PLANT ANIMAL INTERACTION

Vole disturbances and plant diversity in a grassland metacommunity

Erin J. Questad · Bryan L. Foster

Abstract We studied the disturbance associated with prairie vole burrows and its effects on grassland plant diversity at the patch (1 m^2) and metacommunity (>5 ha) scales. We 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, we expected burrows to increase resource heterogeneity and have a community composition distinct from the matrix. We 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, we compared community similarity among burrow and matrix plots. Using Sorenson's similarity index, which considers only presence–absence data, we 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, we 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 we observed are consistent with several diversity-maintaining mechanisms, including a successional mosaic and alternative successional trajectories. We also found evidence that prairie voles may be ecosystem engineers.

Keywords Beta diversity · Succession · Community assembly · Metaecosystem · Ecosystem engineer

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 (Chesson and Huntly 1997; Connell 1978; Huston 1979, 1994; Platt and Connell 2003; Sousa 1979). 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 (Gibson 1989; Hobbs and Huenneke 1992; Huntly and Inouye 1988; Reichman and Seabloom 2002b; Seabloom and Richards 2003) as well as granivory (Howe and Brown 2001; Howe et al. 2002) by mammals are forms of disturbance that shape

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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 and Richards 2003). Another pattern caused by disturbance is a successional mosaic, a collection of patches at various stages along the same successional trajectory (Chesson and 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 and Connell 2003; Seabloom and 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 we 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 and Seabloom 2002a, 2002b). These alterations to the ecosystem can have cascading influences on many types of organisms, including the engineering organism itself. We 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.

We 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 m^2) 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 we studied, discrete disturbed patches existed within a continuous matrix habitat.

We 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, we 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, we 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, we expected greater similarity among burrow patches than among matrix patches. If a successional mosaic existed, we expected the drawdown of resources to vary among burrows, thus increasing the spatial heterogeneity of resources in the metacommunity. At the ecosystem level, we expected reduced plant uptake and increased mineralization on burrows to increase the mean level of available resources. We discuss the effects of burrows on resources in the context of ecosystem engineering.

Materials and 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 and Getz 1994) and have a mean aboveground area of 5.7 m^2 (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

We 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 our study site is representative of the dominant current land cover in the regional landscape (Jog et al. 2006).

Most of the site has 3–7% slopes and Pawnee clay loam soils (Dickey et al. 1977). The site was taken out of agricultural production in the mid-1970s and has not been managed since 1998 when it was mowed (D. 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, we 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 and Kalisz 1992; Kalisz and Davis 1992). We marked all visible burrows ($N = 90$) in their centers with identifying pin flags and recorded their geographic location with a Garmin (Olathe, KS, USA) GPS 76 (accuracy < 5 m).

Of the 90 burrows, 30 were randomly selected for observation. We 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, we 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

We identified plant species from 11 to 14 June 2003 in 1-m^2 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, we 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). We 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. We 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 (Valencia, CA, USA) 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.

We 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 into 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, we 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, we 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.

We 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. We used 16 plots from each group to calculate the CV for LAI. We 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, we 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. We 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 arcsine 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 $1/D$), we 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, we 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, we 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. We 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), we 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 $-\ln(D)$.

We further analyzed metacommunity patterns by using community similarity indices to describe community similarity among burrows and among matrix plots. We 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. We calculated the difference between mean burrow similarity and mean matrix similarity (D_s) for both similarity indices:

$$D_s = S_{matrix} - S_{burrow} \tag{1}$$

A similarity value of $S = 0$ indicates that the two communities have completely different compositions, whereas a value of $S = 1$ indicates that the two communities have identical compositions. A positive value of D_s demonstrates that the matrix plots are more similar to each other than the burrow plots. A negative value of D_s shows that the burrow plots are more similar to each other than the matrix plots. We 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), we 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). We 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).

We used Fisher's exact test of two-by-two contingency tables to determine the association of individual species with burrow or matrix plots (Sokal and 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, 10.0 m).tpb 1

Soil and canopy resources

Soils from burrows had lower bulk densities, higher total carbon and nitrogen contents, and lower C:N ratios than those from matrix plots (Table 1). Burrow soils were marginally drier than matrix soils ($P = 0.051$; Table 1). Burrows had more visible bare ground (Table 1), lower grass biomass, and lower litter accumulation (Table 1). Total live biomass and forb biomass were not different

Table 1 Group means, one standard error, and results of paired *t*-tests (*df* = 30) for resource variables

Resource	Burrow mean	Matrix mean	*t*
Soil bulk density (g/m³)	480 ± 10	540 ± 10	−4.72**
Soil moisture (% volumetric 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**

* $P < 0.05$, ** $P < 0.005$

between plot types (Table 1). Plant tissue from burrows had higher nitrogen and lower C:N than that from matrix plots (Table 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). 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 bur-

Table 2 Coefficient of variation (CV) over burrow and matrix plots for ten resource variables. Asterisks indicate significantly greater CVs based on a two-tailed test and resampling data 1,000 times

Resource	Burrow CV	Matrix CV
Soil bulk density (g/m³)	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

* $P < 0.05$, ** $P < 0.005$

rows, 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. 1c). This effect was entirely due to differences in species richness (S) because community evenness ($E_{1/D}$) did not differ significantly (Fig. 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 ($S = 11.8 + 0.0861 \times$ bare ground; $R^2_{adj} = 12.9$). Soil carbon was the best predictor of $E_{1/D}$ ($E_{1/D} = 0.535 - 0.112 \times$ soil carbon; $R^2_{adj} = 12.4$) and 1/D ($1/D = 6.79 - 1.43 \times$ soil carbon; $R^2_{adj} = 9.6$). 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. 1a). $E_{1/D}$ and 1/D were significantly greater over all burrows than over all matrix plots (Fig. 1b,c). H, E, 1−D, and −ln (D) showed qualitatively similar significant differences.

The difference in Sorenson's similarity index between burrow and matrix patches (D_{s_1}) was negative, but not significantly negative ($D_{s_1} = -0.048$, $P > 0.10$), demonstrating that, based on species presence–absence only, community similarity did not differ significantly among burrow plots and matrix plots. This result was
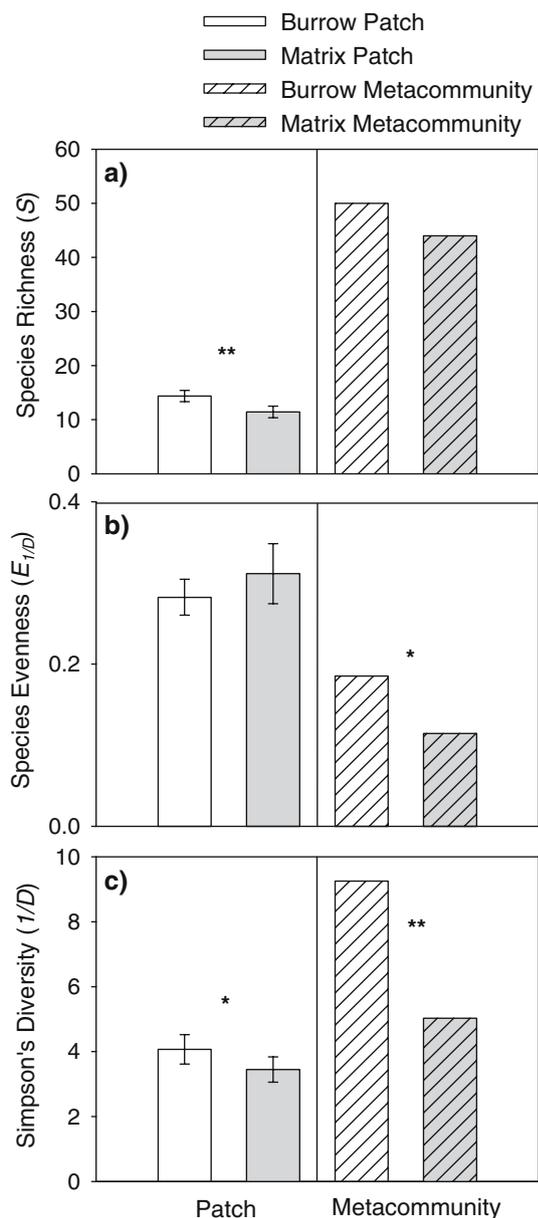
Fig. 1a–c Results from paired *t*-tests for patch-scale diversity and randomization tests for metacommunity-scale diversity (**a** species richness; **b** species evenness; **c** Simpson's diversity). * $P < 0.05$, ** $P < 0.001$

hereafter. Of the five species significantly associated with burrows, four were annual or short-lived perennial forbs (Table 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 4). Only one species, *Ambrosia*, was associated with matrix plots (Table 3). Its relative cover was greater on matrix plots than burrow plots (Table 4), and it is an annual forb.

The identity of dominant species varied more among burrows than matrix plots (Table 5). There were three species with >50% relative cover on burrow plots, and only one, *Bromus inermis*, on matrix plots (Table 5). Ten species had between 30 and 50% relative cover on burrow plots, compared to seven species on matrix plots (Table 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 our results, we 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

Our 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 undisturbed matrix (Table 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 and Baskin 1998). In contrast,

qualitatively similar for all other presence–absence indices tested. In contrast, D_{s_2} was significantly positive ($D_{s_2} = 0.14$, $P < 0.001$) 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 3; we will refer to them by their genus names

Table 3 Species associated with plot types. Significant results of Fisher's exact test for 21 species

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

* $P < 0.05$, ** $P < 0.005$, [+]P < sequential Bonferroni P-value for 21 tests

Table 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

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

* $P < 0.05$, ** $P < 0.005$

Ambrosia, the species associated with matrix plots, is a spring-germinating annual and undergoes seed dormancy in late spring or early summer (Baskin and Baskin 1998). In at least one study, disturbance in the fall increased populations of *Ambrosia*, but disturbance in early summer did not (Squiers 1989). We suggest that the timing of disturbance affects the species present in the grassland we 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 our 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 and Bartolome 2002; Seabloom and Richards 2003). In our 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 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 we observed are consistent with two potential processes occurring in the metacommunity: (1) asynchrony of successional pathways among

Table 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%			
Poa pratensis L.	Kentucky bluegrass	2	0
Solidago canadensis L.	Canada goldenrod	2	0
Sporobolus compositus (Poir.) Merr.	Dropseed	1	0
Bromus inermis Leyss.	Smooth brome	0	9
Relative cover 30–50%			
Bromus inermis Leyss.	Smooth brome	10	11
Poa pratensis L.	Kentucky bluegrass	4	1
Apocynum cannabinum L.	Hemp dogbane	3	1
Solidago canadensis L.	Canada goldenrod	3	5
Sporobolus compositus (Poir.) Merr.	Dropseed	3	2
Carex sp. L.	Sedge	1	0
Carduus nutans L.	Musk thistle	1	0
Cornus drummondii C.A. Mey.	Roughleaf dogwood	1	0
Schedonorus phoenix (Scop.) Holub	Tall fescue	1	0
Brickellia eupatorioides (L.) Shinners	False boneset	1	0
Asclepias verticillata L.	Whorled milkweed	0	3
Toxicodendron radicans (L.) Kuntze	Poison ivy	0	1

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 (Chesson and Huntly 1997; Huntly and Inouye 1988; Tilman 1983), which is consistent with our 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) Our 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 and Goldberg 1989). The abundance of bare ground on burrows may result in increased soil temperatures that could lead to greater water evaporation.

We 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 and 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). We suspect that the greater total N observed on burrows largely reflects increased inorganic N, the form usable 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.

We 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. We 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. We did not find an effect of disturbance on mean light levels, but we 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 (Glenn-Lewin et al. 1990; Grubb 1977; Inouye et al. 1987; Platt 1975). 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 and 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 (Huntly and Inouye 1988; Tilman 1983). We 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 that they cultivate species they prefer to eat (Huntly and Inouye 1988; Reichman and Seabloom 2002b). In general, prairie voles exhibit little species preference, eating species in proportion to their abundance in the community (Pascarella and Gaines 1991). Of the six species that were associated with burrow or matrix plots in our 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 and Gaines 1991). Studies of meadow voles suggest that they prefer to eat large-seeded species (Howe and Brown 2001). The burrows we studied had a higher occurrence of small-seeded species (Table 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 (Huntly and Inouye 1988; Platt 1975) or release from competition are more likely to be mechanisms that allow these fugitive species to be locally abundant.

Voles do not appear to engineer the species available on their burrows, but our 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 and Batzli 1978; Getz et al. 2001). We observed higher nitrogen and lower C:N in aboveground biomass collected from burrows, which indicates a higher nutritional quality of vegetation on burrows than vegetation 5 m from burrows. We 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, we are 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.

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