ML & Diamond JM), pp. 342-444. Harvard University Press, Cambridge, MA
- Dickey H.P., Zimmerman J.L., Plinsky R.O. & Davis R.D. (1977a) *Soil survey of douglas county, kansas*. United States Department of Agriculture, Soil Conservation Service.
- Dickey H.P., Zimmerman J.L. & Rowland H.T. (1977b) *Soil survey of jefferson county, kansas*. United States Department of Agriculture, Soil Conservation Service.
- Downton W.J.S. (1975) The occurrence of c_4 photosynthesis among plants. *Photosynthetica*, 9, 96-105
- Drake J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist*, 137, 1-26
- Fargione J., Brown C.S. & Tilman D. (2003) Community assembly and invasion: An experimental test of neutral versus niches processes. *PNAS*, 100, 8916-8920
- Fehmi J.S. & Bartolome J.W. (2002) Species richness and california voles in an annual and a perennial grassland. *West N Am Nat*, 62, 73-81
- Foster B.L. & Dickson T.L. (2004) Grassland diversity and productivity: The interplay of resource availability and propagule pools. *Ecology*, 85, 1541-1547
- Foster B.L. & Gross K.L. (1998) Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *Ecology*, 79, 2593-2602
- Foster D., Swanson F., Aber J., Burke I., Brokaw N., Tilman D. & Knapp A. (2003) The importance of land-use legacies to ecology and conservation. *Bioscience*, 53, 77-88
- Fukami T., Bezemer T.M., Mortimer S.R. & van der Putten W.H. (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecol Lett*, 8, 1283-1290
- Getz L.L. (1985) Habitats. In: *Biology of new world microtus* (ed. Tamarin RH), pp. 286-309. The American Society of Mammalogists
- Getz L.L., Gudermuth D.F. & Benson S.M. (1992) Pattern of nest occupancy of the prairie vole *microtus ochrogaster* in different habitats. *Am Midl Nat*, 128, 197-202
- Getz L.L., Hofmann J.E., McGuire B. & Dolan III T.W. (2001) Twenty-five years of population fluctuations of *microtus ochrogaster* and *m. pennsylvanicus* in three habitats in east-central illinois. *J Mammal*, 82, 22-34
- Gibson D.J. (1989) Effects of animal disturbance on tallgrass prairie vegetation. *Am Midl Nat*, 121, 144-154
- Glenn-Lewin D.C., Johnson L.A., Jurik T.W., Akey A., Leoschke M. & Rosburg T. (1990) Fire in central north american grasslands: Vegetative reproduction, seed germination, and seedling establishment. In: *Fire in north american tallgrass prairies* (eds. Collins SL & Wallace LL), pp. 28-45. University of Oklahoma Press, Norman, OK
- G.P.F.A. (1986) *Flora of the great plains*. University of Kansas Press, Lawrence, KS.

- Grime J.P. (2001) *Plant strategies, vegetation processes, and ecosystem properties*. Second edn. John Wiley & Sons Ltd., West Sussex, England.
- Gross K.L., Mittlebach G.G. & Reynolds H.L. (2005) Grassland invasibility and diversity: Responses to nutrients, seed input, and disturbance. *Ecology*, 86, 476-486
- Grubb P.J. (1977) The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol Rev*, 52, 107-145
- Harrison S. & Inouye B.D. (2002) High beta diversity in the flora of californian serpentine 'islands'. *Biodivers Conserv*, 11, 1869-1876
- Higgins K.F. (1984) Lightning fires in north-dakota grasslands and in pine-savanna lands of south-dakota and montana. *J Range Manag*, 37, 100-103
- Hobbs R.J. & Huenneke L.F. (1992) Disturbance, diversity, and invasion: Implications for conservation. *Conserv Biol*, 6, 324-337
- Hobbs R.J. & Mooney H.A. (1985) Community and population dynamics of serpentine grassland annuals in reaction to gopher disturbance. *Oecologia*, 67, 342-351
- Hobbs R.J. & Mooney H.A. (1995) Spatial and temporal variability in california annual grassland: Results from a long-term study. *J Veg Sci*, 6, 43-56
- Holyoak M., Leibold M.A. & Holt R.D. (2005) *Metacommunities: Spatial dynamics and ecological communities*. University of Chicago Press.
- Houseman G.R., Mittelbach G.G., Reynolds H.L. & Gross K.L. (*in press*) Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology*
- Howe H.F. (1994a) Managing species diversity in tallgrass prairie: Assumptions and implications. *Conserv Biol*, 8, 691-704
- Howe H.F. (1994b) Response of early- and late-flowering plants to fire season in experimental prairies. *Ecol Appl*, 4, 121-133
- Howe H.F. & Brown J.S. (2001) The ghost of granivory past. *Ecol Lett*, 4, 371-378
- Howe H.F., Brown J.S. & Zorn-Arnold B. (2002) A rodent plague on prairie diversity. *Ecol Lett*, 5, 30-36
- Hubbell S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Huntly N. & Inouye R. (1988) Pocket gophers in ecosystems: Patterns and mechanisms. *Bioscience*, 38, 786-793
- Huston M.A. (1979) A general hypothesis of species diversity. *Am Nat*, 113, 81-101
- Huston M.A. (1994) *Biological diversity: The coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Hutchinson G.E. (1951) Copepodology for the ornithologist. *Ecology*, 32, 571-577
- Inouye R.S., Huntly N.J., Tilman D. & Tester J.R. (1987) Pocket gophers (*geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central minnesota. *Oecologia*, 72, 178-184
- Jameson E.W. (1947) Natural history of the prairie vole (mammalian genus *microtus*). *University of Kansas Museum of Natural History*, 1, 125-151

- Jog S., Kindscher K., Questad E.J., Foster B. & Loring H. (2006) Floristic quality as an indicator of native species diversity in managed grasslands. *Nat Areas J*, 26, 149-167
- Kalisz P.J. & Davis W.H. (1992) Effect of prairie voles on vegetation and soils in central kentucky. *Am Midl Nat*, 127, 392-399
- Kansas Agricultural Statistics Service (2006) Kansas farm facts. In:
- Klopatek J.M., Olson R.J., Emerson C.J. & Jones J.L. (1979) Land-use conflicts with natural vegetation in the united states. *Environ Conserv*, 6, 191-199
- Knapp A.K., Blair J.M., Briggs J.M., Collins S.L., Hartnett D.C., Johnson L.C. & Towne E.G. (1999a) The keystone role of bison in north american tallgrass prairie. *Bioscience*, 49, 39-50
- Knapp A.K., Briggs J.M., Hartnett D.C. & Collins S.L. (1998) *Grassland dynamics: Long-term ecological research in tallgrass prairie*. Oxford University Press.
- Knapp A.K., Hartnett D.C., Collins S.L. & Briggs J.M. (1999b) A caution against grazing - response. *Bioscience*, 49, 600-601
- Kneitel J.M. & Chase J.M. (2004) Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecol Lett*, 7, 69-80
- Knops J.M.H. & Tilman D. (2000) Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology*, 81, 88-98
- Lande R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5-13
- Leach M.K., Henderson R.A. & Givnish T.J. (1999) A caution against grazing. *Bioscience*, 49, 599-600
- Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., Holt R.D., Shurin J.B., Law R., Tilman D., Loreau M. & Gonzalez A. (2004) The metacommunity concept: A framework for multi-scale community ecology. *Ecol Lett*, 7, 601-613
- Lennon J.J., Koleff P., Greenwood J.J.D. & Gaston K.J. (2001) The geographical structure of british bird distributions: Diversity, spatial turnover and scale. *J Anim Ecol*, 70, 966-979
- Levin S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967
- Lin Y.K., Keane B., Isenhour A. & Solomon N.G. (2006) Effects of patch quality on dispersal and social organization of prairie voles: An experimental approach. *J Mammal*, 87, 446-453
- Lindenmayer D., Hobbs R.J., Montague-Drake R., Alexandra J., Bennett A., Burgman M., Cale P., Calhoun A., Cramer V., Cullen P., Driscoll D., Fahrig L., Fischer J., Franklin J., Haila Y., Hunter M., Gibbons P., Lake S., Luck G., Macgregor C., McIntyre S., Nally R.M., Manning A., Miller J., Mooney H., Noss R., Possingham H., Saunders D., Schmiegelow F., Scott M., Simberloff D., Sisk T., Tabor G., Walker B., Wiens J., Woinarski J. & Zavaleta E. (2007) A checklist for ecological management of landscapes for conservation. *Ecol Lett*

- Loreau M., Mouquet N. & Holt R.D. (2003) Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecol Letters*, 6, 673-679
- Loreau M., Mouquet N. & Holt R.D. (2005) From metacommunities to metaecosystems. In: *Metacommunities: Spatial dynamics and ecological communities* (eds. Holyoak M, Leibold MA & Holt RD), pp. 418-438. University of Chicago Press
- Lupwayi N.Z., Clayton G.W., O'Donovan J.T., Harker K.N., Turkington T.K. & Rice W.A. (2004) Soil microbiological properties during decomposition of crop residues under conventional and zero tillage. *Can J Soil Sci*, 84, 411-419
- MacArthur R.H. & Wilson W.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Mackey R.L. & Currie D.J. (2000) A re-examination of the expected effects of disturbance on diversity. *Oikos*, 88, 483-493
- Magurran A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, Oxford.
- Mankin P.C. & Getz L.L. (1994) Burrow morphology as related to social organization of *Microtus ochrogaster*. *J Mammal*, 75, 492-499
- McCune B. & Mefford M.J. (1999) Multivariate analysis of ecological data version 4.14
- McGarigal K., Cushman S. & Stafford S. (2000) *Multivariate statistics for wildlife and ecology research*. Springer-Verlag New York, Inc., New York.
- McLean E.O. (1982) Soil ph and lime requirement. In: *Methods of soil analysis. Part 2: Chemical and microbiological properties* (eds. Page AL, Miller RH & Keeney DR), pp. 200-209. American Society of Agronomy, Madison, WI
- McNaughton S.J. (1979) Grazing as an optimization process - grass ungulate relationships in the serengeti. *Am Nat*, 113, 691-703
- Menhusen B.R. (1963) An investigation on the food habits of four species of rodents in captivity. *Trans Kans Acad Sci*, 66, 107-112
- Murphy C.A. (2004) Plant diversity and soil characteristics of managed grasslands in northeastern Kansas. In: *Ecology and Evolutionary Biology*, p. 144. University of Kansas, Lawrence, KS
- Murphy C.A., Foster B.L., Ramspott M.E. & Price K.P. (2006) Effects of cultivation history and current grassland management on soil quality in northeastern Kansas. *Journal of Soil and Water Conservation*, 61, 75-84
- Naeem S. & Wright J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecol Lett*, 6, 567-579
- Natural Resources Conservation Service (2000) *National resources inventory. Summary report, 1997, revised 2000*. United States Department of Agriculture.
- Noss R.F., LaRoe E.T., III & Scott J.M. (1995) Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. In: *Biological Report 28* pp. 1-58. US Department of the Interior: National Biological Service

- Pacala S.W. & Rees M. (1998) Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am Nat*, 152, 729-737
- Pascarella J.B. & Gaines M.S. (1991) Feeding preferences of the prairie vole (*Microtus ochrogaster*) for seeds and plants from an old-field successional community. *Trans Kans Acad Sci*, 94, 3-11
- Petraitis P.S., Latham R.E. & Niesenbaum R.A. (1989) The maintenance of species-diversity by disturbance. *Q Rev Biol*, 64, 393-418
- Pielou E.C. (1977) *Mathematical ecology*. John Wiley and Sons, Inc., New York.
- Platt W.J. (1975) The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecol Monogr*, 45, 285-305
- Platt W.J. & Connell J.H. (2003) Natural disturbances and directional replacement of species. *Ecol Monogr*, 73, 507-522
- Questad E.J. & Foster B.L. (2007) Vole disturbances and plant diversity in a grassland metacommunity. *Oecologia*, 153, 341-351
- Questad E.J. & Foster B.L. (*in press*) Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecol Lett*, 11
- Rees M., Condit R., Crawley M., Pacala S. & Tilman D. (2001) Long-term studies of vegetation dynamics. *Science*, 293, 650-655
- Reichman O.J. & Seabloom E.W. (2002a) Ecosystem engineering: A trivialized concept? Response. *Trends in ecology and evolution*, 17, 308
- Reichman O.J. & Seabloom E.W. (2002b) The role of pocket gophers as subterranean ecosystem engineers. *TREE*, 17, 44-49
- Reynolds H.L., Mittelbach G.G., Darcy-Hall T.L., Houseman G.R. & Gross K.L. (2007) No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *J Ecol*, 95, 723-733
- Rosenzweig M.L. (1996) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Samson F. & Knopf F. (1994) Prairie conservation in north america. *Bioscience*, 44, 418-421
- Scheiner S.M., Cox S.B., Willig M., Mittelbach G.G., Osenberg C. & Kaspari M. (2000) Species richness, species-area curves and simpson's paradox. *Evol Ecol Res*, 2, 791-802
- Seabloom E.W. & Richards S.A. (2003) Multiple stable equilibria in grasslands mediated by herbivore population dynamics and foraging behavior. *Ecology*, 84, 2891-2904
- Shea K., Roxburgh S.H. & Rauschert E.S.J. (2004) Moving from pattern to process: Coexistence mechanisms under intermediate disturbance regimes. *Ecol Lett*, 7, 491-508
- Sokal R.R. & Rohlf F.J. (1995) *Biometry, third edition*. W.H. Freeman and Co.
- Sousa W.P. (1979) Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. *Ecology*, 60, 1225-1239

- Squiers E.R. (1989) The effects of seasonal timing of disturbance on species composition in a first-year oldfield. *J Torrey Bot Soc*, 116, 356-363
- Stevens M.H.H. & Carson W.P. (2002) Resource quantity, not resource heterogeneity, maintains plant diversity. *Ecol Lett*, 5, 420-426
- Temperton V.M., Hobbs R.J., Nuttle T. & Halle S. (2004) *Assembly rules and restoration ecology: Bridging the gap between theory and practice*. Island Press.
- Tilman D. (1983) Plant succession and gopher disturbance along an experimental gradient. *Oecologia*, 60, 285-292
- Tilman D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2-16
- Tilman D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81-92
- Tilman D., Hill J. & Lehman C. (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, 314, 1598-1600
- Tilman D. & Pacala S. (1993) The maintenance of species richness in plant communities. In: *Species diversity in ecological communities: Historical and geographical perspectives* (eds. Ricklefs RE & Schluter D), pp. 13-25. University of Chicago Press, Chicago
- Towne E.G., Hartnett D.C. & Cochran R.C. (2005) Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecol Appl*, 15, 1550-1559
- U.S. Census Bureau (2008) State and county quickfacts. URL <http://quickfacts.census.gov/qfd/states/19000.html>
- Urban M.C. (2004) Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, 85, 2971-2978
- USDA (2007a) Title ii: Conservation. In: *USDA 2007 Farm Bill Proposals* (ed. Agriculture USDo)
- USDA F.S.A. (2007b) Conservation programs. URL <http://www.fsa.usda.gov/FSA/webapp?area=home&subject=copr&topic=crp>
- USDA NRCS (2006) The plants database. National Plant Data Center, Baton Rouge, LA 70874-4490 USA
- Vandvik V. & Birks H.J.B. (2002a) Partitioning floristic variance in norwegian upland grasslands into within-site and between-site components: Are the patterns determined by environment or by land-use? *Plant Ecol*, 162, 233-245
- Vandvik V. & Birks H.J.B. (2002b) Pattern and process in norwegian upland grasslands: A functional analysis. *J Veg Sci*, 13, 123-134
- Vandvik V. & Goldberg D.E. (2006) Sources of diversity in a grassland metacommunity: Quantifying the contribution of dispersal to species richness. *Am Nat*, 168, 157-167
- Veen G.F., Blair J.M., Smith M.D. & Collins S.L. (*in press*) Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie. *Oikos*

- Vinton M.A., Hartnett D.C., Finck E.J. & Briggs J.M. (1993) Interactive effects of fire, bison (bison bison) grazing and plant community composition in tallgrass prairie. *Am Midl Nat*, 129, 10-18
- Vitousek P.M., Mooney H.A., Lubchenco J. & Melillo J.M. (1997) Human domination of earth's ecosystems. *Science*, 277, 494-499
- Vivian-Smith G. (1997) Microtopographic heterogeneity and floristic diversity in experimental wetland communities. *J Ecol*, 85, 71-82
- Wiens J.A. (1989) Spatial scaling in ecology. *Funct Ecol*, 3, 385-397
- Wijesinghe D.K., John E.A. & Hutchings M.J. (2005) Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. *J Ecol*, 93, 99-112
- Wilsey B.J., Martin L.M. & Polley H.W. (2005) Predicting plant extinction based on species-area curves in prairie fragments with high beta richness. *Conserv Biol*, 19, 1835-1841
- Zavesky L.D. & Boatright W.C. (1977) *Soil survey of leavenworth and wyandotte counties, kansas*. United States Department of Agriculture, Soil Conservation Service.
- Zobel M., Otsus M., Liira J., Moora M. & Mols T. (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, 81, 3274-3282