

EFFECTS OF CONNECTIVITY AND REGIONAL DYNAMICS ON
RESTORATION TRAJECTORIES FOR SMALL MAMMAL COMMUNITIES ON
MIDWESTERN GRASSLANDS

BY

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THESIS

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ABSTRACT

Grasslands are among the most imperiled of the North American ecosystems, with $\leq 1\%$ of tallgrass prairie remaining. The State Acres for Wildlife Enhancement (SAFE) is a national conservation program that converts agricultural fields into grasslands with the primary focus on improving habitat for high priority wildlife species. Because small mammals can be important indicators of ecosystem function, I sampled small mammal communities to evaluate restoration efforts under the SAFE program in Illinois. I livetrapped small mammals during 3 summers (2009-2011) on plots that were recently seeded, seeded 1-4 years prior to sampling, or established references (>10 yrs old). Overall, the dominant species were the deer mouse (*Peromyscus maniculatus*), prairie vole (*Microtus ochrogaster*), and meadow vole (*Microtus pennsylvanicus*); which combined represented 92-97% of total captures each year. Typical restoration trajectories for small mammal communities included a shift over time from dominance by generalist *Peromyscus* to communities that included substantial numbers of *Microtus*. During the first year of community assembly following restoration, the abundance of *Microtus* depended on spatial connectivity provided by linear habitats (roadside ditches and grass waterways) within 300 m, which probably served as temporary habitats and movement corridors. Patch size and seeding type (cool-season versus warm-season grasses) were not predictors of initial restoration trajectories. In 2011, populations of *Microtus* experienced a severe regional decline that might have reflected multi-year population cycles. During the crash, most remaining voles occurred on restored SAFE grasslands but not on established grasslands. This surprising outcome suggests young restoration plots could function as refuges for voles during population declines in agricultural landscapes in the Midwest region. Overall, my study highlights the need for adopting landscape mosaic approaches in ecological restoration.

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GENERAL INTRODUCTION

Due to decline of native grasslands ($\leq 1\%$ of tallgrass prairie remains) mainly from the expansion of agriculture, populations of many native animal species in North America are plummeting (Howe 1994; Samson & Knopf 1994; Camill et al. 2004). For instance, North American grassland bird species have shown widespread declines that range from 25-65% between 1980 and 1989 (Knopf 1992) likely due to the fragmentation and removal of native prairie within agricultural landscapes (Brennan & Kuvlesky 2005). Federal and state grassland conservation programs have been created to convert low-quality agricultural fields into habitats that are more beneficial for the ecosystem, and in many cases wildlife (Fletcher & Koford 2002; Richardson 2010). When evaluating restoration efforts, it is imperative to assess the local wildlife to quantify the impacts the conservation program is having on the ecosystem as a whole. Animal biodiversity can alter ecosystem productivity and services through top-down effects on vegetation that can influence a landscape from nutrient runoff and erosion to sequestering carbon dioxide (Balvanera et al. 2006; Donald & Evans 2006; Tilman et al. 2006). Creating grassland habitats to improve wildlife biodiversity will recover these ecosystem services while yielding benefits such as biological pest control, organic waste recycling, pollination, harvest of food, and ecotourism. These ecosystem services from restored grasslands could generate billions of dollars in annual economic and environmental benefits in the United States alone (Pimentel et al. 1997; Losey & Vaughan 2006).

State Acres for Wildlife Enhancement (SAFE; United States Department of Agriculture 2008) is a conservation program that converts agricultural fields into grasslands in select areas with the primary focus on re-establishing wildlife populations. This program is similar to the Conservation Reserve Program (CRP), but unlike CRP whose main focus was to prevent soil

erosion and the runoff of nutrients, SAFE focuses on increasing the abundance of grassland wildlife through habitat restoration. In common with CRP parcels, SAFE parcels are often located on highly erodible land. There are 657,326 ha of SAFE land nationwide, with 11,458 ha in Illinois. In Illinois, there are 31 township-sized focal areas split into the Grand Prairie Natural Region (22 focal areas) and the Southern Till Plain Region (9 focal areas). Focal areas in the Grand Prairie region were selected primarily to improve habitat conditions for game birds such as ring-necked pheasant (*Phasianus colchicus*) and northern bobwhite (*Colinus virginianus*) as well as declining songbirds. Focal areas in the Southern Till Plain region were selected primarily based on improving habitat and landscape connectivity for greater prairie-chickens (*Tympanuchus cupido*) and songbirds. In both regions, focal areas were chosen based on the amount of existing grassland in the area, the lack of forest habitat in the area, and the amount of area with highly erodible land.

To restore grassland ecosystems effectively, one must take a landscape approach. Unfortunately, many restoration studies focus solely on site-level habitat factors and do not consider how landscape context could affect restoration trajectories (Brudvig 2011). In nature, many grasslands are likely part of a loose network of populations, which together form a metapopulation linked through dispersal (Hanski & Ovaskainen 2003). However, limited dispersal in fragmented landscapes can hinder the recolonization of patches (Bakker & Berendse 1999). The probability of regional population survival also increases as size of the patches increases (Harrison & Fahrig 1995). Habitat quality and landscape structure between patches could also affect the connectivity of patches (Wiens 1997; Schooley & Branch 2007) and the general migration rate (Åberg et al. 1995). Understanding landscape-level factors and constraints of patch size, landscape connectivity, and vegetation composition and structure (i.e.,

habitat quality) on the persistence of wildlife should aid in the planning and management of restored grassland patches in agricultural landscapes.

Patch Size

Determining an optimal patch size for grasslands has been a critical factor when evaluating restoration success, because if a patch is too small, then it will become a population sink that cannot sustain a local population without constant immigration (Buechner 1989). Enlargement of existing plots provides a higher percentage of occupied habitats and decreases the extinction probability of local populations (Scott et al. 2001; Langevelde et al. 2002). However, no consistent density-area relationship operates over all systems of patches (Bowers & Matter 1997). That is, each species will have a different “optimal” patch size based on life-history traits, dispersal ability, and home-range size. The species-area relationship also shows that as a patch increases in size the number of species that occupy that patch increase rapidly at first, but then slows down as areas become larger (Lomolino 2001). Assisting land managers in identifying a critical lower patch size would be a key step in establishing a healthy small mammal community on restored grasslands.

Landscape Connectivity

Small mammal presence and abundance are not determined only by patch size, but by the connectivity of habitat patches to other patches within the surrounding landscape (Lidicker 1994). Agricultural practices have increased the patchiness of the landscape while simultaneously fragmenting wildlife habitat, making dispersal by small mammals difficult (Graetz 1994). Wildlife species make movement decisions that are based on environmental

factors at both local and landscape scales. Unfortunately, there is inadequate information on how movement behavior and dispersal of many species are affected by landscape structure (Wiens et al. 1993; Hanski & Thomas 1994). However, even newly created grassland plots that appear relatively isolated by agricultural fields from large source populations still receive immigrants over time. For this reason, the investigation of remnant habitats as sources of dispersers is of great interest.

Vegetation structure and composition

Vegetation structure is crucial in explaining the abundance and distribution of small mammals (Lin & Batzli 2001; Moro & Gadal 2007). Several studies conclude that total small mammal biomass is typically greatest at sites with high cover, low at sites with intermediate cover, and high again at sites with low cover (Grant & Birney 1979; Michel et al. 2006). However, species diversity tended to be low in agricultural landscape fields (such as corn and soybean) with poor vegetation cover most of the year (Michel et al. 2006). Identifying vegetation structure that yields the most diverse small mammal community could facilitate attracting target species to a restored grassland. For example, deer mice (*Peromyscus maniculatus*) favor landscapes with less cover and avoid high cover vegetation such as brome monocultures (Heske 1999). Meadow voles (*Microtus pennsylvanicus*) prefer relatively tall grass vegetation structures, because they nest aboveground on grass nests, whereas prairie voles (*Microtus ochrogaster*) nest in burrows below ground and are primarily concerned with the presence of forbs rather than protection from vegetation cover (Klatt & Getz 1987; Lin & Batzli 2001; Getz et al. 2005). Habitat preferences of voles could influence their use of newly restored grassland plots dominated by warm- versus cool-season grasses. Although there are no

documented general nutritional preferences between warm- or cool-season grass types for voles, cool-season grasses germinate a few months before warm-season grasses (Bramble & Bramble 2008) and could influence early colonization by voles. Species composition of plant communities can also affect habitat selection by small mammals. For instance, plant species richness can explain the greatest part of total variation of small mammal community composition (Michel et al. 2007). Habitat selection by prairie voles can be greatly influenced by the presence of forbs, which are an essential nutrient source (Getz et al. 2005). A diverse mixture of vegetation species could result in greater small mammal diversity.

Study Significance

Although many studies have investigated the effects of grassland restoration on wildlife, there is a lack of information regarding initial colonization and persistence of small mammals at recently created habitat patches (Stone 2007). Understanding dynamics of small mammal communities during early stages of restoration is important to maintain a sustainable population because restoration programs include sites of various ages due to landowners enrolling at different times. My study takes a landscape approach that includes a focus on how landscape connectivity affects initial restoration trajectories, which is rare for restoration studies (Brudvig 2011). Information on colonization and community assembly will assist land managers in creating grasslands that have a diverse and sustainable small mammal population that can serve as food sources for Illinois state endangered raptors such as short-eared owls (*Asio flammeus*) and northern harriers (*Circus cyaneus*) as well as other carnivorous species (Preston 1990; Korpimäki & Norrdahl 1991).

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INTRODUCTION

Native grasslands are among the most imperiled of North American ecosystems, with $\leq 1\%$ of tallgrass prairie remaining, largely due to the expansion of agriculture (Howe 1994; Samson & Knopf 1994; Camill et al. 2004). In response, state and federal agencies have initiated programs to create and restore grasslands (Fletcher & Koford 2002; Richardson 2010). State Acres for Wildlife Enhancement (SAFE; United States Department of Agriculture 2008) is a national conservation program that converts agricultural fields into grasslands with the primary focus on improving habitat for high priority wildlife species. I monitored small mammal communities on newly created grassland plots in the SAFE program to provide a broader perspective on how these restoration efforts are affecting biodiversity and density. Because agricultural conservation programs (e.g., USDA's Conservation Reserve Program) create a mosaic of parcels of different ages due to staggered entry over time, information on early stages of restoration is necessary for understanding overall population dynamics across landscapes.

Small mammals are a relevant focal group for evaluating conservation programs because of their sensitivity to habitat change (Clark 1989; Bock et al. 2002; Stone 2007). Moreover, small mammals can have substantial top-down influences on vegetation (Getz 1986; Hambäck et al. 2004; Howe & Lane 2004) and serve as important prey for predators including Illinois state endangered raptors such as short-eared owls (*Asio flammeus*) and northern harriers (*Circus cyaneus*) as well as snakes (Preston 1990; Korpimäki & Norrdahl 1991). Hence, small mammals form a crucial link in trophic food webs of grassland ecosystems and can be indicators of ecosystem stability (Clark 1989; Stone 2007). Small mammal communities in Midwestern grasslands have low species diversity often with 3 to 5 species at a patch (Getz & Hofmann 1999; Heske 1999). The deer mouse (*Peromyscus maniculatus*) is a common habitat generalist

that persists in agricultural fields and in restored grasslands just after seeding (Henderson & Sample 1995; Getz & Hofmann 1999; Stone 2007). In contrast, both prairie voles (*Microtus ochrogaster*) and meadow voles (*M. pennsylvanicus*) are common in established grasslands but typically absent from agricultural fields (Howe et al. 2006; Stone 2007). A shift in dominance from deer mice toward a community co-dominated by voles is the expected trajectory for a successful grassland restoration project in the Midwest.

Potential constraints to restoration of grassland ecosystems include site conditions, landscape factors, and historical contingencies (Brudvig 2011). Vegetation structure and composition are site-level factors that often explain the distribution and abundance of small mammal species (Grant & Birney 1979; Raymond & Porter 1986; Lin & Batzli 2001; Getz et al. 2005; Moro & Gadal 2007). Cool-season grasses germinate a few months before warm-season grasses (Bramble & Bramble 2008). Thus, cool-season grasses could provide higher cover and a better food supply for colonizing *Microtus* during initial restoration stages.

Landscape factors such as patch size, context, and connectivity should be consequential for restoration processes but are generally ignored in empirical evaluation (Brudvig 2011). Species have critical, minimum space requirements that must be met to persist locally, and effects of patch size constantly fluctuate with changes in resource availability and population density (Gaines & McClenaghan 1980). Large habitat patches not only tend to have a greater number of species (Lomolino 2001), they also are more likely to be colonized (i.e., “target effect”; Hill et al. 1996; Schooley & Branch 2009). Presence and abundance of a species in a habitat patch also may depend on connectivity of the surrounding landscape (Taylor et al. 1993; Crooks & Sanjayan 2006; Schooley & Branch 2009). Hence, grassland remnants that surround restoration areas have the potential to affect colonization rates of grassland species (Davis et al.

2007). Moreover, linear elements such as roadside ditches and grass waterways can serve as habitat refuges and movement corridors for grassland small mammals in agricultural landscapes (Delattre et al. 1992; Gorman & Reynolds 1993; De Redon et al. 2010). In the Midwest, prairie voles and meadow voles are often associated with ditch habitat (Getz et al. 1978; Klatt & Getz 1987; Cummings & Vessey 1994; Kirsch 1997). Rapid immigration of voles into newly created grasslands would suggest use of linear habitat elements as sources containing resident individuals, corridors channeling dispersers from larger grassland patches, or both. Insights on whether linear habitats are used mainly as temporary habitat or corridors can be gained by investigating sex ratios of individuals. For instance, prairie voles that are dispersers have a male-biased sex ratio, whereas residents do not (Solomon & Jacquot 2002; Smith & Batzli 2006). Therefore, linear habitats functioning as corridors should include voles with a male-biased sex ratio.

Multiannual oscillations for species such as voles, which are an indicator group for established grasslands, complicate interpretations of restoration outcomes. Voles and lemmings display tremendous variation in densities among years and can exhibit 3- to 4-year cycles (Getz et al. 2001; Ims et al. 2008). Population cycles of small mammal species have been investigated for many years (e.g., Charles Elton 1924), but much controversy still exists regarding the cause of cycles. Cycles could be driven by multiple processes including predation, food availability, and silica defenses in grasses (Cole & Batzli 1979; Krebs 1996; Massey et al. 2008; Dalkvist et al. 2011).

I examined potential restoration constraints for small mammals to assist future grassland restoration efforts by land managers. Specifically, I tested the following hypotheses and predictions: (1) Dominance of warm-season versus cool-season grasses will affect habitat

selection by small mammals because of differences in vegetation structure and composition. Grassland mammal species will colonize cool-season grass plots earlier in summer compared to warm-season grass plots. (2) Colonization and community assembly by small mammals will depend on patch size because of area requirements and target effects. The speed of expected restoration trajectories (i.e., shift toward community assembly of established references) will be related positively to patch size. (3) Restoration trajectories will depend on landscape connectivity due to dispersal constraints of grassland species. Abundance of voles on restored plots will be related positively to connectivity from established grasslands and linear habitats. My results demonstrate the difficulty of separating community dynamics driven by restoration processes from those inherent to multiannual population fluctuations, and the surprising role of young restoration plots as habitat refuges during regional population declines.

METHODS

Sampling Design and Study Plots

During 2009-2011, I sampled 28 plots that were clustered in six sampling sites located in Illinois within landscapes dominated by row-crop agriculture (Fig. 1; 11 plots in Southern Till Plain region, 17 plots in Grand Prairie region). Individual plots were sampled for one year ($n = 7$), two years ($n = 13$), or three years ($n = 8$). Most restoration plots were in the SAFE program ($n = 10$), whereas plots at the Saybrook site ($n = 5$) were seeded by the Illinois Department of Natural Resources (IDNR) using similar methods. SAFE plots were required to be in row crop production 4-6 years from 1996-2001 and were seeded with cool season grasses or warm season grasses during mid to late April. I classified 13 restored grasslands as ‘new’ plots when sampled during the first year after seeding (4 in 2009, 8 in 2010, 1 in 2011). I classified 14 restored

grasslands as ‘intermediate’ plots that were 1-4 years old when sampled (2 in 2009, 4 in 2010, 14 in 2011). I also included 13 established plots (seeded >10 years before sampling) to serve as references (12 in 2009, 5 in 2010, 7 in 2011). Plot sizes were measured using digital orthophotographs from 2005 updated with current digital orthophotographs from Google Earth (ArcMap; Esri 2010).

Small Mammal Sampling

Each plot was livetrapped for 3 consecutive nights in early summer (2 June – 25 June 2009, 25 May – 8 July 2010, 18 May – 23 June 2011) and again in late summer (10 July – 13 August 2009, 21 July – 15 August 2010, 28 June – 11 August 2011). On each plot, I normally established 6 transects with each containing 15 trap stations (spaced 7 m apart) for a total of 90 traps per plot each night. However, 11 plots contained only 2 to 4 transects due to area constraints. Sherman live traps were baited with birdseed in the evening and checked the next morning. Traps remained closed throughout the day. For analyses using sampling effort, traps sprung overnight were accounted for by subtracting 0.5 trap-nights for each sprung trap (Beauvais & Buskirk 1999). For each captured individual, I recorded species, age (juvenile, subadult, or adult), sex, and body mass. To keep track of recaptures and to estimate total individuals caught, I applied batch marks the first two nights of a trapping period by clipping fur on the hindquarters of all captured individuals.

Landscape Connectivity

To determine whether linear, grassy habitats could promote connectivity by serving as sources or corridors for small mammals, I sampled small mammals in roadside ditches and grass

waterways. Width of roadside ditches ranged from 3.7-11.2 m, and width of grass waterways ranged from 6.9-36.8 m. I sampled linear habitats from 17 June – 8 August 2010 (14 ditches and 5 waterways) and from 26 July – 17 August 2011 (18 ditches and 8 waterways). The total of 31 linear habitats trapped over the two years (9 ditches and 5 waterways were trapped both years) were sampled using a transect of 15 Sherman traps spaced 7 m apart as on the study plots. I trapped each linear habitat twice each year (only once for the 6 Southern Till Plain linear habitats) for 3 consecutive nights unless excessive rain posed a serious risk to captured small mammals. I tested whether sex ratios of species differed from parity using binomial tests (PROC FREQ; SAS Institute Inc. 2009) for linear habitats and study plots for the two species with adequate sample sizes (prairie voles in 2010, and deer mice in 2010 and 2011). I used only data from late summer for plots because that is when I sampled the linear habitats.

To measure structural landscape connectivity for plots, I used digital orthophotographs from 2005 (updated with current digital orthophotographs) to digitize established and restored grasslands, roadside ditches, and grass waterways within 300 m and 2 km of plot edges (ArcMap; Esri 2010). These two buffer sizes were chosen based on estimates of homing distances and natal dispersal distances for prairie and meadow voles that range from 127 m to 1.2 km (Mihok et al. 1988; Ostfeld & Manson 1996; Sutherland et al. 2000). Connectivity measures were calculated as the proportion of grassy habitat cover within buffers. For both buffer sizes, I calculated cover for only established grasslands (EST), only linear habitats (LIN), and all grassy habitats (ALL = EST + LIN). Hence, there were 6 connectivity measures in total. I recognize this measure could reflect both spatial connectivity and landscape context depending on the function of the linear habitats as either movement corridors or primary habitat for small mammals.

Vegetation Sampling

I classified each plot as dominated by cool-season grasses or warm-season grasses based on relative abundances of the three most common species (using visual estimates). Cool-season grasses included smooth brome (*Bromus inermis*), creeping bentgrass (*Agrostis stolonifera*), rye (*Secale cereale*), and fescue (*Festuca pratensis*). Warm-season grasses included giant foxtail (*Setaria faberi*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). I sampled 14 warm-season grass plots ($n = 10$ restored plots, $n = 4$ reference plots) and 14 cool-season plots ($n = 5$ restored plots, $n = 9$ reference plots).

More detailed vegetation sampling was conducted during summer 2010 and 2011. I used line-point intercept sampling (Brady et al. 1995) to estimate percent cover (grass, forb, woody debris, bare soil, moss, or rock). For most plots, a vegetation sampling transect (50 m long) was established 5 m away from and parallel to three trapping transects. For small plots, 1 or 2 vegetation transects were established. On each vegetation transect, I recorded the type of cover every meter. Thus, I sampled 150 total points for cover (3 x 50) on most plots. I use the plant cover data to ask (1) whether there were changes in vegetation between 2010 and 2011 associated with changes in small mammal communities (restricting the analysis to intermediate and reference plots sampled in both years), and (2) whether cover of grasses and forbs differed between cool-season and warm-season dominated plots during the first summer after seeding.

Statistical Analysis

I estimated relative abundances for each small mammal species for each 3-day sampling period using catch-per-unit-effort (CPUE) expressed as number of individuals per 100 trap-nights. For multivariate ordination of communities based on CPUE, I used the 3 most common

species each year from 2009-2011 (Table 1). I also removed all plots from analysis that had <10 total individuals for a given year (Appendix A: Table 1). I used non-metric multidimensional scaling (NMDS; PC-Ord version 6.0, MjM Software, Gleneden Beach, Oregon) to examine potential gradients in community structure among plot types and across years. For NMDS, I used the Bray-Curtis distance matrix and limited the dimensionality to two axes based on stress values.

To evaluate predictors of initial restoration trajectories, I used CPUE for *Microtus* (prairie voles + meadow voles) during the first year after seeding as the response variable because voles are grassland species common on established sites during normal conditions. I restricted the analysis to 2009-2010 ($n = 12$ sites) because of the extreme regional decline in vole abundances in 2011 (see Results). Because I sampled sites twice per year, I used repeated-measures, linear mixed models with maximum-likelihood estimation (PROC MIXED; SAS Institute Inc. 2009). I determined the appropriate covariance structure (first-order autoregressive) by fitting the full model under different covariance structures using restricted maximum-likelihood method and Akaike's information criterion corrected for small sample size (AIC_c ; Burnham & Anderson 2002). Potential predictors of *Microtus* CPUE included time (months since seeding), year (2009 or 2010), grass (cool-season or warm-season), area (ha), and connectivity. I used AIC_c to rank 31 candidate models that each included time and ≤ 2 additional predictors. Models with ΔAIC_c values ≤ 2 are considered competitive (Burnham & Anderson 2002). I evaluated residuals from the top-ranked model for normality using the Shapiro-Wilk test (PROC UNIVARIATE; SAS Institute Inc. 2009). Each of the six connectivity measures occurred in 4 models in a balanced fashion, so I used the sum of Akaike weights (ω_i) for those models to assess overall support for different connectivity metrics.

RESULTS

Abundance Dynamics: Grassland Plots and Linear Habitats

From 2009-2011, I captured 4,390 small mammals (3,072 individuals) from 11 species during 24,750 trap-nights. The three most common species (deer mouse, prairie vole, and meadow vole) represented 95.7% of the total individuals captured (Table 1). Small mammal abundances varied greatly between 2009-2010 and 2011 (Table 1, Fig. 2). In particular, abundance of *Microtus* (prairie and meadow voles combined) declined from 2009-2010 to 2011. Of the 91 voles captured in 2011, only 2 (2.2%) were from established reference plots and the remaining 89 (97.8%) were from restoration plots of intermediate age (Fig. 2). In contrast, abundance of deer mice increased from 2009-2010 to 2011 (Table 1). Deer mice represented 35% of the total individuals caught in 2009-2010 and 85.1% in 2011.

From 2010-2011, I captured 299 individuals of 8 small mammal species in linear habitats during 3,660 trap-nights (Appendix A: Table 2). The four most common species (deer mouse, prairie vole, northern short-tailed shrew, and meadow vole) represented 95% of the individuals captured. Abundance of *Microtus* declined substantially in linear habitats from 96 individuals in 2010 to only 2 individuals in 2011 (Fig. 2) despite increased trapping effort (1,590 trap-nights in 2010; 2,070 trap-nights in 2011). In linear habitats, *Microtus* represented 59.5% of the individuals captured in 2010 ($n = 161$), but only 1.5% of the individuals captured in 2011 ($n = 137$).

Sex Ratios

In 2010, the sex ratio of prairie voles in linear habitats differed from parity ($Z = 3.49$, $P = 0.001$, $n = 74$) and was male-biased (70.3% males, SE = 5.3%). In contrast, populations on

intermediate plots were female-biased (37.5% males, SE = 4.9%, $Z = -2.45$, $P = 0.014$, $n = 96$), and populations on new plots (50.0% males, SE = 6.9%, $Z = 0.00$, $P = 1.00$, $n = 52$) and reference plots (49.5% males, SE = 3.4%, $Z = -0.14$, $P = 0.892$, $n = 218$) had sex ratios not different from parity. The sex ratio of deer mice in linear habitats differed from parity in 2010 ($Z = 2.26$, $P = 0.024$, $n = 33$) and 2011 ($Z = 2.16$, $P = 0.031$, $n = 104$) and was male-biased (69.7% males, SE = 8.0% in 2010; 60.6% males, SE = 4.8% in 2011). Deer mice on new plots in 2010 also had a male-biased sex ratio (63.2% males, SE = 4.2%, $Z = 3.03$, $P = 0.002$, $n = 133$) but the sex ratio was not different from parity in 2011 (53.6% males, SE = 9.4%, $Z = 0.38$, $P = 0.706$, $n = 28$). Populations on intermediate plots in 2010 (46.0% males, SE = 8.2%, $Z = -0.49$, $P = 0.622$, $n = 37$) and 2011 (53.9% males, SE = 3.2%, $Z = 1.21$, $P = 0.225$, $n = 245$) and reference plots in 2010 (64.3% males, SE = 9.1%, $Z = 1.52$, $P = 0.131$, $n = 28$) had sex ratios that did not differ from parity. Deer mice populations on reference plots in 2011 were male-biased (67.6% males, SE = 7.7%, $Z = 2.14$, $P = 0.033$, $n = 37$).

Small Mammal Communities

Species richness increased on newly seeded plots from early summer ($\bar{x} = 1.62$, SE = 0.27) to late summer ($\bar{x} = 3.15$, SE = 0.30; Wilcoxon signed rank sum test, $S = 30.5$, $P = 0.0049$). Richness on intermediate and reference plots did not change substantially within years. Intermediate plots tended to have higher species richness for 2009-2010 ($\bar{x} = 3.42$, SE = 0.36, $n = 6$) compared to 2011 ($\bar{x} = 2.15$, SE = 0.19, $n = 14$) due to the regional *Microtus* decline. Reference plots followed a similar trend with species richness relatively high for 2009-2010 ($\bar{x} = 3.09$, SE = 0.20, $n = 13$) compared to 2011 ($\bar{x} = 1.21$, SE = 0.26, $n = 7$).

Species composition of small mammal communities across plot types reflected expected restoration trajectories during 2009 and 2010, but not in 2011 (Fig. 3). The proportion of captured individuals consisting of *Microtus* species increased with time since seeding for plots sampled in 2009 (0.161 new, 0.454 intermediate, 0.732 reference) and 2010 (0.224 new, 0.571 intermediate, 0.892 reference). In contrast, *Microtus* was a measurable component only on plots of intermediate age in 2011 (Fig. 3), albeit at reduced levels (0.157).

The NMDS ordination also indicated community structure of small mammals on restoration plots was moving over time toward that of reference plots prior to 2011 (Fig. 4; see Fig. 1 in Appendix B for full ordination). In 2009 and 2010, new plots were located in ordination space near the species score for deer mice, whereas intermediate plots were shifted toward reference plots located in ordination space near species scores for prairie voles and meadow voles (Fig. 4). In 2011, all plots were associated with species scores for deer mice.

For intermediate and reference plots sampled in both 2010 and 2011 ($n = 8$), grass cover did not vary between 2010 ($\bar{x} = 80.0\%$, $SE = 5.1\%$) and 2011 ($\bar{x} = 71.9\%$, $SE = 8.0\%$; $S = -9$, $p = 0.24$). Forb cover also was similar in 2010 ($\bar{x} = 18.6\%$, $SE = 4.9\%$) and 2011 ($\bar{x} = 26.5\%$, $SE = 7.5\%$; $S = 9.5$, $p = 0.21$). Therefore, the decline of *Microtus* in 2011 was not associated with an obvious change in general vegetation cover.

Predictors of Initial Community Assembly

Area and connectivity were highly variable among plots (Appendix B: Table 1). For my analysis of initial restoration trajectories on new plots ($n = 12$), size of plots ranged from 8.5 to 64.6 ha ($\bar{x} = 32.0$). Connectivity measured as the proportion of established grasslands within 300 m ranged from 0.07-0.28 ($\bar{x} = 0.17$) and established grasslands within 2 km ranged from

0.02-0.10 ($\bar{x} = 0.07$). Connectivity measured as the proportion of linear habitats within 300 m ranged from 0.01-0.12 ($\bar{x} = 0.06$) and linear habitats within 2 km ranged from 0.02-0.05 ($\bar{x} = 0.04$). Five plots were dominated by cool-season grasses and 7 plots were dominated by warm-season grasses. For new plots in 2010 for which I had vegetation cover data, I detected no differences in grass cover between cool-season plots ($n = 3$) and warm-season plots ($n = 5$) during either early summer (Kruskal-Wallis Test, $X^2 = 0.202$, $df = 1$, $p = 0.65$) or late summer ($X^2 = 0.022$, $df = 1$, $p = 0.88$; Appendix B: Fig. 2). Likewise, forb cover was similar between cool- and warm-season plots in early summer ($X^2 = 0.556$, $df = 1$, $p = 0.46$) and late summer ($X^2 = 0.022$, $df = 1$, $p = 0.88$). Across all new plots ($n = 8$), grass cover increased from early summer ($\bar{x} = 17.9\%$, $SE = 9.0\%$) to late summer ($\bar{x} = 43.0\%$, $SE = 9.5\%$; Wilcoxon signed rank Sum test, $S = 18$, $p = 0.0078$). Forb cover also increased from early summer ($\bar{x} = 19.3\%$, $SE = 4.6\%$) to late summer ($\bar{x} = 39.4\%$, $SE = 7.8\%$; $S = 15$, $p = 0.0391$).

Time since treatment and connectivity to linear habitats were the best predictors of relative abundance of voles on newly restored grasslands (Table 2, Fig. 5). The ΔAIC_c rankings revealed three competitive models ($\Delta AIC_c \leq 2$). The top two models included connectivity based on linear habitats within either 300 m or 2 km, and these had a better fit than the third-ranked model with only time (Table 2). Summed weights (ω_i) also were greater for connectivity measured for linear habitats within 300 m (0.250) and 2 km (0.220) compared to connectivity from established grasslands within 2 km (0.113) and 300 m (0.054), and all grassy habitats (linear + established) within 2 km (0.042) and 300 m (0.036). Based on the top-ranked model, vole abundance was related positively to time ($\beta = 1.188$, $SE = 0.383$) and connectivity ($\beta = 26.133$, $SE = 11.124$), and the normality assumption was not violated ($W = 0.935$, $P = 0.1231$).

DISCUSSION

Small mammal communities can assemble rapidly on newly restored grasslands within Midwestern agricultural landscapes. Colonization of restored plots by grassland species such as voles depended on landscape connectivity provided by linear habitats in the form of roadside ditches and grass waterways. Hence, my study represents a rare example in which a landscape constraint to biodiversity restoration was identified (Brudvig 2011). Extreme population fluctuations of voles, which likely represent multi-annual population cycles, complicated my ability to assess restoration success, but also suggested recently restored grasslands could serve as refuges for voles during regional declines.

The best model for predicting abundance of voles on newly restored grassland plots during the first year after seeding included time since treatment and cover by linear habitats within 300 m. This result indicates linear habitats in highly modified ecosystems provide a source of small mammals that can colonize new grasslands. Likewise, studies in Europe concluded that roadside ditches and grass waterways may function as habitat refuges for small mammals in agricultural landscapes (Delattre et al. 1992; Gorman & Reynolds 1993; Tattersall et al. 2002; De Redon et al. 2010; Sabino-Marques & Mira 2011). In my study system, further investigation is needed to determine the relative importance of linear habitats as sources of residents versus movement corridors (Bennett et al. 1994). The male-biased sex ratio of prairie voles in linear habitats (70% males), which contrasts with even or female-biased sex ratios on grassland plots, suggests linear habitats could be dispersal corridors for this species. These sex ratios agree with another study on prairie voles in Illinois in which dispersers were approximately 70% male but residents were 45% male (Smith and Batzli 2006). Sex ratios of deer mice also were male-biased in linear habitats, which suggests ditches and grass waterways

could function generally as dispersal corridors for small mammals. However, new plots in 2010 and reference plots in 2011 also were male-biased for deer mice, so the picture is less clear for this habitat generalist. Width of linear habitats could be important to their function as corridors. Grassland strips that are too narrow are typically avoided by voles, whereas wide corridors are hindered by cross-directional movements or aggression by conspecifics that take up residence in the corridors, creating a “social fence” (Hestbeck 1988; Andreassen et al. 1996; Smith & Batzli 2006). Movements of voles within linear habitats could also expose individuals to high predation rates (Peles & Barrett 1996; Smith & Batzli 2006). Despite these complexities, unmowed ditches and grass waterways likely contribute to persistence of grassland species in agricultural landscapes.

I detected no evidence that patch size or seeding type (warm- or cool-season grasses) strongly affected abundances of voles during the first year after seeding. Therefore, colonization and initial community assembly seemed unrelated to area requirements or target effects. The smallest patch of 1.55 ha might have exceeded any critical patch size for colonizing small mammals. Potential target effects (Hill et al. 1996) could have been muted by the strong influence of spatial connectivity from linear habitats. The lack of an effect of seeding type could be due to rapid growth of weedy species such as Canada goldenrod (*Solidago Canadensis*), horseweed (*Conyza Canadensis*), bull thistle (*Cirsium vulgare*), redroot pigweed (*Amaranthus retroflexus*), and wild carrot (*Daucus carota*) on warm-season plantings providing adequate cover for grassland mammals. These forbs could also have provided a good initial source of nutrition that is preferred by prairie voles (Getz et al. 2005).

Spatio-temporal dynamics of voles make assessments of restoration success for small mammals exceptionally difficult. Intended directional trajectories are overlaid on inherent

oscillations including possible 3- to 4-year population cycles. This interaction partly resets trajectories during years exhibiting population declines, while also turning references into moving targets. The drivers of vole population dynamics remain a mystery (Krebs 1996; Klemola et al. 2000), and climate change could further complicate the picture in some regions (Ims et al. 2008). The most intriguing result regarding the extreme population decline of voles in 2011 was the differential response among plot types. The vole decline was steepest on reference grasslands. As a result, of the remaining voles captured on plots in 2011, only 2% were on reference plots compared to 98% on restored plots. Hence, during years with high vole numbers, established grasslands and linear habitats serve as potential sources for colonizers to recently restored grasslands. During low density periods, however, restored grasslands could serve as habitat refuges. This hypothesis requires additional scrutiny, especially given that I do not know what mechanisms might produce the refuge effect for young restoration plots.

The main goal of the SAFE program is to restore target species on grasslands within focal areas chosen because of their connectivity and proximity to established grasslands. When attempting to restore grasslands for small mammals, which represent critical trophic links (Getz 1986; Cadenasso et al. 2002; Hambäck et al. 2003; Howe & Lane 2004; Moro & Gadal 2007), land managers should also focus on the connectivity provided by linear habitats. This management recommendation should apply to other taxa such as ground-dwelling arthropods and herpetofauna, and thus to animal biodiversity in general. Given the observed interplay between ages of restored plots and vole dynamics, land managers would benefit from creating a mixture of established and early successional stages of grasslands connected through linear habitats. In sum, my study highlights the need for a landscape mosaic approach to ecological restoration of small mammal communities in agricultural landscapes (Donald & Evans 2006).

SUMMARY

In a highly fragmented agriculturally-dominated landscape that has $\leq 1\%$ of tallgrass prairie remaining (Howe, 1994; Samson and Knopf, 1994; Camill et al., 2004), it is important to carefully implement a restoration effort. Small mammals, especially grassland species such as prairie and meadow voles, serve as indicators of ecosystem stability and health (Clark, 1989; Stone, 2007) and attract various predators including raptors and snakes to restored grasslands (Schmidt, 2008). My research indicates that linear habitats in the form of roadside ditches and grass waterways within a 300 m buffer are the strongest factor leading to an increase of voles on new restoration plots. With these results, I conclude that land managers need to consider the presence of un-mowed ditches and grass waterways when selecting plots to convert from agricultural fields to restored grasslands. In contrast, patch size and seeding type (warm- or cool-season grasses) had little effect on initial colonization of voles.

Regional dynamics including multiannual oscillations for voles, which are an indicator group for established grasslands, complicate interpretations of restoration outcomes (Getz et al., 2001; Ims et al., 2008). However, I found that established grasslands serves as source populations for prairie and meadow voles during years of high population density, whereas voles may rely on restored grasslands as refuge during periods of low population density. This finding indicates that we need to take a landscape mosaic approach to ecological restoration.

TABLES AND FIGURES

Table 1. Total number of individuals of each mammal species captured on restored grassland and reference plots in Illinois, 2009-2011.

Species	No. of Individuals		
	2009	2010	2011
Deer mouse (<i>Peromyscus maniculatus</i>)	402	399	653
Prairie vole (<i>Microtus ochrogaster</i>)	543	608	72
Meadow vole (<i>Microtus pennsylvanicus</i>)	145	100	19
Northern short-tailed shrew (<i>Blarina brevicauda</i>)	44	2	1
House mouse (<i>Mus musculus</i>)	13	9	1
Meadow jumping mouse (<i>Zapus hudsonius</i>)	0	1	14
Western harvest mouse (<i>Reithrodontomys megalotis</i>)	8	4	4
Thirteen-lined ground squirrel (<i>Spermophilus tridecemlineatus</i>)	6	5	3
White-footed mouse (<i>Peromyscus leucopus</i>)	5	2	0
Southern bog lemming (<i>Synaptomys cooperi</i>)	0	5	0
Long-tailed weasel (<i>Mustela frenata</i>)	0	4	0

Table 2. Ranking of repeated-measures, linear mixed models for evaluating factors affecting relative abundance of *Microtus* (prairie and meadow voles) on new restoration plots, 2009-2010. Predictors included T = time since treatment, G = grass type (warm- or cool-season), Y = year, A = plot area, LIN = connectivity based on linear habitats within either 300 m or 2000 m, and EST = connectivity based on established grasslands within 300 m or 2000 m. K = number of explanatory variables +3, and $\Delta AIC_c = AIC_c$ of model – minimum AIC_c , where AIC_c is Akaike’s information criterion corrected for small sample size. ω_i is the Akaike weight. Models with a $\Delta AIC_c \leq 4$ are presented.

Model	K	-2 Log-likelihood	ΔAIC_c	ω_i
T, LIN_300	5	98.4	0	0.222
T, LIN_2000	5	99.6	1.1	0.128
T	4	103.0	1.3	0.116
T, EST_2000	5	100.7	2.2	0.074
T, A, LIN_300	6	98.1	3.3	0.043
T, G, LIN_300	6	98.1	3.3	0.043
T, Y, LIN_300	6	98.4	3.6	0.037
T, EST_300	5	102.3	3.8	0.033

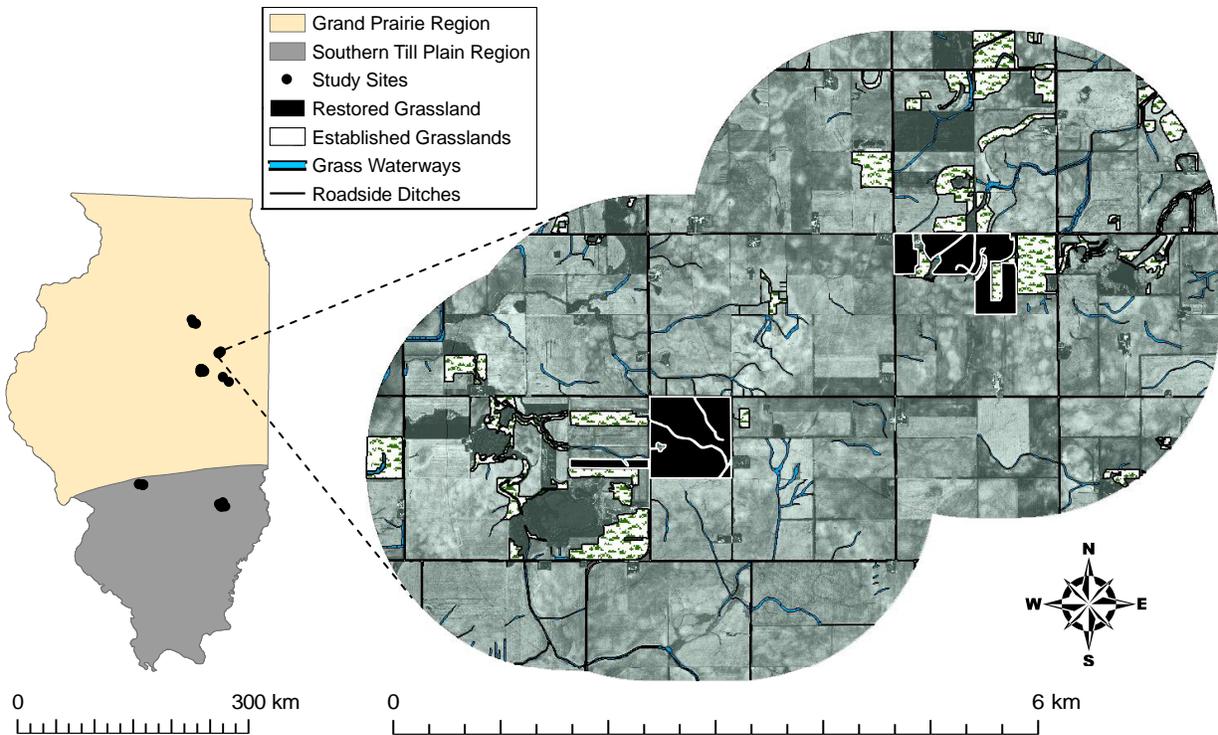


Figure 1. Location of 6 study site clusters that included 28 plots used to assess grassland restoration and small mammal communities in Illinois, 2009-2011. Inset shows 3 restored grassland plots at the Livingston site. Buffers (2-km radius) around each plot were used to measure spatial connectivity based on amount of established grasslands and linear habitats (grass waterways and roadside ditches).

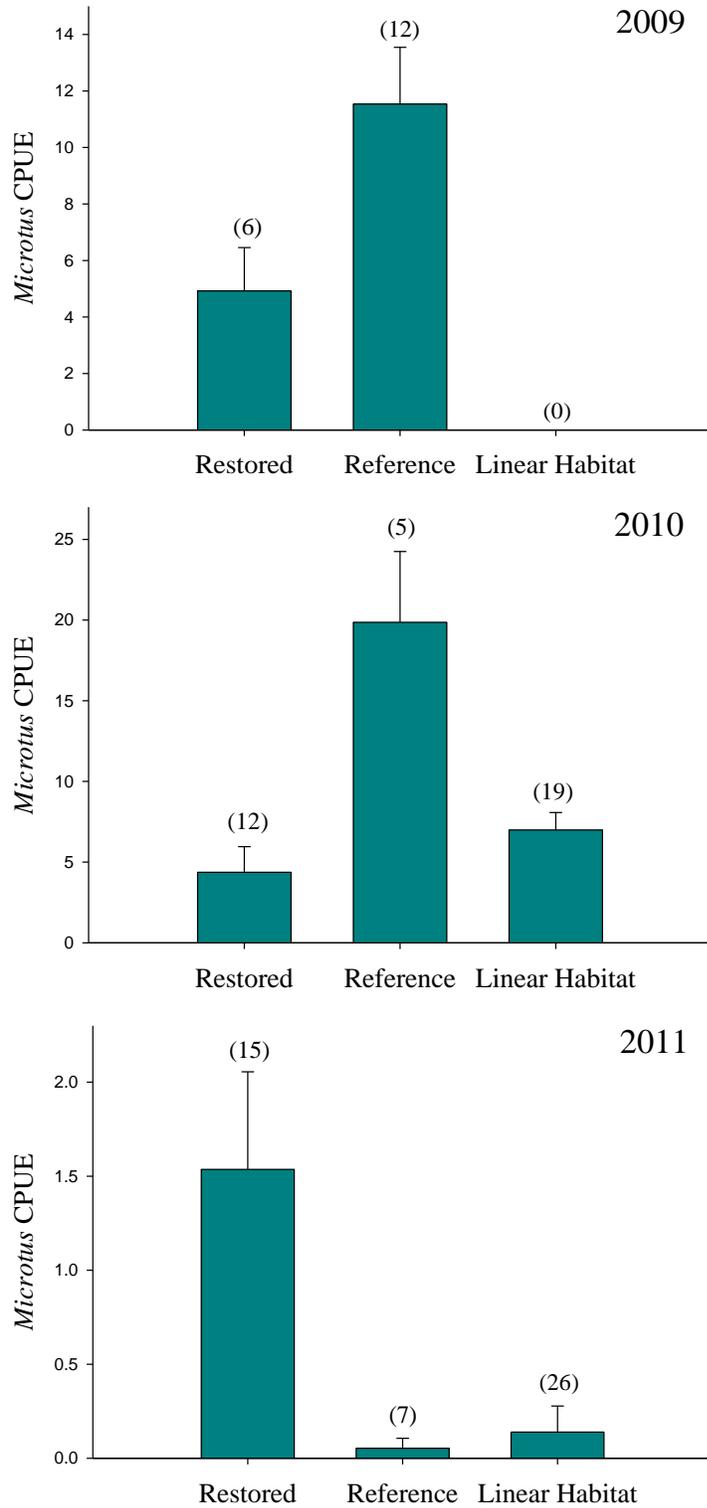


Figure 2. Mean (+1SE) catch-per-unit-effort (CPUE) of *Microtus* (*Microtus ochrogaster* and *M. pennsylvanicus*) during 2009-2011 on three plot types: restored (≤ 4 years since seeding), reference (> 10 years since seeding), and linear habitats (roadside ditches and grass waterways). Numbers above bars are sample sizes for plots. Note Y-axis scale changes among years.

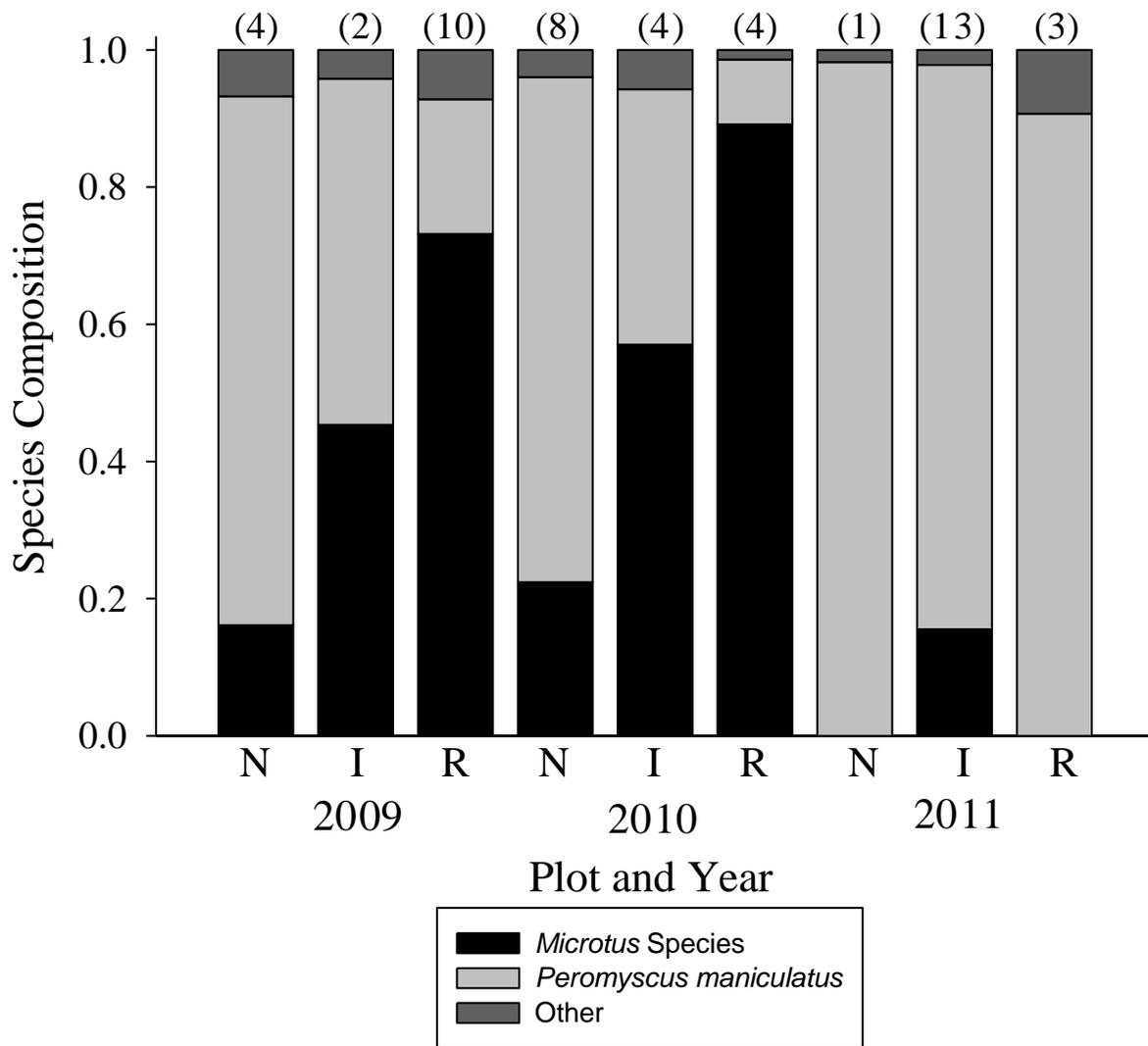


Figure 3. Proportion of the communities comprised of *Microtus* (*Microtus ochrogaster* and *M. pennsylvanicus*), *Peromyscus maniculatus*, and all other species combined based on catch-per-unit-effort. Grassland plots were classified as newly restored (N, <1 year since seeding), intermediate (I, 1-4 years since seeding), and reference (R, >10 years since seeding). Numbers above bars represent sample size for plots. Plots with <10 individuals total captured within a year were removed.

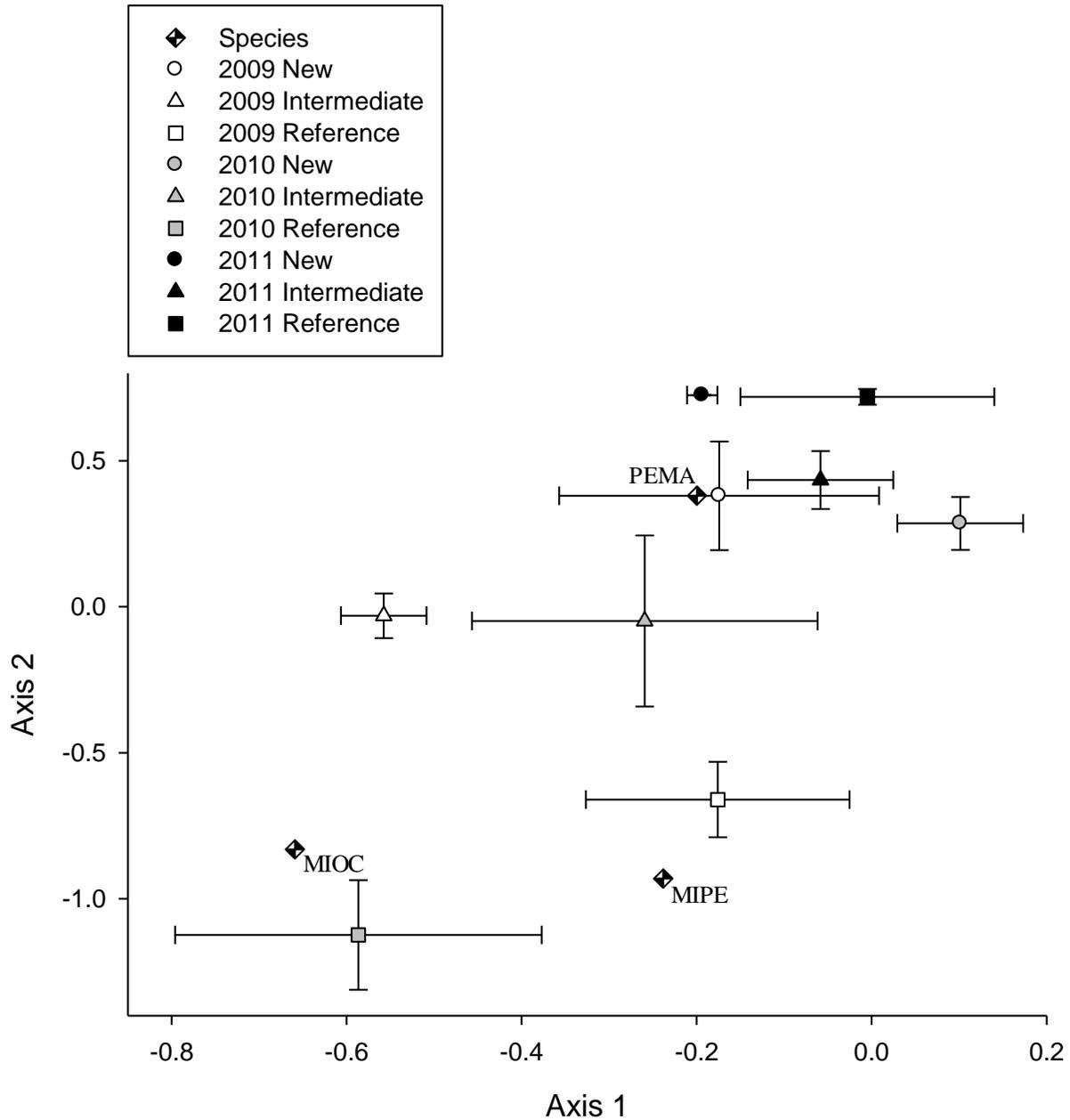


Figure 4. Non-metric multidimensional scaling of small mammal communities from 2009-2011. Mean scores (± 1 SE) are displayed for plots in three categories: new (<1 year since seeding), intermediate (1-4 years since seeding), and references (>10 years since seeding). Species scores are represented in which PEMA = deer mouse, MIOC = prairie vole, and MIPE = meadow vole. All plots with <10 individuals for a given year were removed from analysis.

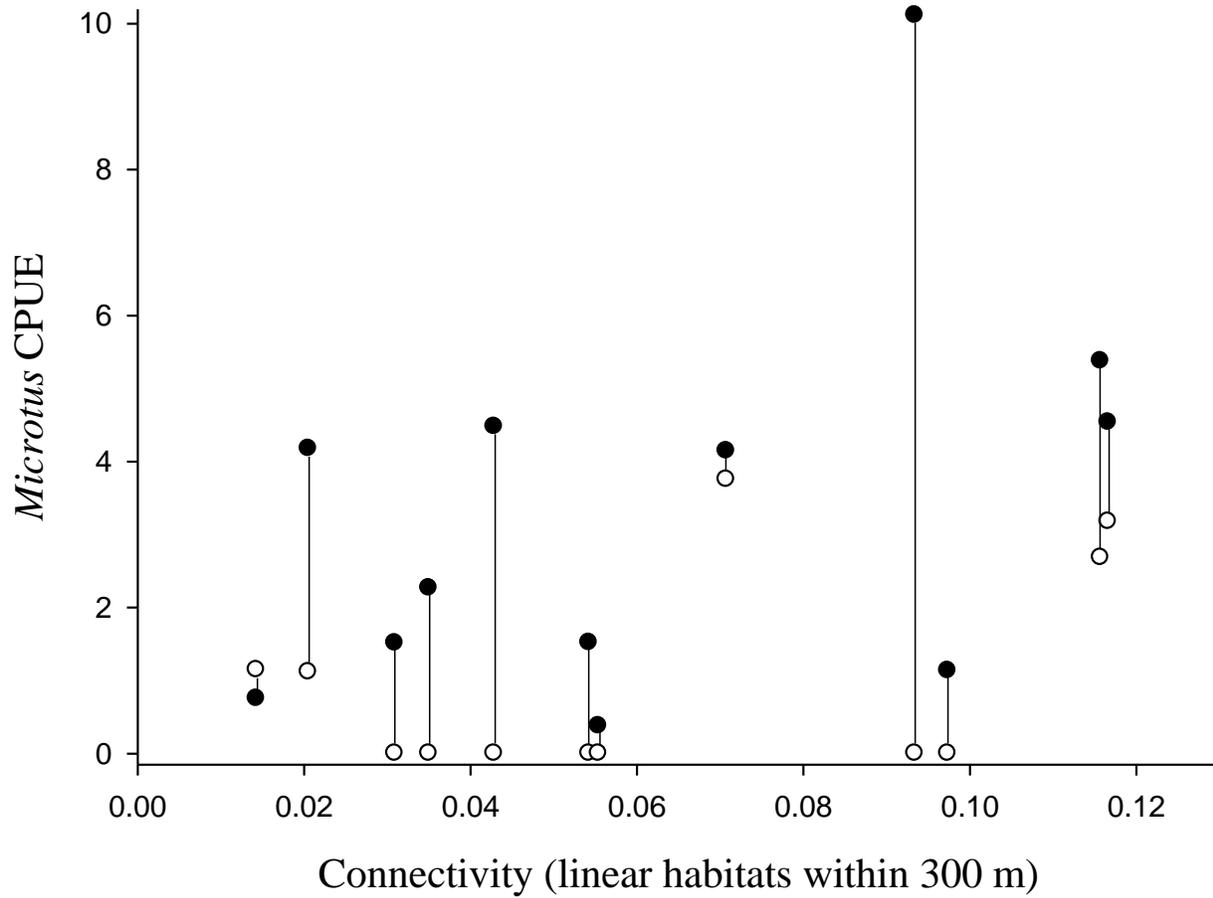


Figure 5. Relationship between relative abundance of *Microtus* (catch-per-unit-effort, CPUE, for prairie voles and meadow voles) and landscape connectivity on new restoration plots, 2009-2010. Lines between points signify changes in *Microtus* CPUE on individual plots between early (open circles) and late (closed circles) summer during the first year post seeding.

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APPENDIX A: Capture Results

Table A.1 Number of individuals captured and catch-per-unit-effort (CPUE) on each plot from 2009-2011.

Plot	2009		2010		2011	
	No. Individuals	CPUE	No. Individuals	CPUE	No. Individuals	CPUE
Old CRP East	59	22.69	56	21.17	21	8.22
Old CRP West	55	20.99	36	13.58	32	12.12
Radio North	97	18.79	.	.	48	8.96
Radio South	72	13.60	65	12.23	88	16.60
Anchor North	142	26.47	.	.	74	13.79
Anchor South East	33	18.54	19	12.32	23	12.78
Anchor South West	58	16.52	28	7.89	54	15.38
Old Say East	114	32.76	.	.	7	1.95
Old Say West	43	24.16	.	.	8	3.90
Hummel	.	.	33	6.21	61	11.42
Marge	.	.	72	13.53	44	8.26
Curve	.	.	44	8.44	41	7.64
Treeline	.	.	62	12.20	31	5.85
Tower	.	.	81	23.30	35	9.80
Dassow	56	10.47
Harvey	34	6.38	157	29.51	1	0.19
Huber South	.	.	39	7.57	53	9.86
Lane	.	.	48	9.07	*10	*3.72
SP Huber South	.	.	24	9.04	26	9.72
SP Huber North	.	.	27	10.31	49	18.46
BW	144	26.93	190	35.82	4	0.74
Tombstone	119	22.50	153	28.87	0	0
Ditch	39	7.30
Hog	6	1.13
Cancer East	12	3.38
Cancer West	3	1.69
B&B	77	13.38
Perdue	68	12.95

*Due to railroad construction, the restored grassland plot Lane was only trapped in the early summer of 2011 and not the late summer.

Table A.2 Number of individuals of each small mammal species captured on roadside ditches and grass waterways from 2010-2011.

Species	No. of Individuals	
	2010	2011
Deer mouse	33	104
Prairie vole	78	2
Northern short-tailed shrew	30	18
Meadow vole	19	0
House mouse	1	5
Meadow jumping mouse	0	4
White-footed mouse	1	3
Western harvest mouse	0	2

Table A.3 Total individuals of each species present on restored grasslands and reference plots in either the Grand Prairie or Southern Till Plain region from 2009-2011.

Species	Grand Prairie Region			Southern Till Plain Region		
	2009	2010	2011	2009	2010	2011
	No. of Individuals			No. of Individuals		
Deer mouse	357	280	573	45	119	80
Prairie vole	259	144	11	284	464	61
Meadow vole	127	55	17	18	45	2
Northern short-tailed shrew	44	2	1	0	0	0
Meadow jumping mouse	0	1	14	0	0	0
House mouse	6	4	1	7	5	0
Western harvest mouse	7	4	4	1	0	0
Thirteen-lined ground squirrel	6	5	3	0	0	0
White-footed mouse	4	2	0	1	0	0
Southern bog lemming	0	0	0	0	5	0
Long-tailed weasel	0	4	0	0	0	0

APPENDIX B: Data Summaries and Supplemental Figures

Table B.1 Plot areas and connectivity (within 300 m or 2 km buffer) of established grasslands (EST), linear habitats (LIN), or a combination (ALL = EST + LIN). EST is the proportion of the buffered area covered by established grasslands, whereas LIN is the proportion of buffers covered by roadside ditches and grass waterways. Warm and cool signify the grass seeding type, and regions (Reg.) are split as the Grand Prairie (G) and the Southern Till Plain (S).

Plot	Area (ha)	EST 300m	EST 2km	LIN 300m	LIN 2km	ALL 300m	ALL 2km	Grass	Years Seeded	Reg.
Radio North Anchor	58.86	0.095	0.043	0.042	0.042	0.138	0.085	Warm	4	G
North Anchor	27.28	0.097	0.061	0.105	0.049	0.202	0.110	Warm	4	G
South West Anchor	20.31	0.280	0.080	0.097	0.049	0.377	0.129	Cool	3	G
South East	8.49	0.249	0.065	0.093	0.050	0.343	0.115	Cool	3	G
Radio South	64.58	0.180	0.081	0.054	0.040	0.234	0.121	Warm	3	G
Harvey	15.74	0.133	0.047	0.021	0.025	0.154	0.072	Warm	3	S
Huber South Lane	27.31	0.112	0.102	0.055	0.027	0.168	0.129	Warm	2	S
SP Huber South	15.74	0.107	0.025	0.014	0.022	0.121	0.047	Warm	2	S
SP Huber North	29.10	0.236	0.087	0.043	0.025	0.279	0.112	Cool	2	S
Hummel	31.76	0.268	0.081	0.035	0.026	0.303	0.107	Warm	2	S
Marge Curve	51.10	0.224	0.070	0.031	0.029	0.255	0.099	Cool	2	G
Treeline	61.54	0.068	0.044	0.071	0.033	0.139	0.077	Warm	2	G
Dassow Old CRP East	37.19	0.146	0.065	0.116	0.046	0.262	0.111	Warm	2	G
Old CRP West	20.31	0.087	0.047	0.117	0.053	0.204	0.100	Cool	2	G
Old Say East	6.48	0.281	0.097	0.023	0.037	0.304	0.133	Warm	1	G
Old Say West	3.06	0.353	0.050	0.080	0.041	0.432	0.091	Cool	≥10	G
Tower BW	5.02	0.486	0.048	0.073	0.043	0.559	0.091	Warm	≥10	G
Tombstone Ditch	27.05	0.044	0.069	0.094	0.043	0.138	0.112	Cool	≥10	G
Hog Cancer East	1.55	0.301	0.109	0.098	0.042	0.399	0.151	Warm	≥10	G
Cancer West	1.96	0.222	0.038	0.108	0.036	0.330	0.074	Cool	≥10	G
B&B	38.76	0.042	0.039	0.026	0.028	0.067	0.067	Cool	≥10	S
Perdue	7.29	0.216	0.085	0.041	0.038	0.257	0.122	Warm	≥10	S
	52.28	0.055	0.057	0.032	0.016	0.086	0.073	Cool	≥10	S
	8.48	0.076	0.071	0.040	0.036	0.116	0.107	Cool	≥10	S
	18.99	0.167	0.060	0.003	0.019	0.170	0.078	Cool	≥10	S
	11.31	0.254	0.052	0.003	0.018	0.257	0.070	Warm	≥10	S
	4.25	0.041	0.032	0.033	0.054	0.074	0.085	Cool	≥10	G
	47.57	0.017	0.021	0.036	0.041	0.053	0.062	Cool	≥10	G

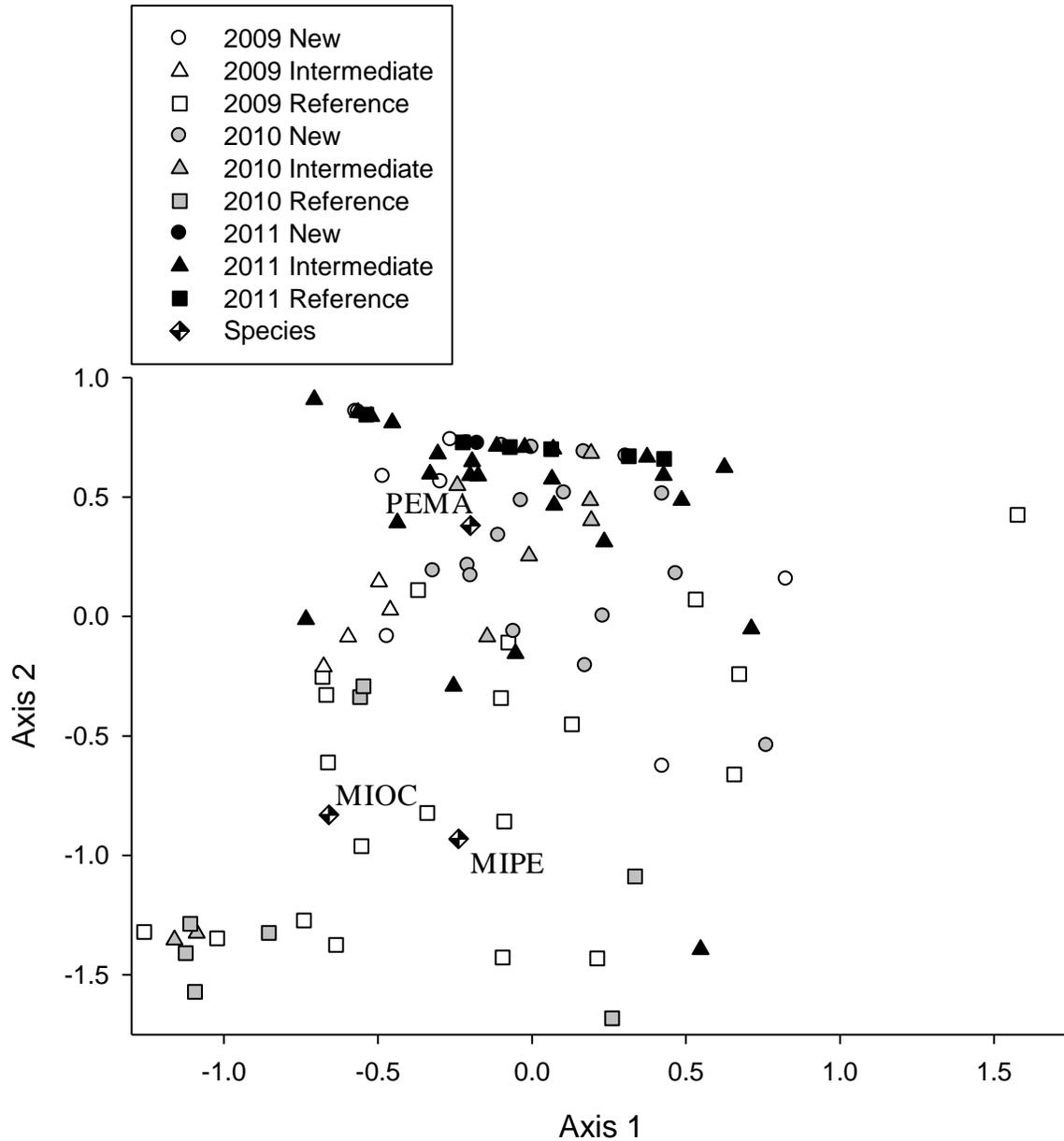


Figure B.1 Non-metric multidimensional scaling of small mammal communities from 2009-2011. Plots are displayed in three categories: new (<1 year since seeding), intermediate (1-4 years since seeding), and references (>10 years since seeding). Species scores are represented in which PEMA = deer mouse, MIOC = prairie vole, and MIPE = meadow vole. All plots with <10 individuals for a given year were removed from analysis.

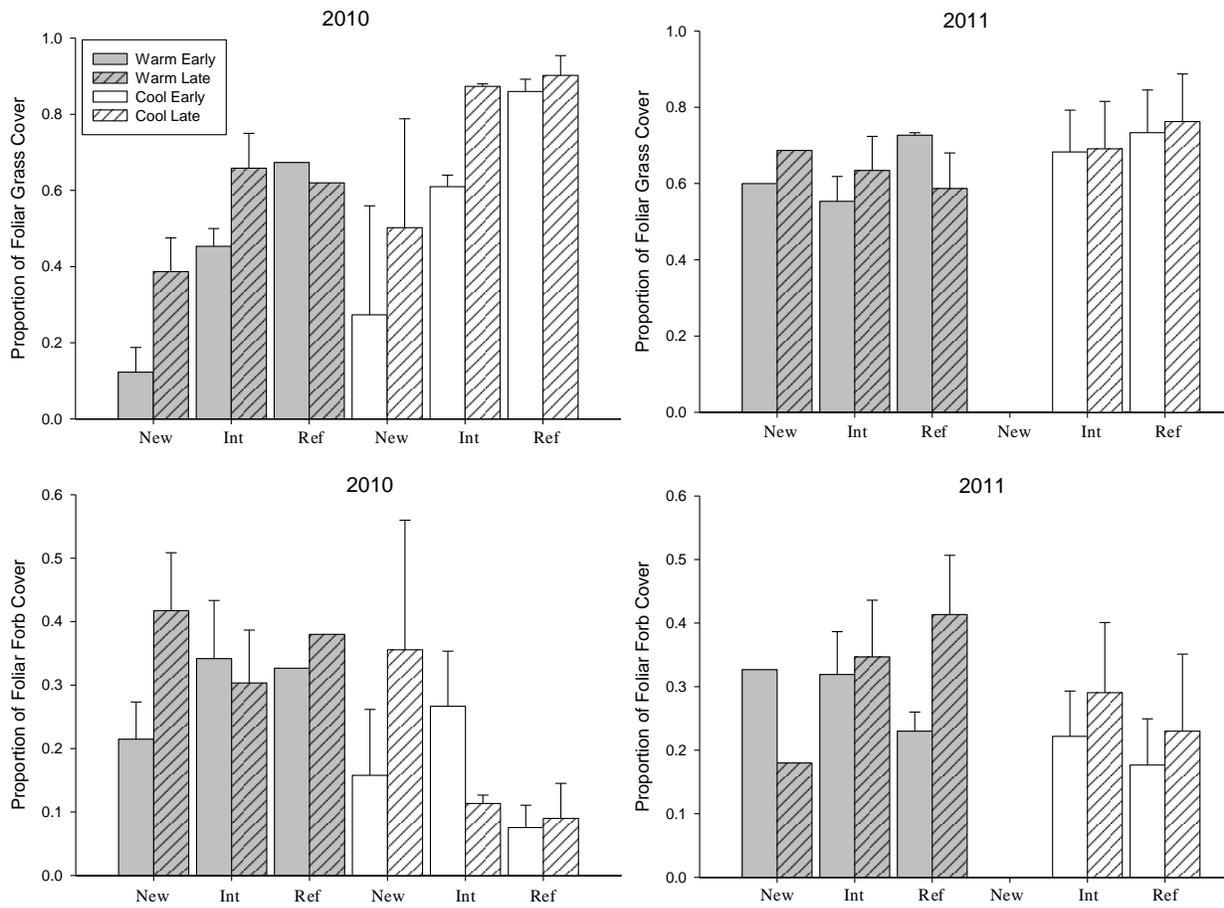
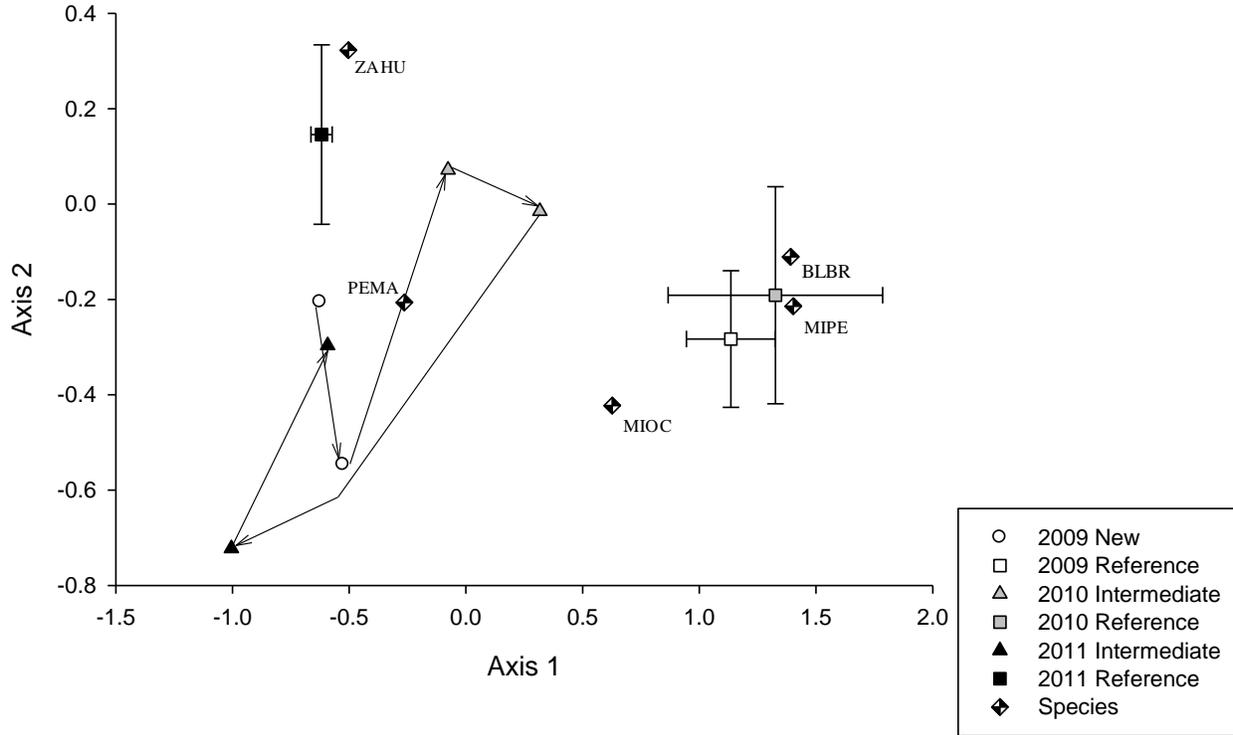


Figure B.2 Comparison of warm- and cool-season grass seeding early (mid-May to late June) and late (early July-mid August) summer from 2010-2011. Cool-season grass plots tend to have greater grass cover while warm-season grass plots had greater forb cover on all plots (New = <1 year since seeding; Int = 1-4 years since seeding; Ref = >10 years since seeding).

Grand Prairie Region



Southern Till Plain Region

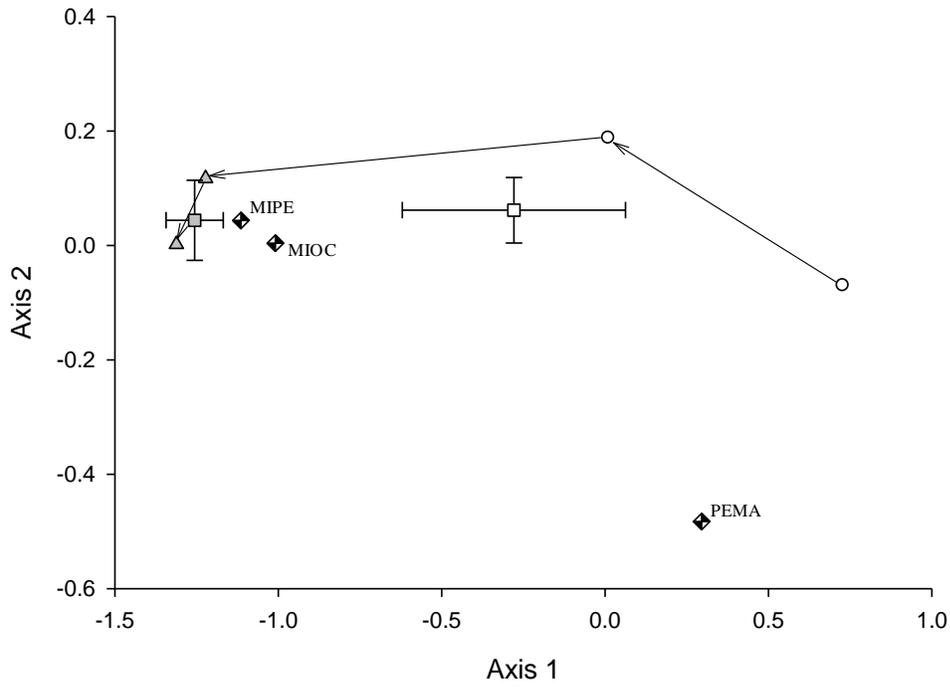


Figure B.3 (cont.)

Figure B.3 Transition of two separate plots in the Grand Prairie (Radio South) and Southern Till Plain (Harvey) regions using non-metric multidimensional scaling. Species scores are represented in which PEMA = deer mouse, MIOC = prairie vole, MIPE = meadow vole, BLBR = northern short-tailed shrew, and ZAHU = meadow jumping mouse. All points with <10 individuals were removed from analysis. The 2011 points for Harvey and average reference point are not shown for the Southern Till Plain region because there were <10 individuals for those plots that year.