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IMPLICATIONS OF INVASION BY *JUNIPERUS VIRGINIANA* ON SMALL MAMMALS IN THE SOUTHERN GREAT PLAINS

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Changes in landscape cover in the Great Plains are resulting from the range expansion and invasion of eastern red cedar (*Juniperus virginiana*). By altering the landscape and local vegetation, red cedar is changing the structure and function of habitat for small mammals. We examined effects of invasion by eastern red cedar on small mammals in 3 plant communities (tallgrass prairie, old field, and cross-timbers forest) in the cross-timbers ecoregion in Oklahoma. We sampled small mammals seasonally from May 2001 to August 2002 by using Sherman live traps and mark–recapture techniques on 3.24-ha, 450-trap grids in each plant community. We sampled vegetation in two hundred twenty-five 12 × 12-m cells within each grid. The structure of the small-mammal community differed among the 3 habitat types, with higher species diversity and richness in the tallgrass-prairie and old-field sites. Overall, the small-mammal community shifted along a gradient of increasing eastern red cedar. In the old-field and tallgrass-prairie plots, occurrence of grassland mammals decreased with increasing red cedar, whereas only 1 woodland mammal species increased. In the cross-timbers forest site, percent woody cover (<1 m in height), rather than cover of red cedar, was the most important factor affecting woodland mammal species. Examination of our data suggests that an increase in overstory cover from 0% to 30% red cedar can change a species-rich prairie community to a depauperate community dominated by 1 species, *Peromyscus leucopus*. Losses in species diversity and changes in mammal distribution paralleled those seen in avian communities invaded by eastern red cedar. Our results highlight ecological effects of invasion by eastern red cedar on diversity and function at multiple trophic levels.

Key words: community, cross timbers, eastern red cedar, invasion, *Juniperus virginiana*, old-field vegetation, small mammals, tallgrass prairie

Invasion and displacement of grasslands by woody species are global phenomena (Archer 1995), believed to result from large-scale changes in disturbance regimes and resource abundance (Briggs et al. 2002). Individual, and often interacting, factors considered as drivers of woody-plant expansion (summarized by Hoch et al. [2002]) include alteration of fire regimes, intensive livestock grazing, climate change, intentional planting, and removal of native herbivores (Weltzin et al. 1997). Increases in woody cover can affect ecosystem processes in these grasslands in several ways, including increasing aboveground net primary productivity and carbon storage (Norris et al. 2001) and reducing plant species richness (Hoch et al. 2002).

Range expansion by a native tree, eastern red cedar (*Juniperus virginiana*), in the Great Plains of North America is rapidly converting remnant native grassland habitats to red cedar savannas and woodlands (Coppedge et al. 2001; Engle et al. 1996; Gehring and Bragg 1992; Hoch et al. 2002). Fire historically limited the spread of eastern red cedar, a fire-intolerant species that reproduces solely by seed. In contrast, most native woody plants of the Great Plains reproduce vegetatively and can resprout after fire (Briggs et al. 2002).

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In the absence of fire, eastern red cedar spreads rapidly across the landscape (Bragg and Hulbert 1976), mostly from animal-driven dispersal of the ripened, fruitlike cones (Holthuijzen and Sharik 1985; Horncastle et al. 2004). Increased abundance of eastern red cedar in the Great Plains has been associated with changes in ecosystem function and structure, including reduced herbaceous biomass in the canopy zone (Engle et al. 1987; Hoch et al. 2002; Smith and Stubbendieck 1990), reduced plant species richness (Hoch et al. 2002), altered plant species composition, reduced understory light and soil water content (Gehring and Bragg 1992), and altered biological and physical soil factors (Arend 1950; Broadfoot 1951; Norris et al. 2001).

Changes in woody cover by succession or invasion can alter structure of grassland faunal communities. Several recent studies have demonstrated shifts in avian communities in southern mixed-grass prairies associated with red cedar encroachment (Chapman et al. 2004a; Coppedge et al. 2001, 2004; Fuhlendorf et al. 2002). Grassland-obligate avian species, such as lesser prairie-chicken (*Tympanuchus pallidicinctus*), upland sandpipers (*Bartramia longicauda*), burrowing owls (*Athene cunicularia*), and western meadowlarks (*Sturnella neglecta*), were either too scarce to model, declined with increasing woody cover (mostly eastern red cedar—Coppedge et al. 2001; Fuhlendorf et al. 2002), or were predicted to decline with the current rate of red cedar expansion (Coppedge et al. 2004). Open-habitat generalists, woodland species, and successional shrub species of birds increased or were predicted to increase with woody or red cedar expansion (Coppedge et al. 2001, 2004).

Small mammals, particularly rodents, are important cogs in the functioning of grassland ecosystems. Succession in small-mammal communities appears to mirror successional shifts in plant composition and habitat structure (Schweiger et al. 2000) because changes in vegetation alter suitability of habitat for individual species of small mammal (Fox 1995; Kaufman and Fleharty 1974; M'Closkey and Lajoie 1975). Mammal communities shift as plant succession proceeds after disturbances such as fire (Fox 1982, 1995), surface mining (Fox 1995; Wetzel 1958), and release from agricultural cultivation (Beckwith 1954; Schweiger et al. 2000; Sietman et al. 1994; Swihart and Slade 1990). Conversely, small mammals can modulate structure and composition of the plant community. For example, meadow voles (*Microtus pennsylvanicus*) shape plant composition of experimental tallgrass communities by selective herbivory (Howe and Brown 1999; Howe et al. 2002) and granivory (Howe and Brown 2001). Seed predation and seedling herbivory by rodents can regulate old-field succession by woody plants (Ostfeld and Canham 1993; Ostfeld et al. 1997).

Our goal was to examine effects of eastern red cedar invasion on community structure of small mammals. Given known effects of eastern red cedar invasion on vegetative communities (i.e., increased woody cover, decreased herbaceous understory, and change in species composition—Gehring and Bragg 1992; Smith and Stubbendieck 1990) and previous studies of small-mammal succession, we predicted several consequences of eastern red cedar invasion on the small-mammal community. We predicted that overall diversity of small mammals would be lower where eastern red cedar was prevalent because red cedar reduces aboveground biomass, cover, and diversity of herbaceous plants. Prairie species, such as deer mice (*Peromyscus maniculatus*), fulvous harvest mice (*Reithrodontomys fulvescens*), plains harvest mice (*Reithrodontomys montanus*), and hispid cotton rats (*Sigmodon hispidus*), should be prevalent in tallgrass-prairie and open old-field habitats, but their probability of occurrence should be negatively associated with cover of eastern red cedar (Goertz 1964; Hanchey and Wilkins 1998; Schweiger et al. 2000). Conversely, probability of occurrence of woodland voles (*Microtus pinetorum*), white-footed mice (*Peromyscus leucopus*), and eastern woodrats (*Neotoma floridana*), which are woodland species (Kaufman et al. 1983; McMurry et al. 1993), should be positively associated with eastern red cedar cover. We tested these predictions by intensive trapping on large (3.24-ha) grids representing 3 distinct plant communities in the cross-timbers ecoregion (Hoagland et al. 1999) of the Great Plains: tallgrass prairie, cross-timbers forest, and old fields. Our specific objectives were to compare small-mammal communities in these 3 communities and evaluate mammalian spatial data relative to vegetation cover and occurrence of eastern red cedar.

Materials and Methods

Study area.—Our study was conducted in 2001–2002 on 3 sites at the Oklahoma State University Research Range located about 11 km southwest of Stillwater in Payne County, Oklahoma (36°03′51″N, 97°12′46″W). The Research Range was situated on the western fringe of the cross-timbers ecoregion, which covers large parts of central Oklahoma and extends into Kansas and Texas (Hoagland et al. 1999). Cross-timbers forest is an upland hardwood type dominated by blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*) with coralberry (*Symphoricarpos orbiculatus*), eastern red cedar, poison ivy (*Toxicodendron radicans*), roughleaf dogwood (*Cornus drummondii*), redbud (*Cercis canadensis*), and American elm (*Ulmus americana*) as understory woody dominants (Ewing et al. 1984). One site in each of 3 plant communities was used to evaluate the interactions between small mammals and eastern red cedar. These communities were tallgrass prairie, cross-timbers forest, and old field, all of which were invaded by eastern red cedar trees to various extents, thus creating gradients of cedar invasion in each community. The Research Range was located within a temperate humid climate zone. Mean annual temperature was 15°C and ranged from an average daily minimum of −4.3°C in January to an average daily maximum of 34°C in August. The average annual precipitation was 831 mm (National Oceanic and Atmospheric Administration 1999).

The tallgrass-prairie site previously was used for livestock grazing during summer, and fires burned the site in 1991 (wildfire) and 1996 (prescribed fire). Dominant herbaceous species were little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and western ragweed (*Ambrosia psilostachya*). The prairie site also contained isolated mottes of sumac (*Rhus*), oaks (*Quercus*), and eastern red cedar. The cross-timbers site was dominated by post oak and blackjack oak in the overstory. The understory was dominated by coralberry, Scribner's panicum (*Dichanthelium oligosanthes*), poison ivy, hackberry (*Celtis occidentalis*), and post oak. The old-field site previously was lightly grazed by livestock during summer, used as a holding pasture, and was burned in 1996. The dominant herbaceous species were little bluestem, threeawn species (*Aristida*), Indiangrass, and western ragweed. In 1996,

invading eastern red cedars were removed mechanically with a rotary saw in the northeastern part of the old-field site, leaving the site about 65% invaded by cedar. The tallgrass-prairie and cross-timbers–forest sites were patches of larger associations, whereas the old-field was isolated on the eastern edge of a larger cross-timbers forest.

Experimental design and trapping.—We established large trapping grids (180 × 180 m, each 3.24 ha) in each of the 3 plant communities. The tallgrass-prairie grid was centered 960 m west–northwest of the cross-timber–forest grid, which in turn was 430 m west–southwest of the old-field grid. Each grid was divided into 225 cells (each 12 × 12 m). We chose this design to include spatial scale as a treatment factor in concomitant, landscape-level studies of growth and survival of eastern red cedar. In essence, we sampled locations within each of 3 distinct plant communities in a single, larger cross-timbers landscape. Replicating such grids in multiple cross-timbers landscapes elsewhere was beyond our logistical means. Oksanen (2001) argued that predictions derived from hypotheses should apply to any system within a defined category, and replication is not germane to testing of that particular system. Therefore, we consider our study to be a landscape-specific test of our hypothesis on the ecological effects of eastern red cedar invasion in multiple plant communities. It also represents the initial work to examine the impact of expanding *Juniperus* woodlands on the community of small mammals. Replication in the form of additional studies and meta-analysis should be conducted.

We trapped animals by using Sherman live traps (7.6 × 8.9 × 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, FLorida) baited with oatmeal and provided with cotton for warmth during cold weather (<1.7°C). Two traps were placed in each cell, and each trap was 6 m away from other traps within each cell and 6 or 12 m from traps in adjacent cells throughout the grid. We trapped seasonally (May, August, November, and February) from May 2001 to August 2002 for a total of 6 trapping periods. Within a season, one grid was trapped for 5 consecutive days, followed immediately by a 5-day trapping session on another grid until all 3 grids were sampled. We randomly determined the order in which grids were trapped in each season. We set traps each night and checked them the following morning.

All captured rodents were sexed, aged (adult or juvenile), and weighed with a spring scale. We marked larger rodents (e.g., cotton rats and wood rats) with ear tags (National Band and Tag Co., Newport, Kentucky), and toe-clipped all other species for future identification. Trapping and handling procedures were approved by the Institutional Animal Care and Use Committee at Oklahoma State University and followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Vegetation sampling.—Vegetation data consisted of percent cover of eastern red cedar, understory vegetation, and overstory vegetation. Percent cover of eastern red cedar was visually estimated by using cover classes (1–5%, >5–10%, >10–25%, >25–50%, >50–75%, >75–95%, or >95%) in all 225 cells in each habitat type. Understory vegetation cover (<1 m) was estimated by using cover classes on 1-m^2 quadrats. We visually estimated percent cover of forb, legume, grass, woody vegetation, bare ground, rock, litter, moss, prickly pear (*Opuntia*), and standing dead material. We sampled overstory vegetation by using a densiometer (Lemmon 1957). We sampled 4 points within each cell in each of the 4 cardinal directions for a total of 16 measurements in each cell. Percent cover for a cell was determined as the average of the 16 measurements.

Data analysis.—We used data only from species with enough captures (≥10) to effectively run a particular analysis. Two species (*Chaetodipus hispidus* and *Blarina hylophaga*) had too few captures to be used in any analysis. Composition and structure of small-mammal communities were compared among grid types by using ordination techniques and plots of rank abundance. Overall species composition was 1st evaluated in the 3 plots by using detrended correspondence analysis (DCA) with CANOCO software (ter Braak and Smilauer 1988). DCA is an indirect gradient analysis technique used to identify factors influencing characteristics of communities that vary along compositional gradients (Peet et al. 1988). DCA uses the weighted averages of species abundance to generate species–site joint plots in which sample scores in the ordination diagram lie at the centroids of the positions of species that occur in them. Sites close to a particular species are likely to have a high abundance of that species and those farther away a lower abundance. Eight species were used to ordinate all cells in each habitat type ($n = 675$). The effect of habitat type on species abundance was assessed by comparing sample scores and species scores in the first 2 DCA axes. The eigenvalues produced from the DCA represent the correlation between species' scores and sample scores (maximum value = 1.0). We used correlation of DCA axis scores with vegetation variables to identify gradients represented by the DCA ordination axes.

We used rank–abundance analysis (Begon et al. 1996) to determine differences in the structure of small-mammal communities in the 3 habitat types. The log of the number of individuals was used as a measurement of abundance, and species were assigned a rank from 1 (most abundant) to 7 (least abundant). The slope of the linear regression equation in the rank–abundance curves was an index of species diversity (Southwood 1966). Therefore, we compared the relationship between species rank and abundance in small-mammal communities among the 3 habitats by using multiple linear regression (PROC REG—SAS Institute Inc. 2000).

We used stepwise logistic regression (PROC LOGISTIC—SAS Institute Inc. 2000) to assess the association between the occurrence of individual small-mammal species and eastern red cedar cover and understory vegetation. Total overstory cover was removed from all analyses because of its high correlation with other vegetation variables, as described below. In each habitat type, probability of capture of each species at each cell was regressed against vegetation variables. To determine probability of capture at a given trap site, we considered the probability to be 0 (absent) if an individual was not captured at that site during the course of the study, and to be 1 (present) if an individual was captured at that site. For each habitat type, we reduced the number of vegetation variables by using correlation analyses. For pairs of variables that were highly correlated with each other ($|r| > 0.5$), we eliminated the member of the pair that was most highly correlated with other variables in the data set. Variables eliminated from logistic regression analyses were herbaceous and overstory cover in the tallgrass prairie; herbaceous, litter, and overstory cover in the cross timbers; and forb, litter, and overstory cover in the old field. Models were fitted by using a maximum-likelihood method, and variables were brought into the model by using $P = 0.15$ (Hosmer and Lemeshow 2000). The Hosmer and Lemeshow test (Hosmer and Lemeshow 2000) was used to test goodness-of-fit of the model. P values > 0.05 in the Hosmer and Lemeshow test indicated adequate model fit.

We were interested specifically in the association of eastern red cedar and probability of capture of small mammals. Therefore, we regressed probability of capture for all small-mammal species with adequate data in each habitat type against eastern red cedar as the only independent variable. As a post hoc descriptive analysis, we estimated how relative proportions of the 4 most abundant small-mammal species in our tallgrass-prairie site would vary with changing cover of eastern red cedar. First, by using the above logistic regression equations, we estimated probability of capture of each species over the entire sampling period as a function of red cedar cover. Second, for each cover category

Table 1.—Vegetation cover (%) on 3 study sites that were trapped for small mammals on the Oklahoma State University Research Range from May 2001 to August 2002.

	Site					
	Tallgrass prairie		Cross-timbers forest		Old field	
Cover variable	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Eastern red cedar	3.5	0.8	14.8	0.9	19.3	1.4
Grass	39.9	0.6	5.6	0.4	31.0	0.6
Forb	21.0	0.5	1.1	0.1	13.1	0.4
Understory woody	7.1	0.5	14.0	0.6	0.3	0.1
Legume	2.1	0.2	0.0	0.0	2.3	0.1
Bare ground	0.0	0.1	6.5	0.5	8.3	0.4
Litter	66.1	0.4	86.6	0.6	50.3	0.6
Overstory woody	6.2	0.7	81.5	0.9	15.2	1.1

observed within the cells in our site (2–5% increments up to 85% cover), we determined relative probability of capture of each species such that they summed to 1.0. Finally, we plotted relative probabilities against cover of eastern red cedar.

Results

Small-mammal communities by habitat.—We recorded 1,184 small-mammal captures representing 10 species and 523 unique individuals in 40,500 trap nights between May 2001 and August 2002. Percent cover for each vegetation class varied among the 3 habitats, with old field having the greatest amount of cedar, followed by cross-timbers forest and tallgrass prairie (Table 1).

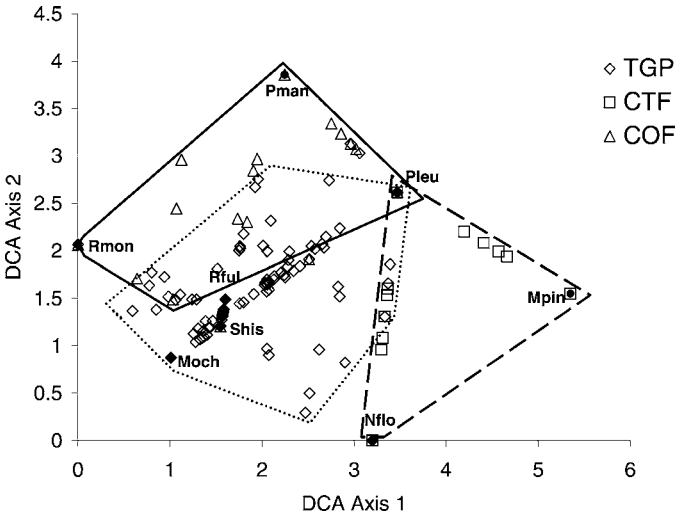


Fig. 1.—Detrended correspondence analysis (DCA) ordination biplot depicting species scores (solid symbols) for small mammals in 3 plant communities: tallgrass prairie (TGP), cross-timbers forest (CTF), and cedar-invaded old field (COF). Each open symbol represents the site or sample score of 1 cell in a habitat. Envelope with solid line (—) represents cells in the old field, envelope with dashed line (- - -) represents cells in the cross timbers, and envelope with dotted line (. . .) represents cells in the tallgrass prairie. Axis 1 depicts a gradient of increasing woody cover and axis 2 depicts a gradient from forb and woody understory cover to cedar and bare-ground cover. Species abbreviations: Moch = *Microtus ochrogaster*; Mpin = *Microtus pinetorum*; Nflo = *Neotoma floridana*; Pleu = *Peromyscus leucopus*; Pman = *Peromyscus maniculatus*, Rful = *Reithrodontomys fulvescens*, Rmon = *Reithrodontomys montanus*, and Shis = *Sigmodon hispidus*.

Table 2.—Results of detrended correspondence analysis for small-mammal composition data from tallgrass-prairie, cross-timbers, and old-field communities on the Oklahoma State University Research Range from May 2001 to August 2002. Axis 1 represents a gradient of increasing woody cover and axis 2 represents a gradient from forb and woody understory cover to cedar and bare-ground cover. Only correlations with $P < 0.05$ are reported.

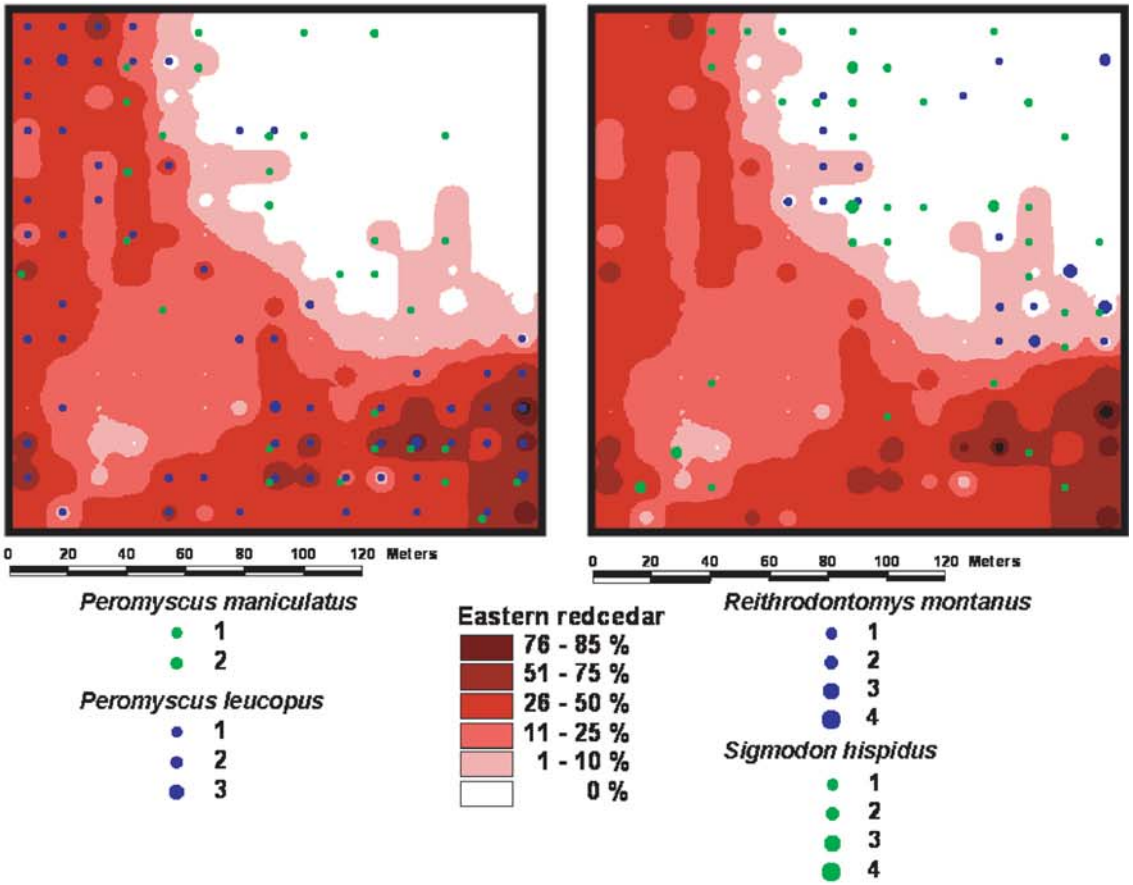
	Detrended correspondence analysis	
	Axis 1	Axis 2
Eigenvalue	0.81	0.57
% variance of all axes	19.5	33.3
Length of gradient	5.35	3.86
Correlations		
% overstory cover	0.687	0.196
% cedar cover	0.464	0.431
% grass cover	−0.497	−0.197
% forb cover	−0.584	−0.207
% woody understory	0.329	−0.222
% bare ground	0.165	0.229
% litter	0.491	
% legume	−0.158	

Detrended correspondence analysis revealed similarity in species composition among cells occurring in tallgrass-prairie and old-field sites compared with cross timbers (Fig. 1). The first 2 axes of the DCA ordination accounted for 33.3% of the variance associated with species data. Small-mammal communities separated along DCA axes 1 and 2 (Fig. 1). Axis 1 separated the small-mammal community in the cross-timbers habitat (e.g., *M. pinetorum*, *N. floridana*, and *P. leucopus*) from mammal communities in the other 2 habitats. This separation was associated with a vegetation gradient from grasses and forbs to greater amounts of woody understory, cedar, litter, and overstory cover (Table 2; Fig. 1). Mammal communities in the old-field and tallgrass-prairie habitats were partially separated on axis 2, which was associated with a vegetation gradient from forb and woody understory cover to increasing cover of eastern red cedar and bare ground (Table 2). The prairie site and open areas of the old-field site were dominated by *S. hispidus*, *P. maniculatus*, *R. montanus*, and prairie voles (*Microtus ochrogaster*; Figs. 1 and 2). Cedar-invaded areas of the old-field site were characterized by both species of *Peromyscus* (Fig. 2).

Rank–abundance analysis showed that species richness and evenness differed between the cross-timbers plot and the other 2 habitats (Fig. 3). Comparison of the slopes in the rank–abundance curves indicated that small-mammal communities inhabiting the cross timbers had a less even distribution of species than those from the old field ($P = 0.005$) and the tallgrass prairie ($P = 0.023$). No difference was found in mammal distribution between the tallgrass-prairie and old-field plots ($P = 0.075$). Species richness and evenness generally were higher in the old field and tallgrass prairie than in the cross timbers.

Species-specific relationships to habitat and vegetation variables.—Results of the Hosmer–Lemeshow goodness-of-fit test indicated that all logistic models presented adequately

A)


0 20 40 60 80 100 120 Meters
0 20 40 60 80 100 120 Meters
Peromyscus maniculatus
1
2
Peromyscus leucopus
1
2
3
Eastern redcedar
76 - 85 %
51 - 75 %
26 - 50 %
11 - 25 %
1 - 10 %
0 %
Reithrodontomys montanus
1
2
3
4
Sigmodon hispidus
1
2
3
4

B)

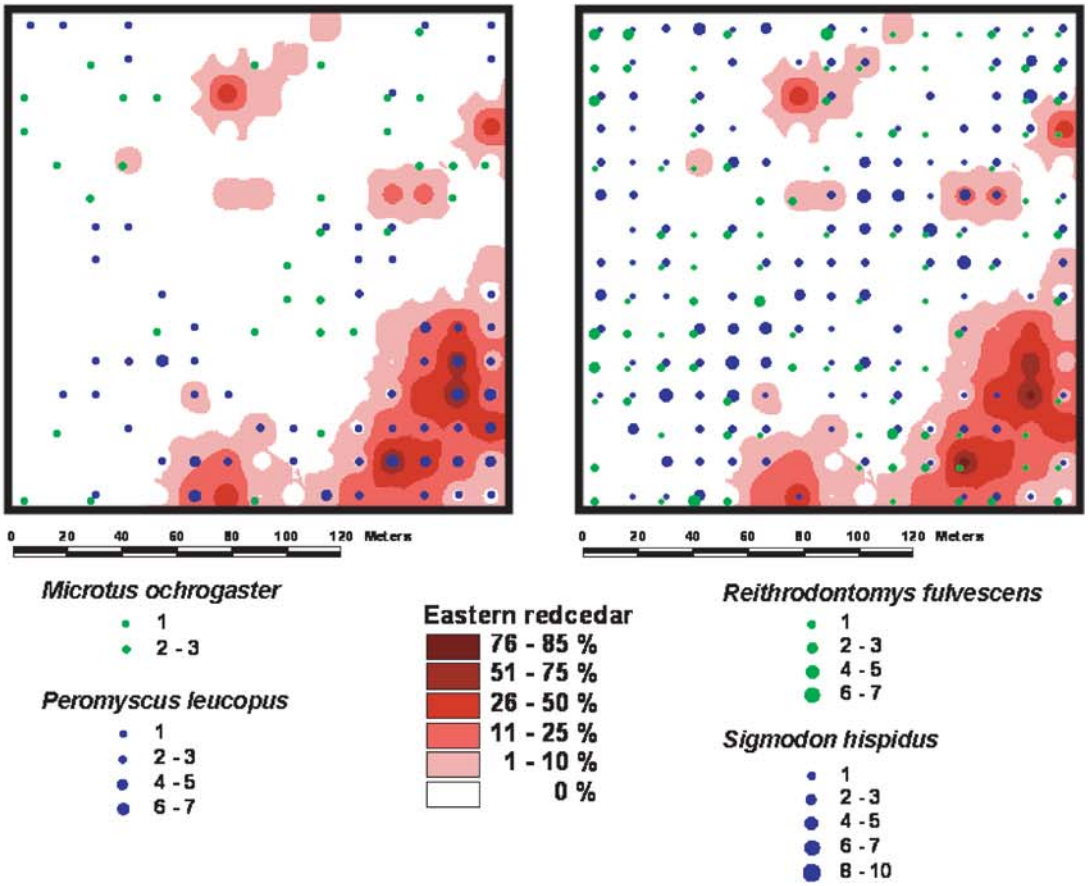

0 20 40 60 80 100 120 Meters
0 20 40 60 80 100 120 Meters
Microtus ochrogaster
1
2 - 3
Peromyscus leucopus
1
2 - 3
4 - 5
6 - 7
Eastern redcedar
76 - 85 %
51 - 75 %
26 - 50 %
11 - 25 %
1 - 10 %
0 %
Reithrodontomys fulvescens
1
2 - 3
4 - 5
6 - 7
Sigmodon hispidus
1
2 - 3
4 - 5
6 - 7
8 - 10

FIG. 2.—Number of captures of 6 small-mammal species (*Peromyscus leucopus* [white-footed mouse], *Sigmodon hispidus* [hispid cotton rat], *Reithrodontomys fulvescens* [fulvous harvest mouse], *Reithrodontomys montanus* [plains harvest mouse], *Peromyscus maniculatus* [deer mouse], and *Microtus ochrogaster* [prairie vole]) in each cell in the A) old-field and B) tallgrass-prairie sites in relation to percentage cover of eastern red cedar, Oklahoma State University Research Range, Payne County, Oklahoma, May 2001–August 2002. ←

fit the data (Table 3). Although many other cover variables were measured, no variable consistently was as important as eastern red cedar in affecting probability of capture among rodent species at the $P < 0.15$ level (Table 3).

In the tallgrass-prairie site, all 4 rodent species that had adequate data to be analyzed were associated with eastern red cedar cover. Occurrence of all 3 prairie species was correlated negatively with cover of red cedar, whereas the 1 woodland species (*P. leucopus*) was correlated positively with red cedar. Three of the 4 rodent species were associated with percent cover of woody understory. Only 2 rodent species, *P. leucopus* and *S. hispidus*, were associated with litter. All other vegetation variables were associated with $\leq$ 1 rodent species in the tallgrass-prairie site (Table 3).

In the cross-timbers site, occurrences of *N. floridana* and *P. leucopus* were associated positively with woody understory cover. Percent cover of red cedar was correlated positively with *P. leucopus* and *M. pinetorum*. *M. pinetorum* also was correlated positively with forb cover, whereas *N. floridana* was correlated negatively. All other vegetation variables were associated with $\leq$ 1 rodent species in the cross-timbers site (Table 3).

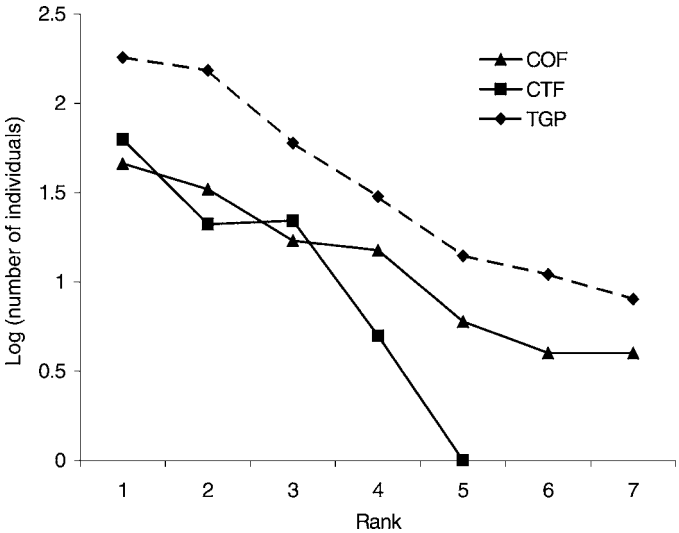


FIG. 3.—Rank–abundance patterns of rodent communities inhabiting 3 sites: tallgrass prairie (TGP), cross-timbers forest (CTF), and cedar-invaded old field (COF) at Oklahoma State University Research Range, Payne County, Oklahoma, May 2001–August 2002. The log number of individuals of each species is ranked from most abundant (1) to least abundant (5–7).

In the old-field site, 3 of the 4 species were associated with eastern red cedar. Occurrences of *R. montanus* and *S. hispidus*, which are considered prairie species, were correlated negatively with red cedar, and occurrence of *P. leucopus* was associated

TABLE 3.—Logistic regression relating probability of occurrence of small-mammal species in tallgrass prairie, cross timbers, and cedar-invaded old field to vegetation cover, Payne County, Oklahoma, 2001–2002. b = regression coefficient; P = probability value associated with cover variable; P (GOF) = Hosmer and Lemeshow goodness-of-fit test.

			Vegetation cover (%)								
Habitat	Species	Statistic	Cedar	Forb	Grass	Understory woody	Bare ground	Rock	Litter	Legume	P (GOF)
Tallgrass prairie	*Microtus ochrogaster*	b	−0.042	−0.042		−0.071					0.607
		P	0.117	0.055		0.032					
	Peromyscus leucopus	b	0.043			0.046		0.309	0.054		0.833
		P	0.036			0.019		0.039	0.016		
	Reithrodontomys fulvescens	b	−0.019								0.414
		P	0.159								
	Sigmodon hispidus	b	−0.034			0.044			−0.045		0.199
		P	0.039			0.028			0.017		
Cross timbers	*Microtus pinetorum*	b	0.026	0.465							0.572
		P	0.143	<0.0001							
	Neotoma floridana	b		−0.683		0.049					0.738
		P		0.059		0.013					
	P. leucopus	b	0.028			0.035	−0.038				0.814
		P	0.009			0.022	0.071				
Cedar-invaded old field	*P. leucopus*	b	0.062		0.030						0.269
		P	<0.0001		0.068						
	P. maniculatus	b			−0.047					0.232	0.817
		P			0.009					0.002	
	Reithrodontomys montanus	b	−0.047								0.151
		P	0.001								
	S. hispidus	b	−0.202				−0.097				0.266
		P	0.008				0.029				

positively with red cedar. Percent herbaceous cover was correlated positively with *P. leucopus*, whereas *P. maniculatus* was correlated negatively. All other vegetation variables were associated with ≤ 1 rodent species in the old-field site (Table 3).

Logistic regression models constructed with red cedar as the sole vegetation variable provided a more detailed illustration of the effect of red cedar on probability of capture of small mammals. *P. leucopus* was correlated positively with red cedar in all 3 habitat types (Table 4), although the model fit poorly in the old-field site. Estimated probability of capture for *P. leucopus* was more sensitive to increases in red cedar cover in the old-field and tallgrass-prairie habitats, doubling with an increase in red cedar cover from 0% to 20%, than in the cross timbers (Fig. 4). Other woodland species were not associated with red cedar cover.

Among prairie species, *S. hispidus* and *R. fulvescens* in the tallgrass prairie, and *R. montanus* in the old field were correlated negatively with eastern red cedar (Table 4). The estimated probability of capture decreased by 50% for *R. montanus* as red cedar cover increased from 0% to 20% in the cedar old field, and decreased by 50% for *S. hispidus* and *R. fulvescens* as red cedar cover increased from 0% to 35% in the tallgrass prairie (Fig. 4). Our post hoc analysis on change in relative proportions of common small-mammal species of the tallgrass prairie suggested increasing dominance by *P. leucopus* as cover of red cedar increased, especially when percent cover of red cedar exceeded 30% (Fig. 5).

Table 4.—Logistic regression results modeling the probability of capture of each species in 3 habitats with percentage of cedar cover as the independent variable. b = regression coefficient; *P* = probability value associated with cover variable; *P* (GOF) = Hosmer and Lemeshow goodness-of-fit test.

Species	Habitat	*n*	b	*SE*	*P*	*P* (GOF)[a]
Peromyscus leucopus	Tallgrass prairie	61	0.057	0.018	0.001	0.006
Sigmodon hispidus	Tallgrass prairie	135	−0.040	0.016	0.014	0.594
Reithrodontomys fulvescens	Tallgrass prairie	105	−0.019	0.014	0.159	0.414
Microtus ochrogaster	Tallgrass prairie	33	−0.219	0.152	0.151	0.456
P. leucopus	Cross timbers	81	0.023	0.010	0.026	0.187
Neotoma floridana	Cross timbers	29	−0.0046	0.015	0.760	0.885
Microtus pinetorum	Cross timbers	17	0.016	0.016	0.317	0.675
P. leucopus	Old field	62	0.059	0.009	<0.001	0.008
P. maniculatus	Old field	31	0.014	0.008	0.088	0.120
Reithrodontomys montanus	Old field	36	−0.047	0.014	0.001	0.151

Discussion

Small-mammal communities by habitat.—The most salient finding of our study was that structure of the small-mammal community shifted along a gradient of increasing eastern red cedar. Overall, eastern red cedar was the most important vegetation factor in modeling probability of capture of most species in old-field and tallgrass-prairie communities. In those habitats, prairie species generally decreased and a single woodland species, *P. leucopus*, increased with increasing red cedar. When we used our equations from logistic regressions that modeled probability of capture on red cedar cover (Table 4) to calculate relative proportions of individual species within the community, examination of our data suggested that an increase in overstory cover from 0% to 40% red cedar can change a species-rich prairie community to a depauperate community dominated by 1 species, *P. leucopus* (Fig. 5). Yet, eastern red cedar did not appear to have as much of an effect on species composition in the cross-timbers forest, perhaps because cedar does not change the physical and vertical structure of cross-timbers forest as drastically as it does in tallgrass prairie and old fields.

Our results did not completely support our a priori predictions. We expected mammal species richness and evenness to decline as cover of red cedar increased in the tallgrass-prairie and old-field plots, and grasses were displaced because of canopy closure. Although cover of eastern red cedar was higher in the old-field site, small-mammal diversity was not lower in that site, probably because about 30% of the site remained in grassland. The majority of species in the old-field plot occurred in open, noninvaded areas (Fig. 2). In addition, the tallgrass-prairie site had an overall greater abundance of small mammals.

Species richness and evenness were higher in the tallgrass prairie and old field than in the cross timbers. In our study, the tallgrass-prairie and old-field sites contained both open and woody areas, whereas the cross-timbers site consisted mostly of overstory cover and little herbaceous understory. Accordingly, we found small mammals normally associated with prairie and woodlands in both tallgrass-prairie and old-field habitats but only woodland species in the cross-timbers forest, a pattern supported by our DCA. Johnson et al. (1979) reported that species richness of small mammals was highest in edge habitat, where all or most of the forest species plus some open-habitat specialists could be found.

Previous studies at an area adjacent to our study sites found that *P. leucopus*, *S. hispidus*, and *N. floridana* responded to successional changes in habitat (McMurry et al. 1993, 1994, 1996). *P. leucopus* and *N. floridana* were captured most frequently in late-successional areas with high amounts of woody dicots, whereas *S. hispidus* had the highest numbers in early-successional habitats with greater amounts of monocots. Densities of all rodents were higher in early and late succession and lowest in forest habitats with little herbaceous cover (McMurry et al. 1993, 1994, 1996). These results correspond to our findings that diversity and abundance were lowest in the cross timbers.

Composition of small-mammal communities also varied among habitats (Fig. 2). Composition in tallgrass prairie was similar to that in old-field plots but highly dissimilar to the cross timbers. Grassland and generalist species were mostly associated with the tallgrass-prairie and old-field sites, whereas woodland species were more associated with the cross-timbers

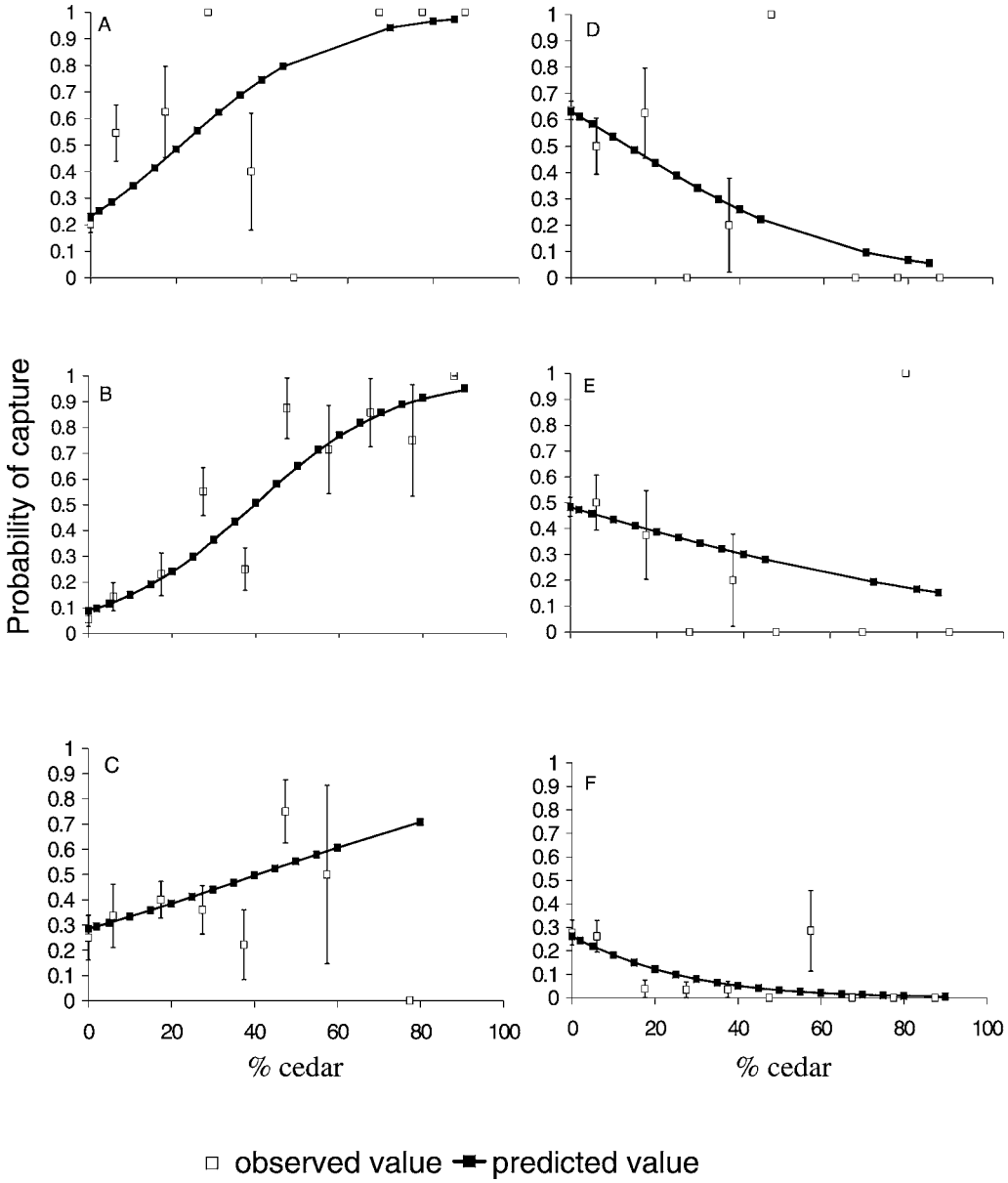


Fig. 4.—Estimated probability of capture of 4 species of rodents in different plant communities: *Peromyscus leucopus* in A) tallgrass prairie, B) old field, and C) cross-timbers forest; D) *Sigmodon hispidus* in tallgrass prairie; E) *Reithrodontomys fulvescens* in tallgrass prairie; and F) *R. montanus* in old field. Observed proportions of captures (±95% confidence interval) averaged across a given level of canopy cover are the plotting points (e.g., if 20 cells contained 20% cover of eastern red cedar and *P. leucopus* was captured in 8 of those cells, the average probability of capture at that cover value would be 0.4). Predictions are based on logistic regression models using percent of eastern red cedar in a 12 × 12-m cell as the independent variable.

site. Several studies of successional dynamics of small mammals in North American old fields have reported similar changes in species composition with an increase in woody cover (Beckwith 1954; Schweiger et al. 2000; Sietman et al. 1994; Swihart and Slade 1990). Others have reported that the change in species communities was greater between grasslands and woodlands than among other habitat types (Hanchey and Wilkins 1998; Kaufman et al. 2000).

Species-specific relationships to habitat and vegetation variables.—Vegetation or structural preferences have been demonstrated for several small-mammal species; however, studies of micro- and macrohabitat use of rodents are inconsistent (Jorgensen and Demarais 1999). Some authors have suggested that small-mammal distributions and habitat-selection strategies are sensitive to variance in local vegetative structure (Dueser and Shugart 1978; Swihart and Slade 1990). Other studies have shown that large-scale features of habitat can affect spatial distribution of small mammals (Barrett et al. 1995; Collins and Barrett 1997; Foster and Gaines 1991; Manson et al. 1999) and constrain microhabitat preferences (Jorgensen and Demarais 1999). Understanding how the interaction between macrohabitat and microhabitat affects species responses to changes in landscape structure warrants further exploration (Schweiger et al. 1999).

Our work did not address the microhabitat–macrohabitat dichotomy but focused on microhabitat features that affect occurrence within larger plant communities. Our results concur with previous work examining associations of effects of microhabitat features on occurrences of the species that we captured. However, species-specific responses to vegetation features emphasize our community-based conclusion that succession to an eastern red cedar woodland would be accompanied by a reduction in small-mammal diversity. Previous work on successional changes in small-mammal communities in old fields and prairies of this ecoregion have not reported similar losses of diversity (Schweiger et al. 2000; Sietman et al. 1994; Swihart and Slade 1990), but neither have they reported invasion of red cedar on their study sites. Therefore, to our knowledge, this is the 1st study that documents the impacts of eastern red cedar invasion on small-mammal communities.

Peromyscus leucopus occurs in deciduous forests, riparian woodlands, and shrub-dominated sites; rarely uses areas without woody structure in the central Great Plains (Kaufman et al. 1983; Schweiger et al. 2000; Swihart and Slade 1990); and is linked to complex vertical structuring of vegetation (Anderson et al. 2003; M'Closkey 1975; M'Closkey and Lajoie 1975). In our study, probability of occurrence of *P. leucopus* was correlated positively with red cedar in all 3 habitats and with woody cover in 2 habitats, which supported previous work. This mammal species also was associated with contiguous patches of red cedar, a result similar to that found by Schweiger et al. (2000), who reported that colonization of old fields by *P. leucopus* was linked to large (0.5-ha) patches of high woody cover that were adjacent to continuous oak–hickory forest. Pearson (1959) reported that *P. leucopus* was the dominant species in an abandoned orchard succeeding to a red-cedar forest, whereas Schnell et al. (1980) found *Peromyscus attwateri* to be restricted to cedar glades in a north-central Oklahoma study area.

Other woodland species were not as closely linked with red cedar as was *P. leucopus*, although we had predicted positive associations. *M. pinetorum*, which occurs in woodland habitats such as savannah edge, upland woods, and bottomland woods (Caire et al. 1989) and which was limited to the cross-timbers–forest site in our study, was only weakly associated with cover of red cedar. It was more strongly associated with forb cover, perhaps because forbs and grasses dominates its diet (Cengel et al. 1978). Occurrence of the other main woodland species, *N. floridana*, was correlated positively with woody vegetation and negatively with forbs. These results were consistent with McMurry et al. (1993), who found that *N. floridana* selects areas with increased woody vegetation for their greater structural complexity, and Schweiger et al. (2000), who reported capturing the species only on large patches of woody vegetation adjacent to continuous forest. Notably in our study, however, *N. floridana* was not captured in the old-field site where there was a high density of woody cover in the form of eastern red cedar.

Occurrences of prairie species were consistent with our predictions relative to their negative association with red-cedar cover and with previous work on their habitat associations. *S. hispidus* in Oklahoma is limited to habitats with dense stands of grass, forbs, or low-growing woody vegetation (Caire et al. 1989). Our results reflected these microhabitat preferences. We found that the probability of occurrence of *S. hispidus* was correlated negatively with red cedar and litter and positively correlated with woody vegetation < 1 m in height. Goertz (1964) also found that this species usually avoids areas where tree canopy shades ground cover. At an area adjacent to our study sites, relative densities of *S. hispidus* increased in response to increased production of monocots (McMurry et al. 1994). When red cedar colonizes an area, it reduces the herbaceous ground cover under the canopy zone (Engel et al. 1987; Smith and Stubbendieck 1990) on which prairie mammals depend.

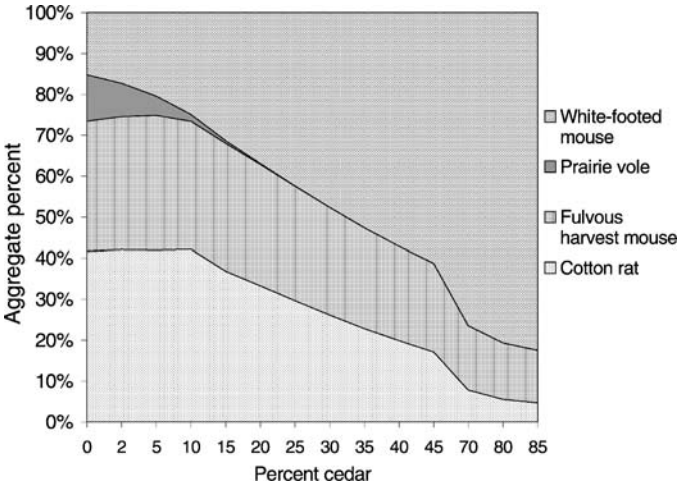


Fig. 5.—Predicted changes in relative composition of the small-mammal community in the tallgrass prairie with changes in percentage cover of eastern red cedar at Oklahoma State University Research Range, Payne County, Oklahoma, May 2001–August 2002. Relative proportion calculated from changes in estimated probability of capture for each species modeled as a function of eastern red cedar cover in a 12 × 12-m cell.

Occurrence of *M. ochrogaster* was correlated negatively with cedar and woody vegetation, as expected. This species commonly is found in grassy areas with legumes (Kaufman and Fleharty 1974; Schweiger et al. 2000). Similarly, occurrences of both species of *Reithrodontomys* were correlated negatively with cedar. Hanchey and Wilkins (1998) also found that abundance of *R. fulvescens* was correlated positively with grasses and was associated negatively with woody material. Both species prefer grassy habitats, with *R. fulvescens* more abundant in areas with heavy grass cover and *R. montanus* more abundant in areas of sparse cover (Spencer and Cameron 1982).

Peromyscus maniculatus was correlated negatively with grass and positively with legumes. Other studies report that it prefers open habitats, is associated negatively with woody canopies (Schweiger et al. 2000), and avoids lowland prairie with forbs and shrubs (Clark et al. 1998). Its preference for habitats with exposed soil and limited vertical structure (Clark et al. 1998) may allow it to persist in prairies invaded by eastern red cedar.

Ecological implications.—Examination of our data suggests that invasion of red cedar will have serious consequences on

diversity and abundance of small mammals in prairie communities. Our results parallel but also differ from those of Chapman et al. (2004a) and Coppedge et al. (2001), who studied avian communities responding to cedar invasion in western Oklahoma. As with prairie-associated small mammals, these authors found that many grassland avian species decreased in abundance with increasing woody plant cover, notably eastern red cedar, reflecting a change in the structure of the preferred herbaceous layer (Chapman et al. 2004a). In contrast to our data on woodland mammals, overall avian species richness was enhanced with red cedar invasion by attracting open-habitat generalist and woodland bird species that generally increased with increasing woody plant cover (Chapman et al. 2004a; Coppedge et al. 2001). However, this enhancement of species richness is at the expense of the few endemic species of grassland birds. We did not observe a similar increase in woodland mammals with increasing cover of eastern red cedar. Although the low diversity of woodland mammals in the Great Plains would prevent a dramatic increase in species diversity, even common woodland species (e.g., *N. floridana* and *M. pinetorum*) were not found associated with red cedar.

Eastern red cedar has become invasive in Oklahoma and other Great Plains rangelands because of a complex interaction of multiple causes, including fire suppression, grazing by domestic ungulates, cultivation of monoculture grasslands, and anthropogenic factors (Chapman et al. 2004b; Hoch et al. 2002; Norris et al. 2001). Our work adds to a growing body of literature demonstrating the ecological effects of invasion by eastern red cedar on biodiversity, both across and within trophic levels. Hoch et al. (2002) concluded that landscape fragmentation, socioeconomic factors, and current land-use practices have made it difficult for land managers to use prescribed fire, the most efficacious management technique for controlling the spread of red cedar and reversing the conversion of Great Plains grasslands to red cedar forest. Once established, forests of eastern red cedar are difficult and expensive to remove. Early detection and selective removal of young seedlings through cutting, mowing, or grazing may be a cheaper yet effective control measure. Preventing establishment of eastern red cedar could focus on efforts to manage seed dispersers by removing potential bird perches such as fences (Holthuijzen and Sharik 1985) or by selectively removing isolated, mature red cedar trees that attract mammals and birds to forest edges where they can consume and deposit red cedar seeds (Horncastle et al. 2004).

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