



Low-basal area treatment and prescribed fire to restore oak-pine savannas alter small mammal communities



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ABSTRACT

Following decades of fire suppression many oak-pine savanna ecosystems have shifted to closed-canopied forests. Restoration of these ecosystems to their savanna condition is seen as a way to reduce woody species encroachment and dangerous fuel loads, and restore community species composition. The management practices to achieve these goals typically involve thinning and prescribed fire. We assessed how thinning to reduce basal area combined with frequent prescribed fire influenced small mammal communities and their habitat. We focused on six habitat variables that can influence small mammal abundance and species composition: stand basal area of live trees and snags, volume of coarse woody debris, percent ground cover, forest floor depth, and distance of vulnerability to predators. Although savanna restoration reduced basal area by 80%, there was no change in snag density or coarse woody debris volume. Savanna restoration significantly increased the ground cover of graminoids, forbs, bare ground, and down woody debris and reduced forest floor depth and distance of vulnerability. These habitat changes likely contributed to the significant differences between small mammal communities in restored and non-restored stands. Restoration treatments caused a large increase in abundance of White-footed Mouse (*Peromyscus leucopus*) and important changes in community assemblages. Least Shrew (*Cryptotis parva*), Fulvous Harvest Mouse (*Reithrodontomys fulvescens*), Eastern Harvest Mouse (*R. humilis*), and Hispid Cotton Rat (*Sigmodon hispidus*) were caught only in restored stands, while House Mouse (*Mus musculus*), Plains Harvest Mouse (*R. montanus*), and Texas Mouse (*P. attwateri*) were caught only in non-restored stands.

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1. Introduction

Oak-pine savannas of south-central United States evolved over thousands of years under a largely anthropogenic fire regime (DeSantis et al., 2010a; Stambaugh et al., 2013). Starting in the 1920's, Euro-American settlers altered this disturbance regime through fire suppression (Guyette et al., 2006; Stambaugh et al., 2013). Increased tree densities, decreased understory herbaceous vegetation biomass, denser midstories, and altered species composition followed, leading to changes in plant communities and vegetation structure (Chapman et al., 2006; DeSantis et al., 2011; 2010b). Restoration treatments have been implemented to reduce stand basal area (BA), with the goal to increase understory productivity and carrying capacity for wildlife. Mechanical or chemical tree thinning followed by frequent prescribed fires was found to

be effective to reduce tree densities and increase understory vegetation productivity (Brose and Van Lear, 1998; Masters et al., 1993). As these savanna restoration treatments gain popularity and become more widespread, it is important to determine their effects on wildlife habitat and wildlife communities to better inform land managers (Fontaine and Kennedy, 2012). It is thus important to assess the response of small mammals to savanna restoration because changes in small mammal communities could potentially alter ecosystem services.

Small mammals provide crucial ecosystem services such as seed and mycorrhizal fungal spore dispersal (Hollander and Vander Wall, 2004; Pyare and Longland, 2001; Schickmann et al., 2012), nutrient cycling (Reichman and Seabloom, 2002), and soil structure (Reichman and Seabloom, 2002). They are also important in the diet of many predaceous avian, reptilian, and mammalian species (Clark, 2002; Korschgen and Stuart, 1972; McVey et al., 2013). Moreover, some species are hypothesized to regulate ectoparasite populations of cervids (Kaunisto et al., 2012), while other species are hosts to parasites and vectors of diseases (Charles et al., 2012; Pitts et al., 2013). As small mammals provide ecological

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services and act as parasite hosts, changes in their community structure and in their habitat use through the direct and indirect effects of land management practices should be monitored carefully.

Savanna restoration can potentially affect small mammals through changes in their predation pressure and basic life requirements: water, food, and shelter. Changes in some environmental characteristics can be indicative of changes in small mammal habitat and small mammal communities. First, changes in stand BA can affect predation rates, food sources, and microclimate through changes in cover and overstory biomass (Hayes, 1996; Heithacker and Halpern, 2006; Torre and Díaz, 2004). Second, changes in the BA of snags (standing dead trees) can affect corridors for movement, nesting ground, food, and cover from predators (Kalies et al., 2012). Third, changes in the volume of coarse woody debris (CWD) can also influence protective cover for movement, nesting habitat, and forage grounds (Fauteux et al., 2012; Pearce and Venier, 2005). Fourth, changes in ground cover may alter shelter, food, and predation pressure, leading to difference in small mammal species and abundance (small mammals show species specific affinities for certain ground cover types; Jones et al., 2003; Kalies et al., 2012; Stancampiano and Schnell, 2004). Fifth, changes in the forest floor (litter and duff) depth can influence the abundance of some small mammal species by influencing the abundance of insects (Churchfield, 1982; Ober and DeGroot, 2011) and providing a moderated micro-climate protecting animals from extreme temperatures and low humidity (Matlack et al., 2002). Finally, changes in the distance of vulnerability (DOV), a measure of understory vegetation structure and animal vulnerability to visual predators, can influence species composition and abundance (Perry and Thill, 2005). Measuring how these six characteristics change with restoration can potentially explain changes in small mammal communities.

Our primary goal was to determine how savanna restoration in oak-pine forests altered small mammal habitat and how these changes altered small mammal communities. We monitored six habitat characteristics pre- and post-restoration: (1) BA of live trees, (2) BA of snags, (3) CWD volume, (4) ground cover, (5) forest floor (litter and duff) depths, and (6) the DOV. We hypothesized savanna restoration would induce significant changes in small mammal habitat which would alter small mammal communities. We expected restoration to decrease the BA of live trees, forest floor depth, and DOV, to increase the BA of snags and CWD volume, and to alter ground cover. We also expected restoration to alter small mammal communities by favoring species that required open spaces and increased forest floor productivity.

2. Materials and methods

2.1. Study site

Research was conducted at Pushmataha Wildlife Management Area (PWMA) in Pushmataha County, southeast Oklahoma (34°32'N, 95°21'W) located near Clayton, Oklahoma, U.S., at the western edge of the Ouachita Mountains. The county has a mean annual temperature of 17 °C (January being the coldest month) and a mean annual rainfall of 1256 mm (Oklahoma Climatological Survey, 2015). The average growing season has 214 days (Oklahoma Climatological Survey, 2015). Following fire suppression, the oak-pine forest was dominated by Post Oak (*Quercus stellata* Wangenh.) and Shortleaf Pine (*Pinus echinata* Mill.) and the understory vegetation was mainly Little Bluestem (*Schizachyrium scoparium* (Michx.) Nash), Big Bluestem (*Andropogon gerardii* Vitman), and Sedges (*Carex* L. spp.) (Masters et al., 1993).

Oklahoma Department of Wildlife Conservation (ODWC) established PWMA as a deer refuge in 1946 (Masters et al., 1993) and it has grown to cover 7690 ha of rugged terrain, with slopes from 0 to 60%. ODWC managed PWMA for game species, such as White-tailed Deer (*Odocoileus virginianus* (Zimmermann)), Elk (*Cervus elaphus* L.), and Eastern Wild Turkey (*Meleagris gallopavo silvestris* Vieillot) (Masters and Engle, 1994). Restoration reduced stand density by timber harvesting and maintained the open condition through prescribed burning. Prior to 1946, PWMA was used for ranching and selective timber harvest (Masters, 1991).

We studied the effects of restoration treatments on small mammal habitat and communities by comparing four restored and four non-restored stands (Fig. 1a, b). Restored stands averaged 57 ha (range: 38–73 ha) and non-restored stands averaged 54.75 ha (range: 23–80 ha). Restored stands were thinned in 2008 and 2009 to a target BA of 7 m² ha⁻¹. Thinning was not done within 15 to 50 m of water courses to maintain riparian corridors and protect streams. Non-restored stands had not been thinned within the past 20 years. Restored stands were burned 5 or 6 times between 1997 and 2012 and again in March 2013 just prior to the start of this study. Two of the four restored stands were burned during the study in February 2014. Non-restored stands were burned 3 to 5 times between 1997 and 2012. One non-restored stand was burned during the study in March 2014. Growing season burns were preferred, although most burns were conducted during the dormant season between January and March, due to logistical constraints. Restored stands were oak-pine savannas, while non-restored stands were closed canopied oak-pine forests. Prior to restoration, all stands were closed canopied oak-pine forests.

Habitat characteristics and small mammal populations were measured along one 370 m transect placed in the middle of each stand. To reduce edge effects, stands were selected to be at least 420 m by 60 m and without roads (active or abandoned), human infrastructure, water bodies, or watercourses. All stands were located on soils of the Carnasaw-Stapp association (Soil Survey Staff – NRCS, 2013).

2.2. Habitat measurements

We measured habitat variables at 10 m intervals along each transect for a total of 37 plots per stand. Measurements were taken between May and August 2013. Not all characteristics could be measure at the same time and repeated visits were required. Each habitat variable was measured across all stands in a period of 10 days or less to minimize variation due to temporal change.

We measured the BA of snags and live trees at the plot center through a variable radius plot design, using a Criterion® RD 1000 (Laser Technology Inc.) set at a BA factor of 2.3 m² ha⁻¹. Tallied trees were recorded as conifer (Shortleaf Pine) or hardwood.

CWD volume (m³ ha⁻¹) was assessed by measuring all logs within a circular six-meter diameter plot. CWD was defined as any woody debris longer than 910 mm, >75 mm in diameter, <45° from horizontal, and detached from a tree. Only the portion of each log within the circle was measured. Length and diameter at the small and large end of all logs were recorded and volume was calculated using the formula of the frustum of a right circular cone. The volume of all logs within a circle was then totaled and transformed to m³ ha⁻¹.

We measured ground cover in the same circular plots using Daubenmire percent cover classes (Daubenmire, 1959). Ground covers were: graminoids with basal rosettes (e.g., Rosette Grass [*Dichanthelium* Gould]), other graminoids, forbs, legumes, litter, woody plants, rocks, bare ground, and down woody debris (DWD). USDA (2015) defined graminoids as “grass or grass-like plant, including grasses (Poaceae), sedges (Cyperaceae), rushes (Juncaceae), arrow-grasses (Juncaginaceae), and quillworts (Iso-

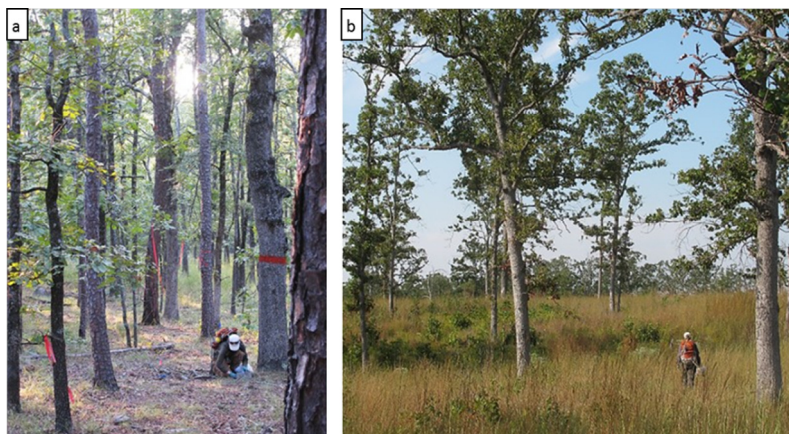


Fig. 1. Non-restored closed canopied forest (a) and restored savanna (b). Photo credits: E.A. Sinnott.

etes)". The percent ground cover of graminoids was divided into two categories (graminoids with and without basal rosettes), because graminoids with basal rosettes can provide forage that is higher in nutrients during late winter and early spring when food is scarce (Masters et al., 1993; Short, 1971). DWD included any woody debris with a diameter ≥ 6 mm, $<45^\circ$ from horizontal, and detached from a tree.

Litter and duff depths were measured to the nearest millimeter in each cardinal direction, one meter from each plot center. Duff was defined as "partially decomposed organic matter lying beneath the litter layer and above the mineral soil" (Brown and Smith, 2000) and forest floor depth was defined as the sum of litter and duff depths.

We used a modified version of the protocol for the "cone of vulnerability" by Kopp et al. (1998) to measure the DOV. Instead of calculating a volume within which an animal was vulnerable to predators (cone of vulnerability), we measured the distance at which the animal was vulnerable to visual predators (distance of vulnerability). To represent a small mammal, we used one half of a tennis ball painted bright blue. We laid the half-ball directly on the ground and recorded the minimum distance at which the object was 100% obscured from view of an observer one meter from the ground, in each cardinal direction. The obstacle responsible for the visual obstruction was recorded as: woody plants, forbs and legumes, graminoids, stumps and snags, topography, rocks, or woody debris.

2.3. Small mammal sampling

Trapping stations were established along each transect in the same location as the 37 plots measured for habitat characteristics. Transects were chosen over grid trapping because transects are more efficient than grids for studying small mammal community composition (Pearson and Ruggiero, 2003). A combination of Sherman live traps ($7.6 \times 8.9 \times 22.9$ cm) and pitfall live traps was used to maximize the number of individuals and species captured (Dizney et al., 2008; Torre et al., 2010). We placed one Sherman trap within 1 m of every plot center and one pitfall trap within 2 m of every third plot center, for a total of 37 Sherman (10 m apart) and 12 pitfall traps (30 m apart) per transect. The pitfall traps were 16.25 cm diameter PVC pipes cut to 20.3 cm length, buried flush to the ground and with aluminum screen at the bottom. Woody debris or rocks found within 1 m (Sherman trap) or 2 m (pitfall traps) of a plot center were used as drift fences directing small mammals into traps. Between trapping sessions, all Sherman traps were removed and pitfall traps were closed.

Small mammal trapping and handling was compliant with protocols from the Institutional Animal Care and Use Committee (ACUP AG-12-16) and followed the guidelines from the American Society of Mammologists (Sikes et al., 2011). Sampling occurred in April, June, and September 2013 (spring, summer, and fall 2013), and in January and March 2014 (winter 2013–2014 and spring 2014). During each sampling period, traps were opened for three nights around sunset. We checked traps in the mornings and closed them during the day to reduce risk of heat-induced mortality. We also added polyester bedding in the traps to reduce risks of hypothermia-induced mortality during colder months (Matlack et al., 2008). Sherman traps were baited with peanut butter and rolled oats (Johnston and Anthony, 2008; Matlack et al., 2008; Stancampiano and Schnell, 2004). Because shrews are mostly caught in pitfall traps and have high metabolic rates putting them at risk of death from starvation (Do et al., 2013), we added approximately 30 g of wet dog food to the pitfall traps. Dog food was not used during the second and third day of trapping in summer 2013, because Red Imported Fire Ant (*Solenopsis invicta* Buren) was attracted to the traps during summer. A modification to the ACUP protocol was approved, allowing for the use of 5% Carbaryl insecticide (GardenTech® Sevin-5 Ready to Use 5% Dust) around all traps in subsequent sampling periods.

Distinction between Deer Mouse (*Peromyscus maniculatus* (Wagner)) and White-footed Mouse (*Peromyscus leucopus* (Rafinesque)) was based on tail and hind-foot length and pelage coloration on the tail.

All animals captured were marked under the chin with a felt-tip permanent marker (Sauvajot et al., 1998), identified to species, and released at the site of capture. The marking technique was chosen because it was non-invasive, required little training, and should have lasted for the duration of each sampling period. Low capture rates in early 2013 did not allow training staff on proper ear-tagging techniques and therefore animals were not ear-tagged. Because of the marking technique chosen, identifying recaptured animals was not always possible.

2.4. Data analysis

Identifying recaptured animals was not possible for all sampling periods because of the marking technique; therefore analyses were performed using new captures and recaptures combined. Due to low capture rates, data was combined as follows: (1) all sampling periods combined and (2) spring 2013 and 2014. We were able to perform analyses for spring only because most captures took place in spring 2014. Bonferroni adjustments were implemented ($\alpha = 0.025$) to account for analyses being performed twice. A third

set of analyses showed that the higher capture rates in spring 2014 were not responsible for the results observed for all sampling periods (not further discussed).

We used the frequency of captured small mammal species (number of traps containing a species divided by the number of adjusted trap-nights) as a measure of abundance. We adjusted the number of trap-nights for Sherman traps to account for unavailable traps (empty sprung traps and closed traps with a captured animal) as per [Beauvais and Buskirk \(1999\)](#): Number of adjusted trap-nights = (number of traps * number of nights opened) – (number of unavailable traps * 0.5).

Analyses were performed for abundant species (≥ 20 captures) and for all species combined. We estimated species richness by rarefaction in EstimateS version 9 ([Colwell, 2013](#)), with the Chao2 estimator ([Brose, 2002](#)).

We calculated Pearson correlation coefficients to assess correlations among habitat covariates (SAS PROC CORR; [SAS Institute, 2012](#)). The effect of savanna restoration on habitat characteristics, small mammal abundance, and species richness was determined by the *t*-test ($n = 8$); there were four experimental units for restored and for non-restored treatments. Levene's test was used to test for homogeneity of variance ([Snedecor and Cochran, 1980](#)). Bonferroni adjustments were performed when necessary: $\alpha = 0.006$ for ground cover and $\alpha = 0.007$ for DOV ($\alpha = 0.05$ for other variables tested). All statistical analyses were performed in IBM SPSS Statistics for Windows version 21.0 ([IBM Corp, 2012](#)).

Canonical Correspondence Analyses (CCA) were conducted to determine effects of stand restoration on small mammal communities ([ter Braak, 1986](#)) using BA as the sole explanatory variable tested. Detrended Correspondence Analyses (DCA; [Hill and Gauch Jr., 1980](#)) were conducted to explore correlations between environmental variables and small mammal species composition. We performed CAAs and DCAs in Canoco 5.03 ([ter Braak and Šmilauer, 2013](#)), log-transformed abundances, and down weighted rare species. For the DCAs, habitat variables were set as supplementary variables.

3. Results

3.1. Habitat

Savanna restoration reduced BA to 4.4 ± 0.6 (SE) $\text{m}^2 \text{ha}^{-1}$ compared to $22.6 \pm 1.1 \text{m}^2 \text{ha}^{-1}$ ($P < 0.001$) in non-restored stands and decreased the relative importance of Shortleaf Pine from 60% of stand BA to 30%. Savanna restoration did not significantly reduce the BA of snags ($0.4 \pm 0.2 \text{m}^2 \text{ha}^{-1}$ in restored stands vs $1.0 \pm 0.2 \text{m}^2 \text{ha}^{-1}$ in non-restored stands, $P = 0.053$) or the abundance of CWD ($7.3 \pm 1.3 \text{m}^3 \text{ha}^{-1}$ in restored stands vs $5.4 \pm 2.0 \text{m}^3 \text{ha}^{-1}$ in non-restored stands, $P = 0.465$). Many habitat variables showed significant correlation within restored and within non-restored stands ([Tables 1, 2](#); [Fig. 2](#)).

Table 1
Pearson correlation coefficients for structural habitat variables in restored stands. The diagonal separates Pearson correlation coefficients (above) from *P*-values (below). BA_live: basal area (BA) of live trees, BA_snags: BA of snags, CWD_vol: coarse woody debris volume, FF: forest floor depth, GC_woody: percent ground cover (GC) of live woody plants, GC_litter: percent GC of litter, GC_rocks: percent GC of rocks, GC_bare: percent GC of bare ground, GC_DWD: percent GC of down woody debris, GC_annual: percent GC of annual plants, DOV: distance of vulnerability.

Pearson Correlation Coefficients, N = 148											
Prob > r under H0: Rho = 0											
	BA_live	BA_snags	CWD_vol	FF	GC_woody	GC_litter	GC_rocks	GC_bare	GC_DWD	GC_annual	DOV
BA_live		−0.20 [*]	−0.04	−0.01	0.14	0.12	−0.25 [*]	0.17 [*]	−0.14	−0.25 [*]	0.39 [*]
BA_snags	0.01		0.17 [*]	0.11	−0.12	−0.12	−0.04	−0.11	0.16	−0.01	−0.18 [*]
CWD_vol	0.61	0.03		0.07	−0.04	−0.04	−0.04	−0.04	0.40 [*]	0.06	−0.18 [*]
FF	0.95	0.18	0.42		0.07	0.06	−0.17 [*]	−0.11	0.16 [*]	0.05	−0.04
GC_woody	0.10	0.14	0.66	0.40		0.17 [*]	0.19 [*]	0.01	0.00	−0.34 [*]	0.04
GC_litter	0.15	0.16	0.62	0.44	0.04		−0.08	0.10	0.14	−0.21 [*]	0.22 [*]
GC_rocks	<0.01	0.62	0.63	0.04	0.02	0.31		−0.12	−0.02	−0.07	−0.20 [*]
GC_bare	0.04	0.18	0.61	0.19	0.94	0.24	0.15		0.14	−0.48 [*]	0.32 [*]
GC_DWD	0.09	0.05	<0.01	0.05	0.98	0.09	0.82	0.08		−0.15	−0.11
GC_annual	0.00	0.89	0.45	0.56	<0.01	0.01	0.39	<0.01	0.07		−0.37 [*]
DOV	<0.01	0.03	0.03	0.60	0.60	0.01	0.01	<0.01	0.18	<0.01	

^{*} Indicate significant correlation ($P < 0.05$).

Table 2
Pearson correlation coefficients for structural habitat variables in non-restored stands. The diagonal separates Pearson correlation coefficients (above) from *P*-values (below). BA_live: basal area (BA) of live trees, BA_snags: BA of snags, CWD_vol: coarse woody debris volume, FF: forest floor depth, GC_woody: percent ground cover (GC) of live woody plants, GC_litter: percent GC of litter, GC_rocks: percent GC of rocks, GC_bare: percent GC of bare ground, GC_DWD: percent GC of down woody debris, GC_annual: percent GC of annual plants, DOV: distance of vulnerability.

Pearson Correlation Coefficients, N = 148 Prob > r under H0: Rho = 0											
	BA_live	BA_snags	CWD_vol	FF	GC_woody	GC_litter	GC_rocks	GC_bare	GC_DWD	GC_annual	DOV
BA_live		0.04	0.01	0.11	0.00	0.41 ⁺	−0.25 ⁺	−0.13	−0.05	−0.42 ⁺	0.19 ⁺
BA_snags	0.67		0.15	−0.08	−0.05	−0.15	0.06	−0.01	0.19 ⁺	0.04	−0.15
CWD_vol	0.89	0.08		−0.07	−0.04	−0.13	0.06	0.00	0.41 ⁺	0.02	−0.25 ⁺
FF	0.19	0.36	0.37		0.29 ⁺	−0.01	−0.07	−0.09	0.03	−0.05	−0.10
GC_woody	0.95	0.54	0.63	<0.01		0.08	−0.11	−0.04	0.08	−0.20 ⁺	−0.24 ⁺
GC_litter	<0.01	0.07	0.13	0.90	0.31		−0.35 ⁺	−0.11	−0.14	−0.72 ⁺	0.46 ⁺
GC_rocks	<0.01	0.49	0.43	0.37	0.17	<0.01		0.07	0.06	0.19 ⁺	−0.12
GC_bare	0.10	0.91	0.98	0.26	0.59	0.18	0.40		0.12	−0.07	0.02
GC_DWD	0.51	0.02	<0.01	0.75	0.36	0.09	0.47	0.16		0.05	−0.22 ⁺
GC_annual	<0.01	0.66	0.80	0.52	0.02	<0.01	0.02	0.41	0.55		−0.44 ⁺
DOV	0.02	0.06	<0.01	0.20	<0.01	<0.01	0.16	0.84	0.01	<0.01	

^{*} Indicate significant correlation ($P < 0.05$).

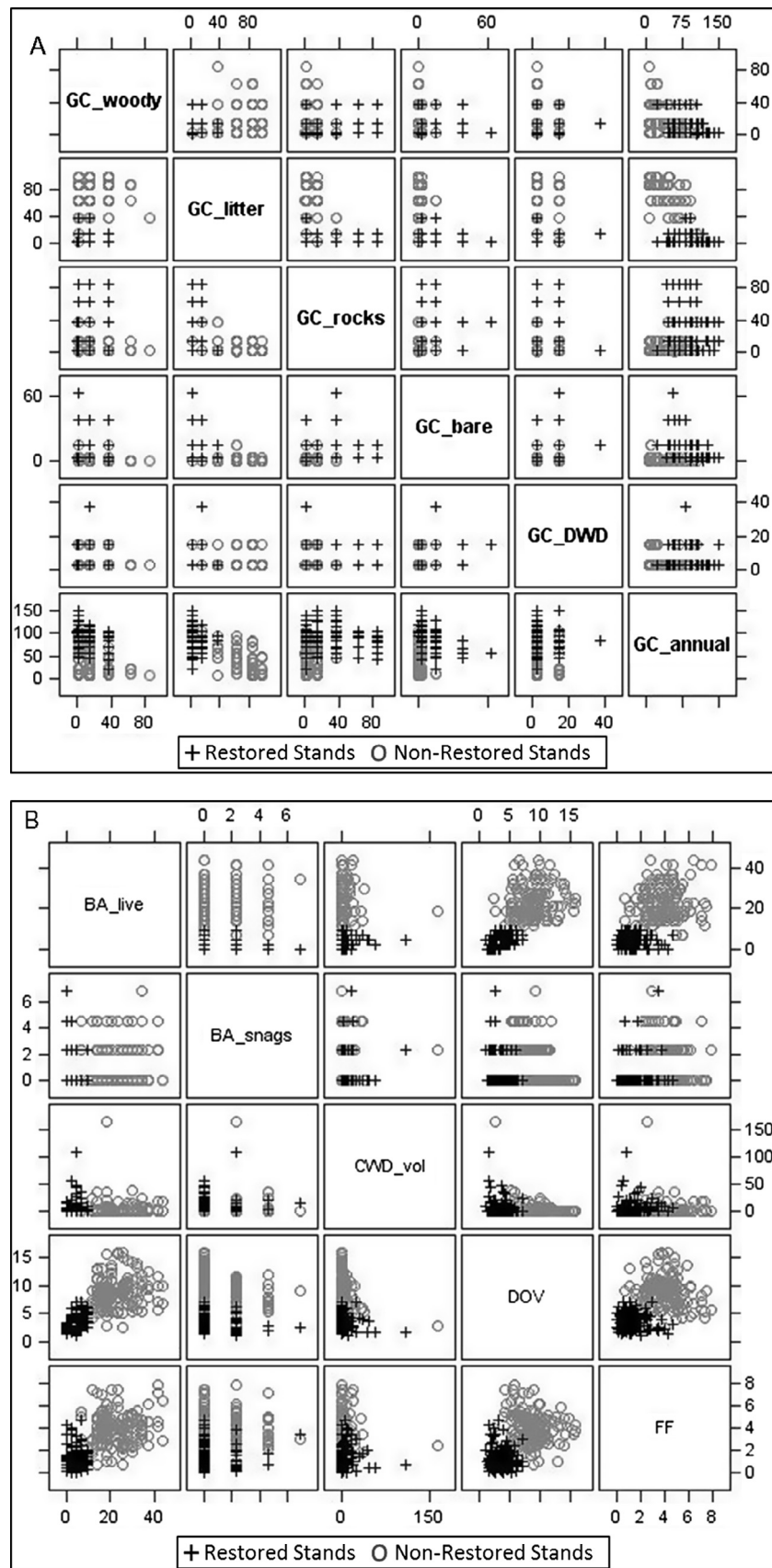


Fig. 2. Matrices showing correlation among structural habitat variables. Restored stands are represented by black crosses; non-restored stands are represented by grey open circles. Each point is the value for a variable from a single plot; closer symbols indicate higher correlation. Graphs above and below the diagonal are mirrored images. (A) GC_woody: percent ground cover (GC) of live woody plants, GC_litter: percent GC of litter, GC_rocks: percent GC of rocks, GC_bare: percent GC of bare ground, GC_DWD: percent GC of down woody debris, GC_annual: percent GC of annual plants. (B) BA_live: basal area (BA) of live trees, BA_snags: BA of snags, CWD_vol: coarse woody debris volume, DOV: distance of vulnerability, FF: forest floor depth.

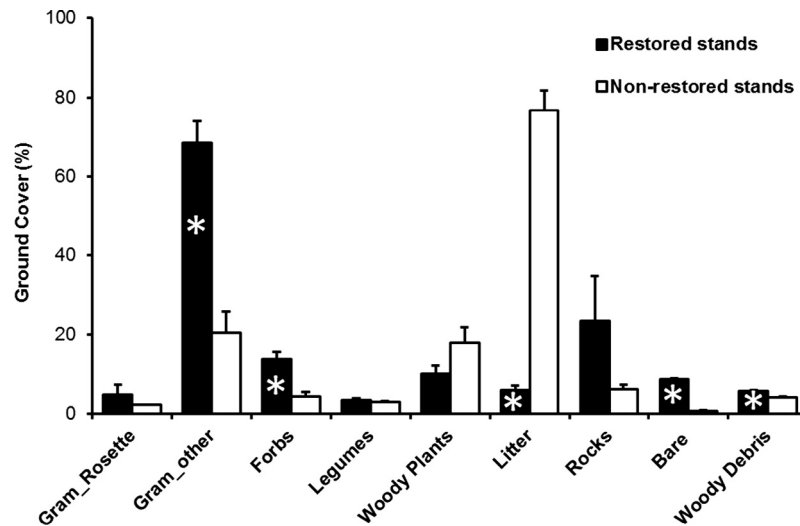


Fig. 3. Effects of savanna restoration on ground covers. Asterisks indicate significant treatment effects ($P < 0.006$). Thin bars represent standard errors. "Gram_Rosette": graminoids with basal rosettes; "Gram_Other": graminoids without basal rosettes.

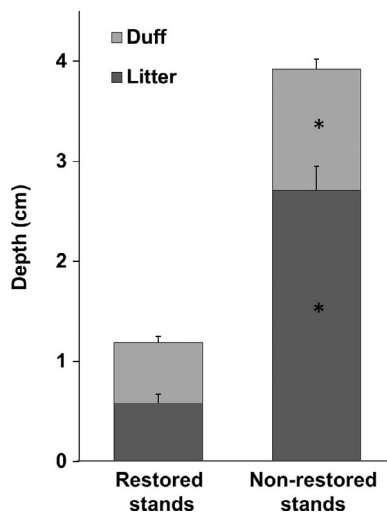


Fig. 4. Effects of savanna restoration on forest floor depth. Asterisks indicate significant treatment effects (litter: $P = 0.001$; duff: $P = 0.002$). Thin bars represent standard errors.

Savanna restoration significantly increased the percent ground cover of graminoids without basal rosettes ($P = 0.001$), forbs ($P = 0.004$), bare ground ($P < 0.001$), and DWD ($P = 0.005$), and significantly decreased the percent ground cover of litter ($P < 0.001$), but had no significant effect on the percent ground cover of graminoids with basal rosettes ($P = 0.422$), legumes ($P = 0.552$), woody plants ($P = 0.131$), or rocks ($P = 0.224$) (Fig. 3). The most prevalent ground covers in restored stands were graminoids without basal rosettes ($68.4 \pm 5.7\%$), rocks ($23.4 \pm 11.3\%$), and forbs ($13.8 \pm 1.7\%$), and in non-restored stands were litter ($76.6 \pm 5.1\%$), graminoids without basal rosettes ($20.4 \pm 5.4\%$), and woody plants ($17.8 \pm 3.9\%$). Forest floor depth was reduced nearly 80% in restored stands and litter was reduced more than duff (litter: $P = 0.001$; duff: $P = 0.002$; Fig. 4).

The DOV was significantly shorter in restored stands (3.6 ± 0.5 m) compared to non-restored stands (8.7 ± 0.3 m, $P < 0.001$). The most important visual obstacles in restored stands were graminoids ($75.2 \pm 4.5\%$), woody plants ($10.1 \pm 2.9\%$), and forbs and legumes ($7.9 \pm 2.4\%$), and in non-restored stands were

woody plants ($58.2 \pm 4.6\%$), graminoids ($20.3 \pm 5.8\%$), and topography ($11.1 \pm 3.2\%$). Graminoids were significantly more important visual obstacles in restored stands than in non-restored stands ($P < 0.001$), while woody vegetation was a significantly less important visual obstacle in restored stands than in non-restored stands ($P < 0.001$). Other obstacles were not significantly different between restored and non-restored stands.

3.2. Small mammals

We captured 274 small mammals from 10 species over 5397 adjusted trap-nights. The number of adjusted trap-night per transect was: 500, 521, 522, and 523 in restored stands and 499, 527, 535, and 535, in non-restored stands. Only one species, Least Shrew (*Cryptotis parva* (Say), $n = 2$), was captured in pitfall traps; all other species were caught in Sherman traps. Capture rates (number of traps containing an animal divided by the number of adjusted trap-nights) were low, ranging from 1.9% in winter 2013–2014 to 12.5% in spring 2014, with an average trapping success of 5.1% per sampling period.

The pooled capture rate for all species from all sampling periods was not significantly different between restored and non-restored stands ($n = 274$, $P = 0.031$). Only three species were caught ≥ 20 times: White-footed Mouse ($n = 176$), Deer Mouse ($n = 32$), and Fulvous Harvest Mouse (*R. fulvescens*, J.A. Allen; $n = 33$). Savanna restoration significantly increased the capture rate of White-footed Mouse ($P = 0.002$), but not Deer Mouse ($P = 0.271$). Fulvous Harvest Mouse was only caught in restored stands. Results from pooled spring sampling periods alone were very similar and will not be discussed separately.

The CCA for all sampling periods combined revealed different small mammal community compositions between restored and non-restored stands ($P = 0.002$, Fig. 5). The CCA primary axis (BA) had a fairly high eigenvalue of 0.3070 while the eigenvalue of the 1st residual axis (0.1953) was lower. This implied that restoration had a relatively strong influence on small mammal communities. Least Shrew, Fulvous Harvest Mouse, Eastern Harvest Mouse (*R. humilis* [Audubon and Bachman]), and Hispid Cotton Rat (*Sigmodon hispidus* Say and Ord) were only caught in restored stands; House Mouse (*Mus musculus* L.), Texas Mouse (*P. attwateri* Allen), and Plains Harvest Mouse (*R. montanus* (Baird, 1855)) were only captured in non-restored stands; Cotton Mouse (*P. gossypinus* (LeConte)), White-footed Mouse, and Deer Mouse were caught in

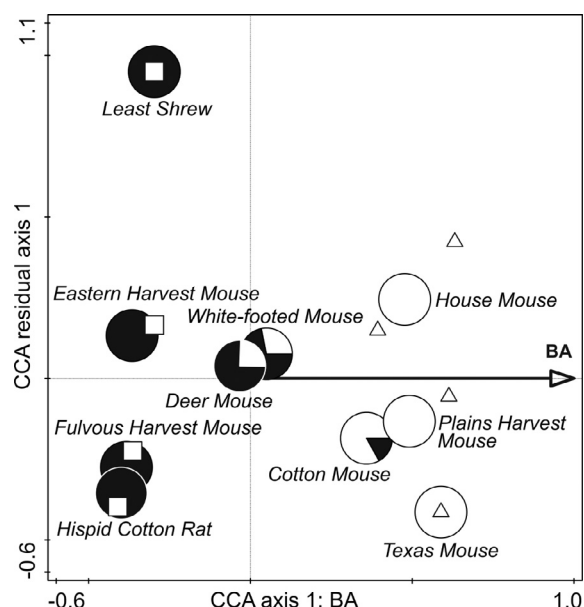


Fig. 5. Canonical Correspondence Analyses (CCA) results for all sampling periods combined: effects of restoration on small mammal community composition. Treatment effects were significant ($P = 0.002$). For each species, a pie chart shows the proportion of captures in restored (black) and non-restored stands (white). Species towards the left of the graph were more closely associated with restored stands, and species towards the right, with non-restored stands. Squares represent restored stands and, triangles, non-restored stands. The CCA primary axis was basal area (BA).

both restored and non-restored stands. The CCA for captures from spring 2013 and 2014 combined showed similar patterns ($P = 0.002$).

Restored and non-restored stands also formed two distinct groups along the DCA primary axis for all captures combined, and for pooled spring captures (Fig. 6a). The primary axes thus likely represented BA. When habitat characteristics were included as supplementary variables for the DCA for all sampling periods combined (similar results were obtained for spring only trapping events) the following habitat variables were strongly positively correlated: snags and tree BA, woody plant and litter ground covers, litter and duff depths, and DOV (Fig. 6b). These variables were strongly negatively correlated with rocky ground cover, graminoids without basal rosettes ground cover, forbs ground cover, bare ground cover, woody debris ground cover, and CWD volume. Because of the strong positive and negative correlations between habitat variables, we were not able to determine which variables caused small mammal communities to respond to savanna restoration.

The results suggested weather conditions during the study may have affected measurements of small mammal communities. Severe and moderate drought conditions that persisted until April of 2013 (NOAA, 2014a, 2014b) likely partly explained low capture rates in 2013. The large increase in capture rates in spring 2014 may have resulted from more normal moisture conditions for the rest of 2013 and early 2014 allowing small mammal populations to recover from the drought.

4. Discussion

Our findings indicate that savanna restoration resulted in expected changes in vegetation composition and structure and concurrent changes in small mammal communities. Although overall small mammal abundance did not change, restoration resulted in a significant increase in White-footed Mouse and a dif-

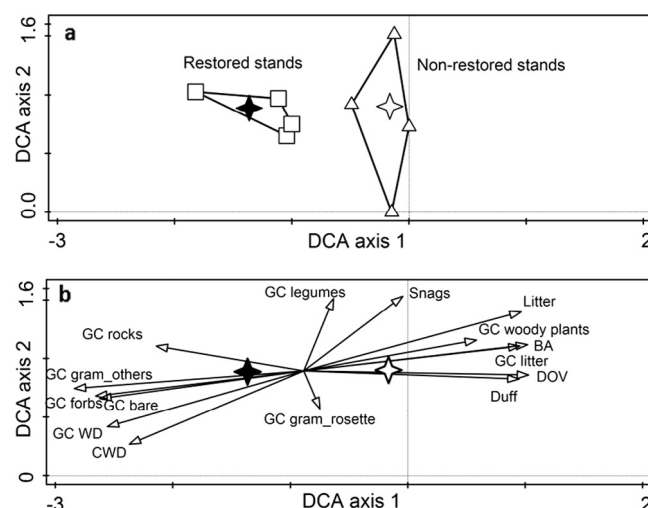


Fig. 6. Positions of stand scores along Detrended Correspondence Analyses (DCA) axis 1 and 2 (a), and relationships among 15 habitat variables on the same DCA axes (b), analyzed for all sampling periods combined. The treatment (restoration) was set as supplementary variables (represented by stars). Squares represent restored stands and, triangles, non-restored stands. GC_woody plants: percent ground cover (GC) of live woody plants, BA: basal area (BA) of live trees, GC litter: percent GC of litter, DOV: distance of vulnerability, Duff: duff depth, GC gram_rosette: percent GC of graminoids with basal rosettes, CWD: coarse woody debris volume, GC WD: percent GC of down woody debris, GC bare: percent GC of bare ground, GC forbs: percent GC of forbs, GC gram_others: percent GC of graminoids without basal rosettes, GC rocks: percent GC of rocks, GC legumes: percent GC of legumes, Snags: BA of snags, litter: litter depth.

ferent assemblage of small mammal species. Least Shrew, Fulvous Harvest Mouse, Eastern Harvest Mouse, and Hispid Cotton Rat were caught only in restored stands, while House Mouse, Plains Harvest Mouse, and Texas Mouse were caught only in non-restored stands. Savanna restoration caused important changes in habitat; however, interpreting influences of individual habitat characteristics on small mammal communities was complicated by high correlations among habitat characteristics. For example, thinning reduced stand BA, which allowed more light to reach the ground layer causing increased production of forbs and graminoids which led to shorter DOV.

4.1. Habitat

Thinning reduced stand BA by over 80%, well below target BA of $7 \text{ m}^2 \text{ ha}^{-1}$, and decreased the relative importance of Shortleaf Pine. Because small mammal species have shown different preferences for types of foods (Lobo et al., 2009; Plucinski and Hunter, 2001), the large reduction in tree density and major shift in canopy species composition could have long-term effects on small mammal abundance and species composition. For example, acorns can be an important source of food for White-footed Mouse and Deer Mouse, especially in winter (Elkinton et al., 1996; McCracken et al., 1999; Ostfeld et al., 1996; Plucinski and Hunter, 2001; Schnurr et al., 2002; Stancampiano and Caire, 1995). By reducing the availability of acorns in winter, a large reduction in oak species could impact the winter survival rates of these species.

Although reduced tree cover due to thinning should produce fewer snags and less CWD in the long-term, this effect was not seen four to five years post thinning. The greater fire frequency in the thinned stands (6–7 burns vs 3–5 burns over 17 years) was not likely to affect the quantity of snags or CWD, as low intensity winter burns do not typically consume significant amounts of large fuel (Polo et al., 2013). Snags and CWD can benefit small mammal species by providing cover, nesting habitat, forage grounds, and running corridors (Fauteux et al., 2012; Kalies et al.,

2012; Pearce and Venier, 2005). The inevitable decline in snags and CWD that will result from reduced stand density can be delayed by encouraging loggers to leave more standing dead trees and slash.

Our results also revealed that the percent ground cover of woody vegetation was not significantly different between restored and non-restored stands. This finding was consistent with earlier work that showed prescribed burning (Burton et al., 2011) and thinning and prescribed burning (Masters et al., 1993) produced no change or only a weak increase in woody vegetation. Most of the woody plants in the understory were sprouts dependent on root systems of established trees. The fact that fire stimulates sprouting while killing existing sprouts may explain the weak response of woody vegetation to prescribed burning (Clark and Hallgren, 2003; DeSantis et al., 2011). The increase in down woody debris cover was understandably small given there was no restoration treatment effect on CWD biomass. This small increase (1.76%) in the ground cover of down woody debris may not be biologically meaningful to small mammals (Greenberg, 2002).

The greatly increased percent cover of bare ground and reduced litter cover and litter and duff depth in restored stands was due, at least in part, to recent burning. Litter depth is closely related to time since last burn (Burton et al., 2011) and the restored stands were burned less than a full growing season before measurements were made while the non-restored stands had been burned 2 and 10 growing seasons earlier. According to litter accumulation equations from earlier research (Bale, 2009; Stambaugh et al., 2006), litter depth would be nearly 98% of equilibrium depth in stands burned in 2003; 53% of equilibrium depth in stands burned in 2011, and less than 10% of equilibrium depth in stands burned in 2013. Plans to prescribe burn all restored stands every three years at PWMA will place a limit on litter accumulation, and maximum litter depth and cover will be far below equilibrium (Burton et al., 2011; Stambaugh et al., 2006). It was not certain whether thinning reduced litter inputs, because the increase in understory herbaceous plants may have made up for what was lost in overstory litter production. When the fire return interval is long enough, as in the non-restored stands, the accumulation of greater forest floor depth can provide protection from extreme temperatures and low humidity, a habitat requirement for some species such as Elliot's Short-Tailed Shrew (*Blarina hylophaga* Elliot) (Matlack et al., 2002). Although this species was not observed in our study it is known to inhabit surrounding areas (Thompson et al., 2011). Stand restoration may eliminate the possibility of this species inhabiting these stands.

The much greater productivity of the understory grasses in the restored stands caused a greater than 50% reduction in the DOV. A change in habitat of this magnitude could affect small mammal behavior and abundance. By integrating multiple structural characteristics of the habitat (Harrell et al., 2001; Harrell and Fuhlendorf, 2002), the DOV provided a valuable index of hiding cover for small mammals. The greater DOV of non-restored stands suggested they were characterized by a scarcity of visual obstacles which indicated a less complex understory structure. In restored stands, predators relying mainly on visual cues would have to be closer to small mammals to see them (and vice versa). This could alter the behaviors of both prey and predators.

4.2. Small mammals

White-footed Mouse is a generalist species that inhabits a diversity of habitats but tend to be more abundant in areas with greater structural complexity of understory vegetation (Anderson and Meikle, 2006). The greater abundance of White-footed Mouse within restored stands may have reflected this species being a generalist, and the positive response to savanna restoration may have been due to increased ground layer productivity and understory

complexity. Previous research showed habitat selection by White-footed Mouse can be influenced by multiple factors such as burning regime, tree density, vertical vegetation structure, structural complexity of understory vegetation, volume of woody debris, and density of shrubs, graminoids, and forbs (Anderson and Meikle, 2006; Greenberg, 2002; Kaufman et al., 1983; Masters et al., 2002). In contrast to our results, previous studies found White-footed Mouse in greater densities in non-thinned stands (Baker, 1968; Linzey et al., 2012). On the other hand, White-footed Mouse was reported to favor grasslands with a high canopy (Stancampiano and Schnell, 2004). Conflicting findings (1) may reflect differences in detection probabilities between restored and non-restored stands, or (2) may reflect geographic differences for the preferred habitat of White-footed Mouse, or (3) may have resulted from differences in weather conditions leading to variation in habitat suitability. Problems with the marking technique prevented an analysis partialling out the effect of detection probabilities.

The finding that Least Shrew, Fulvous Harvest Mouse, Hispid Cotton Rat, and Eastern Harvest Mouse were only captured in restored stands was consistent with previous research that found they were typically grassland species (Cameron and Spencer, 1981; Spencer and Cameron, 1982; Stancampiano and Schnell, 2004; Wilkins, 1995). Because Hispid Cotton Rat uses ground layer monocots as forage (Masters et al., 1998), it was not surprising that it would be associated with restored stands at PWMA. The cover of graminoids and forbs showed a strong increase in restored stands consistent with earlier research (Masters et al., 1993). Another study found C3 (cool-season, temperate) grasses showed strong increases in cover and diversity with increasing burn frequency (Burton et al., 2011). Small mammal species that feed primarily on understory vegetation, such as Fulvous Harvest Mouse and Hispid Cotton Rat (Fleaharty and Olson, 1969; Kincaid and Cameron, 1985; Masters et al., 1998) should benefit from increased herbaceous productivity resulting from savanna restoration.

That Deer Mouse was captured in both restored and non-restored stands was consistent with it being a generalist species that usually inhabits grassland, but can persist in forests or shrublands (Kamler and Pennock, 2004; Mayfield et al., 2000; Merkt, 1981). The species is omnivorous, and primarily feeds on acorns, insects, and miscellaneous vegetation (Kritzman, 1974; Pitts and Barbour, 1979; Stancampiano and Caire, 1995; Whitaker, Jr., 1966). The broad diet and overall adaptability of this species likely allowed it to inhabit both restored and non-restored stands at PWMA.

Strong inferences about habitat preferences cannot be made for species caught infrequently including: Least Shrew ($n = 2$), House Mouse ($n = 4$), Texas Mouse ($n = 1$), Cotton Mouse ($n = 6$), Fulvous Harvest Mouse ($n = 3$), and Plains Harvest Mouse ($n = 3$). However, it is important to point out that House Mouse was the only non-native species caught at PWMA. Most studies have shown that House Mouse is most commonly associated with human infrastructure such as houses and barns (Caire et al., 1989). Even though no infrastructure was located within 30 m of any transects, remnants of old fences, roads, and building foundations were scattered throughout PWMA. Captures from this species likely reflected the ranching history of PWMA.

5. Conclusions

Oak-pine savanna restoration altered key habitat characteristics (reduced basal area, increased ground cover of graminoids, forbs, bare ground, and down woody debris, and reduced forest floor depth and distance of vulnerability) which resulted in important changes in small mammal communities, although overall

abundance remained unchanged. Restored stands favored small mammal species whose niche requirements included high graminoid production, such as Fulvous Harvest Mouse and Hispid Cotton Rat. In contrast, non-restored stands favored species whose niche requirements include deep litter and duff depths or higher BA of live trees. Therefore, different specialist small mammal species occupied restored and non-restored stands. Because small mammals exercise key ecosystem functions, savanna restoration could have indirect effects on nutrient cycling, food webs, and seed germination.

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