

Consumer roles of small mammals within fragmented native tallgrass prairie

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Abstract. Grassland ecosystems globally are being negatively impacted by changes in climate, disturbance regimes, nutrient flux, and consumer guilds. Changes in the trophic ecology of consumers can substantially influence local resources, contributing to shifting diversity, community turnover, and other processes of ecosystem change. Small mammals are diverse and abundant within grasslands and yet the impact of changing ecosystems on small mammals and the role of these mammals as consumers are still both under-studied. We assessed small mammal resource use within grassland and woodland vegetation types that have resulted from landscape-scale experimental disturbance through fire treatments within the tallgrass prairie ecoregion of the North American Great Plains. We predicted that resource use would vary significantly among grassland vs. woodland communities, in turn reducing the role of small mammals in contributing to future maintenance of native prairies. We sampled five dominant species of rodents across three years and multiple habitats. Using stable isotope analysis, we investigated isotopic niche area and overlap to infer variation in diet, both within and among species. Resource use shifted in bivariate isotopic space seasonally but not across years when combining all species and habitats. Inferred spring diet (based on fur samples) was highly diverse and overlapping. Summer isotopic values (based on liver tissue) in woody habitat treatments were narrower and overlapped less than within grassland habitats. Consumers generally shifted from C_4 herbivory to C_3 herbivory, or greater omnivory, when analyzing grassland, shrubland, and woodland habitats respectively. Within the tallgrass prairie ecosystem, small mammal populations in herbaceous-dominated habitats use a broader variety of resources than small mammals in proximate woody-dominated habitats. As native grasslands experience woody encroachment, small mammal assemblages experience turnover of dominant species and associated changes in diet. Ecosystem changes such as cessation of frequent fire resulting in more woody habitats may include reduced roles by native small mammals as consumers/dispersers/propagators of native grassland plants.

Key words: climate change; community turnover; grassland; resource use; rodent diet; stable isotope ratio; wildfire; woody encroachment.

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INTRODUCTION

Grasslands constitute the largest single terrestrial biome type and historically represented ~40% of total global land cover (Dixon et al. 2014). Through the Anthropocene, a combination of human-induced climate, land-use and associated

floral and faunal community changes have resulted in substantial fragmentation, reduction in grassland extent, and corresponding loss of the ecosystem services that they provide (Hoekstra et al. 2005, Alstad et al. 2016). Temperate grasslands persist through a range of precipitation zones, including the Great Plains prairie habitats

of North America that exhibit a strong longitudinal precipitation gradient (Epstein et al. 1996). At the eastern edge of the Great Plains, sufficient rainfall allows for alternate ecosystem states of either grassland or woodland, given the presence or absence of major ecological drivers that may include dominant consumer groups (i.e., herbivory pressure), natural disturbance regimes (i.e., fire), and changing long-term climate (Briggs et al. 2005, Ratajczak et al. 2014, O'Connor et al. 2020). The North American tallgrass prairie ecoregion is one such area, where remaining fragments of native grassland are experiencing widespread woody encroachment, potentially attributable to extirpation of native mega-herbivores, cessation of natural fire regimes, and various other yet unresolved factors (e.g., increasing atmospheric CO₂, Bond and Midgley 2000, Collins and Calabrese 2012). Maintenance of existing grasslands and restoration of historic prairie habitats will depend in part on a greater understanding of linkages between major ecological drivers and the constituent roles and responses of species comprising local communities (Collins 2000, Bruckhoff et al. 2020). Here, we investigate the trophic niche dynamics of small mammal assemblages to assess the bottom-up responses of small mammals to other major drivers (climate variables and fire) through time (e.g., Báez et al. 2006) and to infer their potential roles as consumers (top-down), within an experimental prairie-woodland mosaic.

Grassland, woodland, and intermediate shrubby habitats occur throughout contemporary tallgrass prairie and support different assemblages of small mammals that rely on respective floral and faunal assemblages for food and shelter (Matlack et al. 2008). A change from grassland to intermediate shrubland to climax woodland through time is reflected by small mammal reordering of dominant species (Jones et al. 2017) and community turnover (Clark et al. 1987), with subsequent potential shifts in resource use. Alternatively, the trophic dynamics of generalist mammalian species that occupy multiple habitats may simply reflect dietary switches to use prevailing resources through time (Randolph and Cameron 2001). As such, knowledge of both species-specific ecology and inter-specific interactions is important for understanding community change and associated resource use in any given ecoregion (Supp et al.

2015). We investigate if there is predictability in trophic resource use by small mammals that may provide insight into ongoing mechanisms and consequences of ecosystem change (Bergstrom 2013).

The Konza Prairie Biological Station and Long-Term Ecological Research Site (herein Konza) provides a landscape-scale experimental system for resolving the impact of primary ecosystem drivers on local habitat change (Knapp et al. 1998). Experimental treatments include a factorial design of presence or absence of mega-herbivore grazers (American bison and domestic cattle) and variable fire return intervals. These fire and grazing combinations reflect predominant forms of land use in the region, which include substantial areas burned annually and areas that rarely burn (Ratajczak et al. 2016). Major habitat change through cessation of fire has been accompanied by changing diversity among both plant and animal assemblages (Briggs et al. 2005, Fuhlendorf et al. 2006). In addition, American bison have demonstrated a role of native grazers as drivers of change in floral diversity (Collins et al. 1998, Elson and Hartnett 2017). The relative role of other taxonomic guilds as consumers (e.g., grasshoppers) for maintaining dominant habitats, or conversely for driving progressive change, has also been investigated (e.g., Reed et al. 2004, Joern 2005) but are not yet well-resolved.

Studies of small mammal trophic ecology have a rich history in the literature and provide a foundation from which to develop nuanced alternative hypotheses for resource consumption, ranging from ecological competition for resources (e.g., Codron et al. 2015) and predation pressure (e.g., O'Brien et al. 2018) to evolutionary phylogenetic distance among focal species (Manlick et al. 2019). However, predictive power from analysis of trophic resource use for understanding small mammal consumer roles is complicated by the potential for multiple realistic alternative responses to the same trophic pressures. For instance, in times of abundant resources, a more diverse trophic niche and greater overlap of diet between species may reflect increased dietary choice and reduced competition among individuals (Bauduin et al. 2013). However, we might also predict that a flush of food sources could lead to smaller trophic niche and reduced

overlap as small mammals focus more narrowly on plentiful and species-specific food resources (Reid et al. 2013). Alternatively, if resources are pulsed through mast crops from a single source (e.g., acorns or cicada emergence) as opposed to habitat-wide increased productivity, trophic niche may be very narrow across species but highly overlapping (Stephens et al. 2019). Finally, changes in mammalian abundance may also impact results in combination with other variables (Eckrich et al. 2018).

In the present study, we assess isotopic niche variability from wild small mammal populations across three years using multiple tissue types, considering experimental manipulation of fire frequency coupled with long-term climate trends in order to infer trophic variability. On Konza, herbaceous-dominated habitats coupled with frequent prescribed fire results in a dynamic ground-level microclimate, whereas woody habitats are burned infrequently and the vertical structure provided by woody shrubs dampens ground-level environmental fluctuation (Logan and Brunsell 2015). We therefore expect mammals occupying open grasslands to consume more diverse trophic resources and with greater temporal variability in diet to reflect greater change in available resources across both seasons and years than mammals within more stable woodland habitats. Within isotopic niche space, a more diverse diet could be demonstrated by a large dietary ellipse reflecting many individuals focusing on consumption of different foods or by a smaller centralized ellipse reflecting a generalist diet across all individuals. In addition, the tallgrass prairie ecoregion is co-dominated by warm season C_4 photosynthetic pathway grasses in open native prairie habitats and by C_3 photosynthetic pathway floral assemblages within woody habitats, providing a prediction that grassland and woodland mammals should be using different plant resources, reflected by offset carbon stable isotopic signatures (Haveles et al. 2019). Finally, the degree of overlap in resource use among mammal species should vary by both seasonal and inter-annual changes in primary productivity coupled with small mammal demographic change. We predict that trophic overlap will be greater during periods of limited resources, and as such, amount of overlap between species should fluctuate seasonally

reflecting more opportunistic feeding during spring and more targeted feeding during summer (Rusch et al. 2014).

MATERIAL AND METHODS

Study area, field sampling, and focal species

The Konza field site is a 3487 ha native tallgrass prairie preserve located in the Flint Hills region of northeastern Kansas, USA (39°05' N, 96°35' W). Konza maintains replicated watershed-level experimental treatments including combinations of grazed or non-grazed watersheds and a variable fire regime from annually burned to complete fire exclusion treatments. Fire treatments have had predictable impacts on habitat state where annual burns maintain native grasslands, 4-yr burn intervals are sufficiently infrequent to allow for development of shrubby habitats, and 20-yr burn intervals result in significant woodland encroachment (Ratajczak et al. 2014). Konza also implemented fire reversal treatments (unburned to annual burn) in 2000 to investigate the hysteretic response of grassland recovery from woody encroachment. Prescribed fires are normally conducted in spring although seasonal burn experiments are in place. In 2016, a modified small mammal sampling protocol (Hope 2019) was initiated across a subset of eight non-grazed watershed treatments previously monitored for small mammals (Kaufman 2019). These include three watersheds burned annually (herein grassland), two watersheds burned once every 4 yr (herein shrubland), one watershed burned every 20 yr (herein woodland), and one fire reversal treatment which was unburned from 1979 to 1999 and then burned annually since 2000 (herein recovering grassland).

Two 285 m linear small mammal sampling transects were located in each watershed with 20 permanent trapping stations situated 15 m apart. Small mammal sampling occurred in 2016–2018 during summer for four consecutive weeks per year (between 29 May and 4 August depending on year), consisting of four consecutive nights of trapping per transect using two Sherman live traps (H.B. Sherman, Tallahassee, Florida, USA) per trapping station, resulting in 160 trap nights per transect (40 traps each, set for four nights) per year. In each watershed, one transect was surveyed through capture–mark–release methods to

glean population data consistent with legacy methodologies, and these individuals were not sampled for isotopic analysis. From the second transect per watershed, we removed all small mammal captures and specimens were euthanized under approved protocols (KSU IACUC #3579, #4055) and guidelines (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016).

We analyzed 329 small mammal samples from removal transects (both fur and liver, Table 1), representing the five numerically dominant species: Three predominantly associated with grassland and shrubland treatments including deer mice (*Peromyscus maniculatus*), prairie voles (*Microtus ochrogaster*), and western harvest mice (*Reithrodontomys megalotis*), the remaining two species were predominantly associated with shrubland and woodland treatments, including white-footed mice (*Peromyscus leucopus*) and hispid cotton rats (*Sigmodon hispidus*). Species for analysis were chosen based on sample sizes of at least five individuals during the first sampling year, and sampling of these species in subsequent years produced fewer specimens in only

three instances (Table 1). Shrubland and recovering grassland treatments supported similar small mammal diversity. Cotton rats were sampled from all habitats due to an extreme population eruption during sampling years, a phenomenon previously recorded on Konza but with unknown periodicity (Rehmeier et al. 2005). Based on previous dietary studies of these species, we can infer some feeding preferences. Both *Peromyscus* species are known to be omnivorous, feeding on both arthropods and seeds of grasses and forbs (Whitaker 1966). Similarly, *S. hispidus* have a broad potential diet on leaves of forbs and grasses, seeds, and arthropods that can be variable across seasons (Randolf and Cameron 2001). The diet of *M. ochrogaster* is more strictly folivorous on grass and forbs leaves and stems (Zimmerman 1965) and that of *R. megalotis* is more strictly granivorous, focusing on grass seed, but with some variability, including arthropod consumption (Hope and Parmenter 2007).

Other species did not yield adequate sampling for rigorous analysis. Additional species detected from each burn treatment, along with numbers captured per year and trapping effort are provided

Table 1. Corrected Bayesian standard ellipse areas (SEA_C) in $\%_0^2$ for Konza small mammals.

Treatment/ sampling time	<i>Peromyscus maniculatus</i>	<i>Microtus ochrogaster</i>	<i>Sigmodon hispidus</i>	<i>Peromyscus leucopus</i>	<i>Reithrodontomys megalotis</i>
Grassland					
3-yr total	(28) 13.1/7.9	(14) 11.1/4.9	a	a	a
2016	(8) 12.2/5.3	(8) 2.0/2.1	a	a	a
2017	(10) 19.0/4.4	(5) 16.5/3.0	a	a	b
2018	(10) 1.7/2.2	a	a	a	b
Shrubland					
3-yr total	a	(7) 7.2/3.9	(8) 14.0/4.5	(10) 17.2/0.8	(7) 4.7/2.2
2016	a	(3) 0.4/0.4	a	b	(5) 2.0/2.7
2017	a	(4) 1.9/1.8	(5) 8.0/2.3	(5) 20.3/0.1	a
2018	a	b	a	(5) 6.4/0.3	b
Woodland					
3-yr total	b	b	(18) 9.2/2.3	(24) 10.9/2.4	a
2016	b	b	(7) 3.4/2.0	(7) 15.5/1.2	a
2017	b	b	(8) 5.1/0.3	(8) 4.4/2.8	b
2018	b	b	a	(9) 4.1/1.4	b
Recovering grassland					
3-year total	(5) 1.8/0.5	(11) 12.6/3.3	(19) 14.7/9.0	(15) 20.1/2.1	b
2016	b	(5) 2.2/1.5	(4) 10.1/2.2	(5) 9.2/1.4	b
2017	a	(5) 13.4/2.1	(5) 28.7/12.4	(5) 20.2/1.6	b
2018	a	a	(10) 5.0/1.5	(5) 4.1/1.0	b

Notes: Trophic areas are provided for spring/summer (based on fur or liver tissues respectively) of each year of sampling and for all three years combined. Sample sizes used for isotopic analyses are indicated in parentheses. See Appendix S1: Table S1 for total capture data. Abbreviations are a, samples were collected but too few were available for analyses; and b, no samples were collected during this sampling period.

in supplementary materials (Appendix S1: Table S1). Species richness by treatment was similar, given detection of multiple rare species. Shrubland treatments supported the lowest densities of small mammals, followed by grassland, recovering grassland, and woodland with increasing densities respectively.

Stable isotope data collection

We measured the stable isotopic ratios for the five dominant small mammal species collected. Only adult individuals (based on body measurements and full adult non-molting pelage) were used for isotopic analysis to control for out of season molt for sub-adults and potential differences in feeding behavior among age classes. Full-length fur was removed from the dorsal posterior (rump) pelage and stored dry. Most adult small mammals at temperate latitudes experience two annual molts (spring and fall; Reid et al. 2013). Given that average last frost in the study region is mid-April, onset of spring reproduction and subsequent molting had occurred by timing of sampling in all years. Fur from summer captures is therefore presumed to provide coarse isotopic resolution of diet spanning late spring following the molt period. In addition, a piece of liver tissue was sampled from the same individuals. Liver tissue has a relatively rapid turnover time in small mammals and although variable, is considered to provide isotopic data reflecting diet within ~10 d previous to specimen sampling (Miller et al. 2008). Together, these tissues provide insight to trophic ecology of small mammals spanning both spring and summer from single sampling events.

Tissues were prepared for stable isotope analysis of carbon and nitrogen according to well-established methods (e.g., Smith et al. 2010, Miller et al. 2011). In brief, fur samples were soaked in a 2:1 chloroform to methanol solution overnight specifically to remove contaminants (Ben-David and Flaherty 2012), rinsed in deionized water, air-dried, and cut finely, cleaning tools in between samples with ethanol. Uncontaminated liver samples were dissected, rinsed with deionized water, desiccated overnight at 60°C, and then chopped into a fine powder without removing lipids (Caut et al. 2008). Approximately 0.5 mg of sample was analyzed using a continuous-flow Thermo Finnigan Delta Plus

Mass Spectrometer coupled to a Carlo Erba 1110 elemental analyzer in the Stable Isotope Mass Spectrometry Lab at KSU. Four internal secondary isotopic reference standards were analyzed approximately every 10–12 samples and were used to develop a calibration curve for each run. These internal reference materials have been previously calibrated against the international standards (VPBD for $\delta^{13}\text{C}$ and atmospheric air for $\delta^{15}\text{N}$), and isotopic ratios were expressed in per mil (‰). The mean and SD of the internal standards for each run are provided in Appendix S1: Table S2. These data illustrate that the accuracy and precision of the internal standards was typically within 0.05 for $\delta^{13}\text{C}$ and <0.1 for $\delta^{15}\text{N}$. A subset of samples was cross-validated at the Stable Isotopes for Biosphere Science Laboratory at Texas A&M University. Ten percent of samples were run in duplicate to quantify analytical variability. Duplicate samples produced values consistent with the reported variance from the duplicate standards (standard deviation <0.05 for $\delta^{13}\text{C}$ and <0.1 for $\delta^{15}\text{N}$).

Statistical analyses

All analyses were conducted in the R statistical environment 3.5.2 (R Core Team 2017). Given that trophic enrichment determination was not possible within our study system, all output isotopic values were adjusted for enrichment by standard values of 3‰ for nitrogen and 1‰ or 3‰ for carbon values of liver or fur respectively (Ben-David and Flaherty 2012). The latter adjustment considers recognized differences in discrimination of carbon for these tissues (Tieszen et al. 1983). We acknowledge that enrichment factors can vary markedly (by habitat, by tissue type, through time, etc.). These factors have been applied only as a qualitative comparison to broad trophic reference groups and do not impact inferences of quantitative analyses of isotopic ellipse area. To compare isotopic area and overlap between all five species in spring and summer, we used the package Kernel Isotopic Niches in R (rKIN, Eckrich et al. 2019). rKIN compares kernel use density (KUD) metrics that measure the extent of spacing within the bivariate isotopic space, representing isotopic niche area. The package also estimates the position of taxa relative to each other and reports isotopic niche overlap. The niche represents an area

encompassed by contours of data (50%, 75%, 95%). Overlap between species is asymmetric, defined as the ratio of overlap between two species relative to the niche area of the focal species.

We also estimated isotopic niche area for each burn regime treatment (grassland, shrubland, recovering grassland, and woodland) by calculating corrected standard ellipse areas (SEAC) across species to assess temporal and community variability using the R package SIBER version 2.1.3 (Jackson et al. 2011). This package uses individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as model inputs to calculate isotopic niche area and overlap which represents the core mean of the group SEAC, regardless of sample size. Standard ellipses contain only the core 50% of populations to reduce bias across the range of sample sizes. We used `baysianOverlap` in SIBER to test for pairwise overlap between burn treatments and species reflecting shared resource use.

RESULTS

Temporal variability

To address fundamental trophic niche of the Konza small mammal community, we measured isotopic signatures across years and season, combining all species and treatments for each category (Fig. 1). Spring and summer dietary ellipses, respectively, were highly overlapping across years indicating consistent trophic resource use in spring and in summer, but did exhibit seasonal differences in ellipse area. Ellipse area also varied by year in both seasons, increasing from 2016 to 2017, followed by a decrease and smallest ellipse areas in 2018 for both spring and summer (Fig. 1). A seasonal decrease in ellipse area was generally consistent across years, experimental treatment, and by individual species (Figs. 1–4; Appendix S1: Fig. S1).

Treatment variability

To assess trophic niche of small mammal assemblages by habitat type (fire treatment), we combined all species within a given treatment, but separated by tissue type to assess seasonal diet (Fig. 2). Spring ellipse areas were large and overlapping among all treatments indicating similar broad collective resource consumption across fire treatments. However, summer ellipses

for all fire treatments were smaller and were distinctly structured across the carbon axis, with grassland assemblages feeding further toward C_4 signatures (larger values), woodland assemblage feeding more exclusively within the C_3 carbon range (smaller values), and shrubland and recovering grassland mammals situated intermediate to these extremes. Grassland and woodland treatments were non-overlapping in isotopic niche for all summer sampling combined, and there was a corresponding increase in $\delta^{15}\text{N}$, respectively (Fig. 2).

Species and assemblage variability

Independent of treatment or sampling year, all species overlapped when considering spring diet inferred from fur isotopic values (Fig. 3; Appendix S1: Table S3). However, summer isotopic niches were segregated among species (Fig. 3; Appendix S1: Fig. S1, Table S3). A few general observations emerged when considering dietary reference categories, focusing here on summer diet (Fig. 3). Isotopic ellipse of *P. maniculatus* was furthest toward C_4 plant resources, whereas *S. hispidus* was furthest toward C_3 plants. Isotopic values of $\delta^{15}\text{N}$ were relatively higher for *P. leucopus* (inferred as greater omnivory with respect to arthropod reference values), and both *M. ochrogaster* and *R. megalotis* exhibit centralized positions within isotopic niche space. No small mammals were strongly associated with consumption of either predatory arthropods or purely C_4 plant materials. When species were considered independently, both *P. leucopus* and *S. hispidus* exhibited consistent dietary shifts toward more exclusively C_3 plant sources by treatment, from recovering grassland to woodland treatments, with *P. leucopus* also exhibiting a corresponding increase in nitrogen isotopic ratio (Appendix S1: Fig. S1). The narrowest isotopic niche space was consistently exhibited by *P. leucopus*, followed by *M. ochrogaster*, *S. hispidus*, and with *P. maniculatus* having the broadest isotopic niche within grassland treatments (Table 1). Considering mammal assemblages associated with different treatments, summer segregation of diet was again evident when compared with values of spring isotopic overlap, except for grassland treatments where *P. maniculatus* and *M. ochrogaster* were highly overlapping in isotopic space and no significant shift was detected between

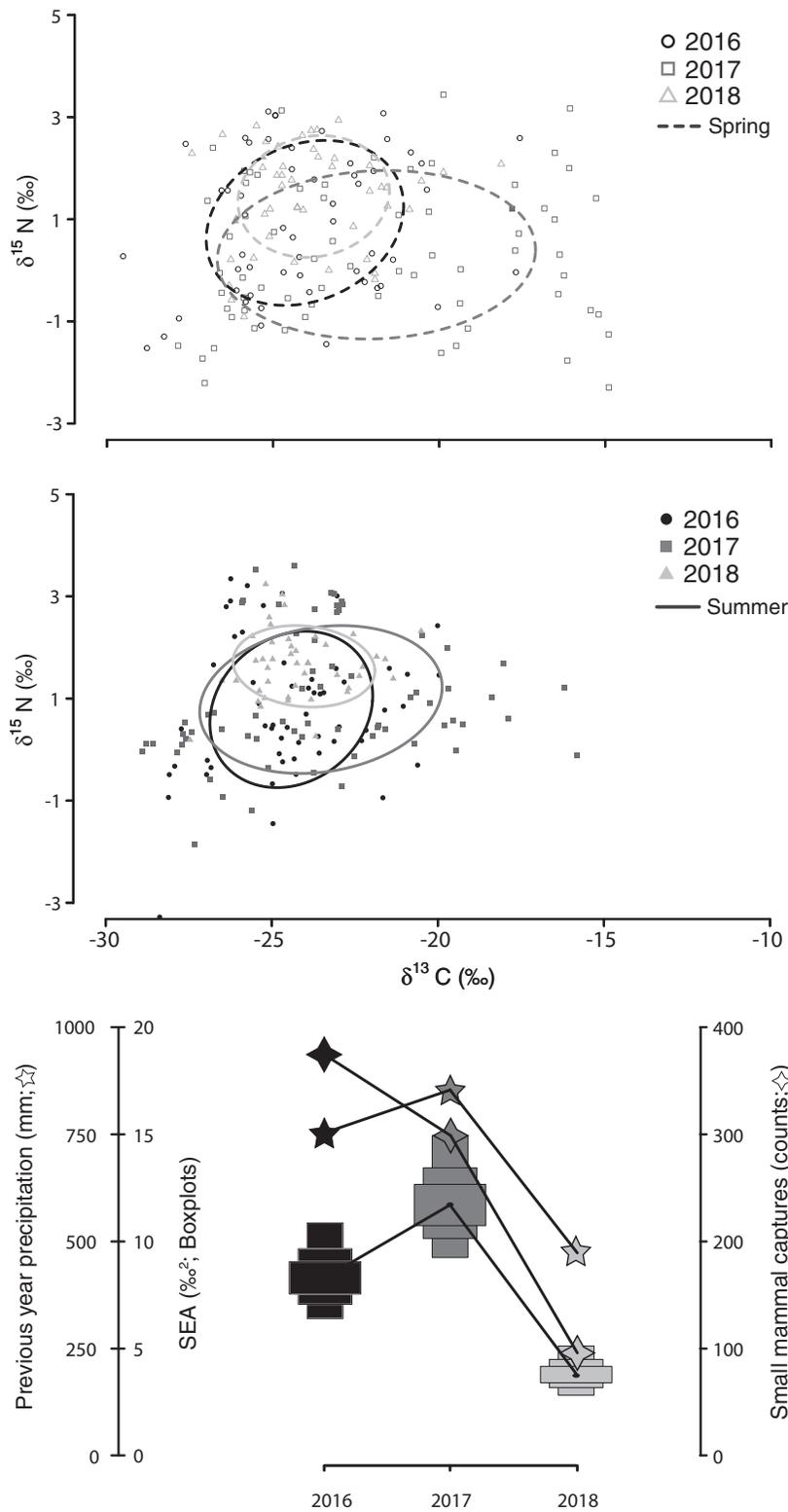


Fig. 1. Top: plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche space across three years for small mammals in spring (inferred

(Fig. 1. *Continued*)

from fur tissue). Middle: plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche space across three years for small mammals in summer (inferred from liver tissue). Bottom: plot of 50% Bayesian standard ellipse areas (SEA_C) in $\% ^2$ based on summer ellipses, growing season precipitation and rodent counts across three years. For each category, all species and all experimental landscape treatments are combined. Isotopic values have been adjusted to account for trophic enrichment.

seasons (Fig. 4, Table 2). The woodland treatment exhibited the narrowest total isotopic niche for summer with *P. leucopus* and *S. hispidus* completely separated within isotopic space, both within the range of $\delta^{13}\text{C}$ signatures indicating consumption of C_3 plant species, and *P. leucopus* with much higher $\delta^{15}\text{N}$ (Fig. 4).

DISCUSSION

We performed a study to assess how changes in vegetative communities within a single ecosystem impact the diet of co-existing small mammal species. Our results show clear evidence of (1) different resource use by species, (2) seasonal shifts in diet from spring to summer, and (3) clear impacts of changing vegetative community (from grassland to woodland) on the trophic structure of this ecosystem. Our results demonstrate key impacts of woody encroachment on a major trophic assemblage (small mammals). Given that small mammals are themselves a key resource for higher-level consumers (e.g., mammalian carnivores, raptors, snakes), the observed changes in ecology of grassland prairie small mammals may have cascading impacts on species abundance and the role of small mammals as engineers of habitat structure and function.

Our primary finding was that small mammal isotopic niches, and therefore trophic niches, were predictable across a gradient of ecosystem change. This was true both within and among species and according to seasonal and inter-annual variability. First, the collective diet of all small mammals (reflected by niche position within isotopic space) was relatively consistent across years (Fig. 1). However, the ellipse areas for all species combined varied in size and shape across years. This was strongly correlated to average annual precipitation from the previous year (and resulting net primary productivity) and overall small mammal abundance

(Fig. 1). The smallest niche area was associated with a drought year and low rodent densities (2018) and the largest area followed a very wet year with very high rodent densities (2017). This suggests that either density dependence or greater availability of resources plays a role in diversifying diet and indicates varying facultative specialization among species (Shipley et al. 2009).

Temporal variability in dietary specialization was further supported by consistent isotopic shifts on a seasonal basis, both in SEA_C (smaller in summer) and also displaced across isotopic space (Figs. 1–4). Competitive release and seasonal limitation of preferred resources may explain this phenomenon (Codron et al. 2015). Springtime rodent densities are generally lowest following winter mortality, presenting less opportunity for competitive interaction. Reduced ellipse size following a drought year also suggests that total spring resources during more productive years are not as limited (higher availability of the same pool of resources than in drought years). As such, reduced area of isotopic niche during drought is likely a result of resource limitation (low availability/abundances of resources) but also strongly combined with very low rodent population densities. As such, fewer individuals are all feeding on a broad mix of scarce resources. In general, we posit that broader spring ellipses than summer reflects early season generalist feeding considering the species as a whole, but with individuals focusing on different resources within the same available pool, as encountered. This was supported by high inter-annual variability in spring ellipse position, size, and overlap among species (Tables 1, 2). Subsequently, dietary overlap and ellipse size decreased in summer. Given higher summer resource availability (both by diversity and biomass), this may reflect either that each species specialized on different preferred resources with disproportionate abundance

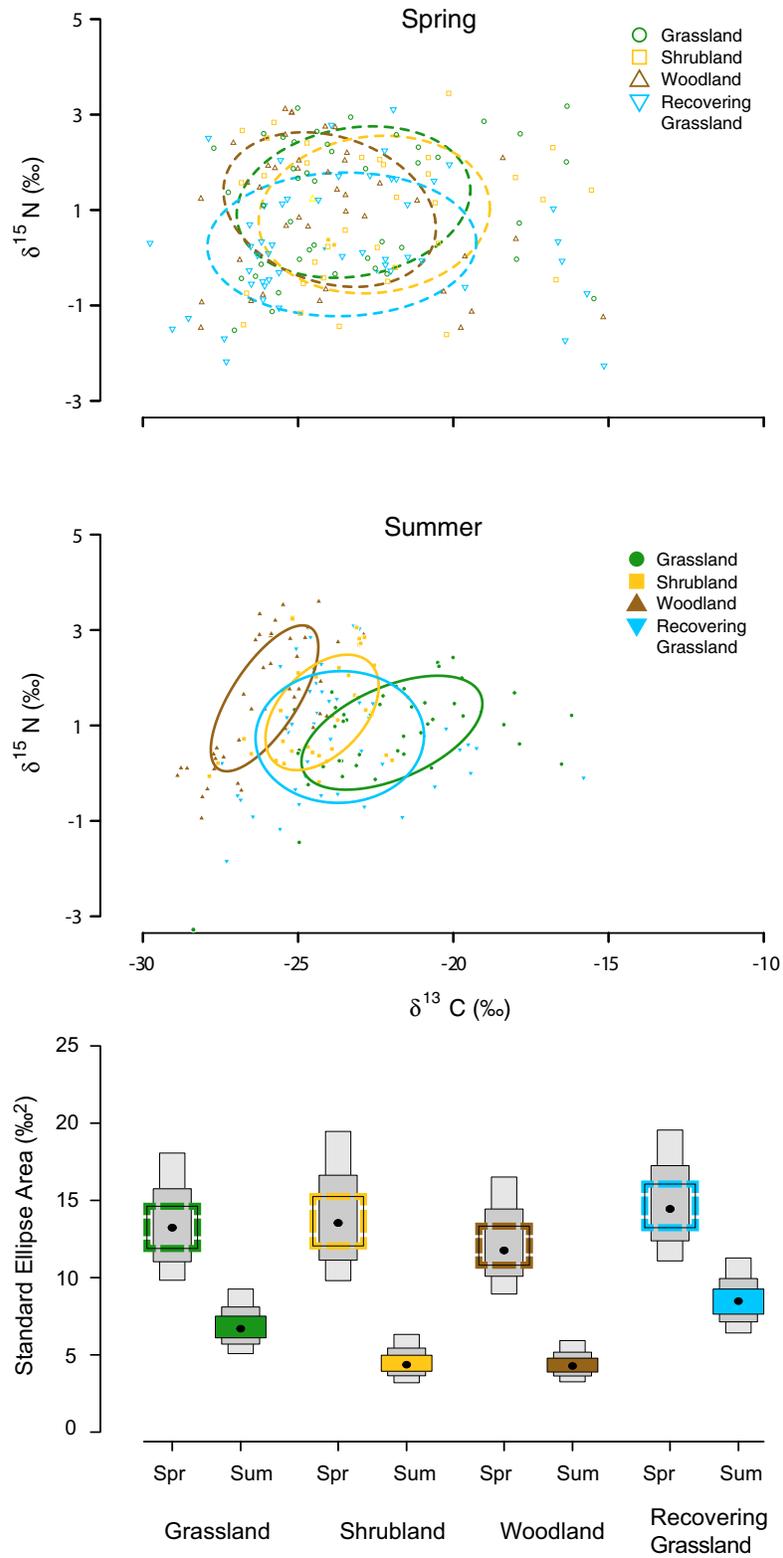


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niche space for Konza small mammals across four experimental landscape treatment

(Fig. 2. Continued)

categories for Top: Spring diet inferred from fur tissue; Middle: Summer diet inferred from liver tissue. For each category, all species across three years of sampling were combined. Included are 50% Bayesian standard ellipse areas (SEA_C) in ‰². Convex hulls connect ellipse center-points across treatments. Isotopic values have been adjusted to account for trophic enrichment. Bottom: Box plots representing seasonal changes in SEA_C values across all treatment categories. Box edges represent 50% (color), 75% (dark gray), and 95% (light gray) credible intervals, with black dots indicating mean values of posterior probability distributions.

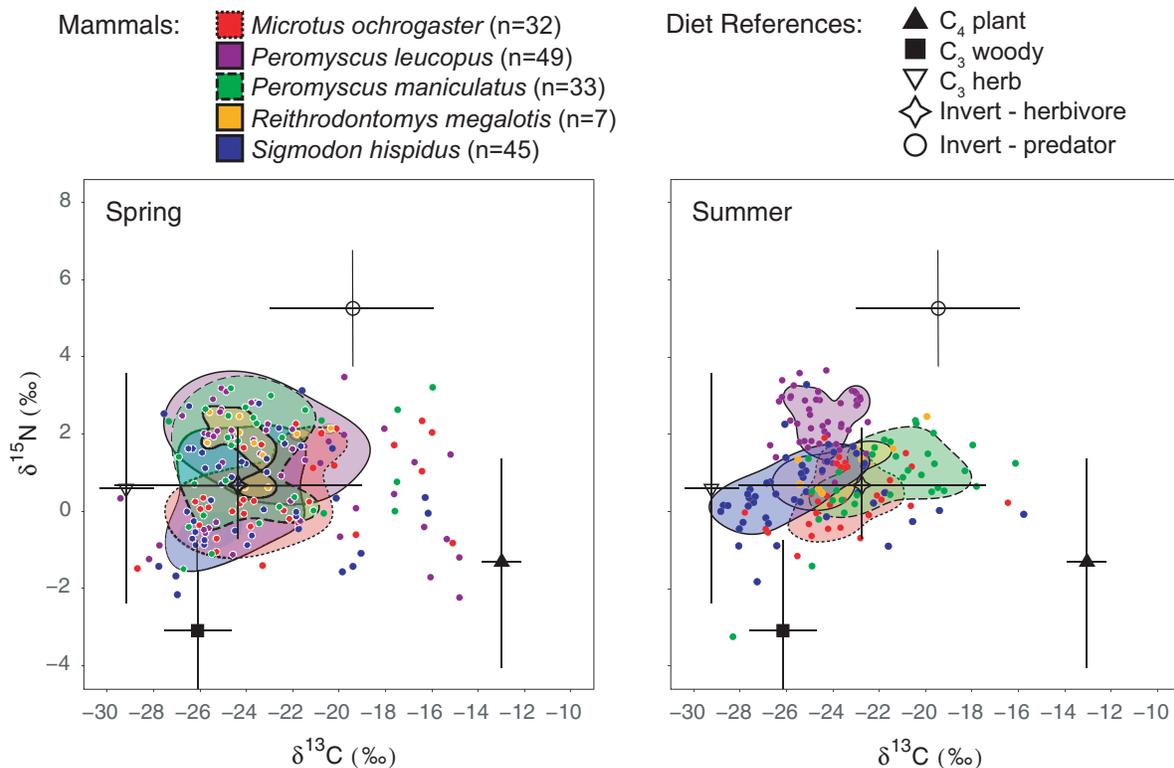


Fig. 3. Plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche space for separate Konza small mammals across two seasons (left, spring; right, summer). For each species, data from all three years of sampling are combined. Shaded areas represent 50% Kernel Utilization Densities (KUD) calculated in rKIN. Provided are average \pm 95% CI isotopic values for broad dietary reference categories. Mammalian isotopic values have been adjusted to account for trophic enrichment.

(Smith et al. 2002) or that all individuals within a species are acting as generalists, but with each species on average sampling different subsets of the total abundant resource pool, resulting in smaller and spatially distinct isotopic niches (Bearhop et al. 2004). We also note that a broader spring ellipse may be indicative of an extended dietary sampling period, considering the longer turnover time of fur (weeks) compared with liver

(days), reflecting spring and summer diets, respectively.

A second finding was that small mammal species occupied distinct isotopic niches during summer compared to spring, and this pattern was consistent across years (Table 2). This is likely to some extent reflective of differential C₃ and C₄ annual productivity in grasslands, whereby many C₃ species emerge early in spring and seed-

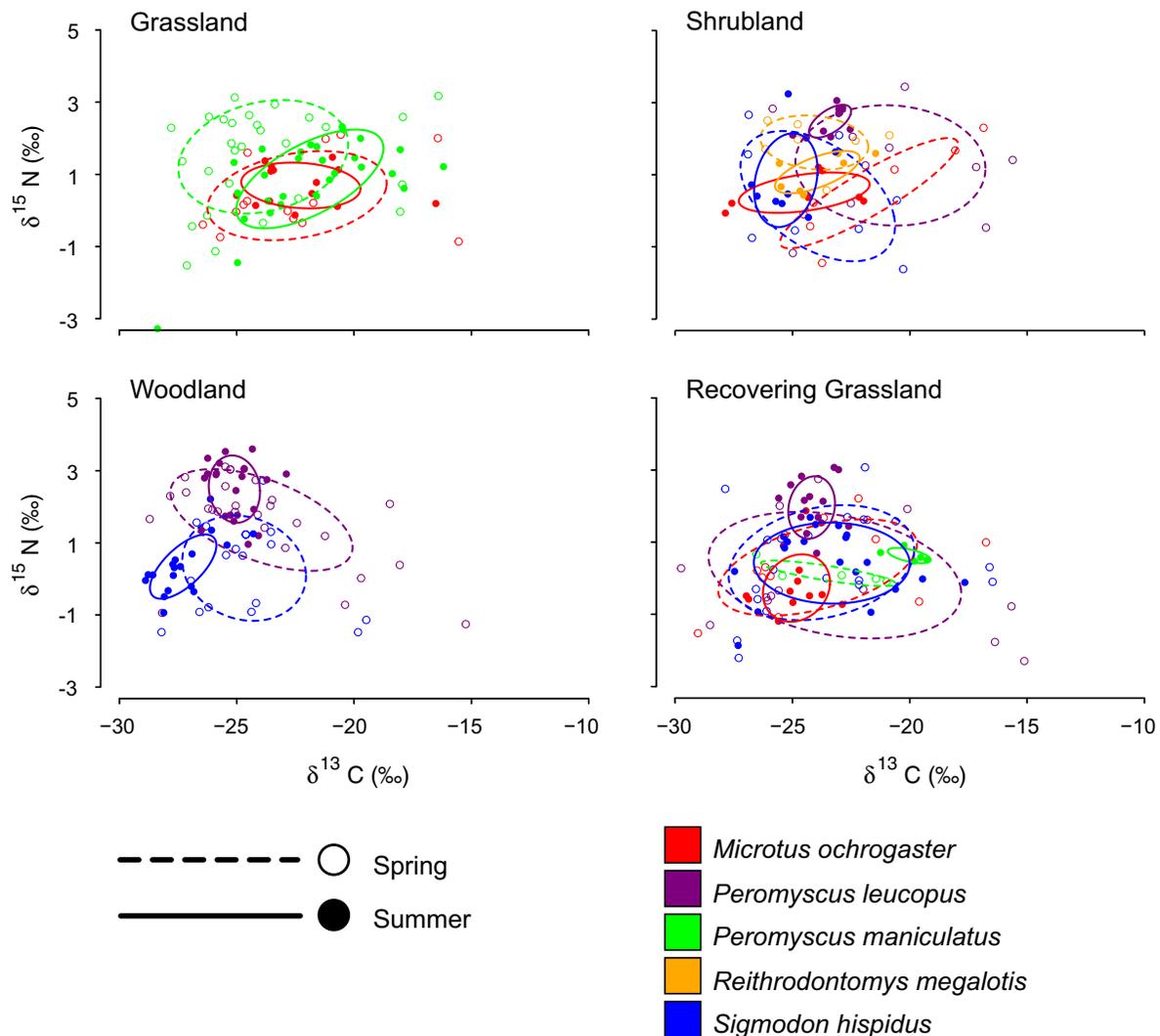


Fig. 4. Plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche space for small mammal assemblages within each experimental landscape treatment category, considering two seasons (spring inferred from fur tissue and summer inferred from liver tissue). For each category and season, data across all years are combined. Included are 50% corrected Bayesian standard ellipse areas (SEAC) in ‰^2 . Isotopic values have been adjusted to account for trophic enrichment.

set by early summer, whereas many C_4 emerge later and seed set in autumn. As such, spring granivory is likely dominated by previous season C_4 resources through overwinter seed bank. Summer herbivory may reflect C_4 new growth, whereas summer granivory is more likely dominated by C_3 seed set. Additional factors including reduction of spring C_3 biomass following prescribed wildfire, and a highly diverse floral ecology on Konza make inferring dietary niche

difficult. Additionally, the rodent species are ecologically diverse in their trophic niche across treatments. Within the woodland treatment, *P. leucopus* and *S. hispidus* could be considered facultative specialists, with small isotopic ellipses very high on the nitrogen axis or strongly focused on C_3 plant resources, respectively. A narrow diet for *P. leucopus* focused on woodland-associated resources has been shown previously (Hope and Parmenter 2007). Given the distinct shift of both

Table 2. Overlap in corrected Bayesian standard ellipse areas (SEA_C) in ‰² for Konza small mammals.

Treatment/Sampling time	<i>Pm/Mo</i>	<i>Mo/Sh</i>	<i>Mo/Rm</i>	<i>Sh/Pl</i>	<i>Sh/Rm</i>	<i>Pl/Rm</i>
Grassland						
3-yr total	47.1/20.4					
2016	8.5/11.3					
2017	50.2/9.1					
2018						
Shrubland						
3-yr total		37.4/11.0	10.8/8.9	54.1/2.9	22.2/9.4	52.2/3.2
2016			0.3/3.6			
2017		13.3/3.1		33.5/<0.1		
2018						
Woodland						
3-yr total				36.0/3.7		
2016				19.1/2.2		
2017				7.5/0.1		
2018				1.6/1.9		
Recovering grassland						
3-yr total	10.9/0.2	59.6/16.6		76.8/9.6		
2016		5.7/1.9		7.0/2.1		
2017	7.9/0.1	43.3/10.3		56.8/3.2		
2018				11.2/1.6		

Notes: Areas of overlap are provided for spring/summer (based on fur or liver tissues respectively) of each year and for all three years combined where samples allowed. Abbreviations are *Pm*, *Peromyscus maniculatus*; *Mo*, *Microtus ochrogaster*; *Sh*, *Sigmodon hispidus*; *Rm*, *Reithrodontomys megalotis*; *Pl*, *Peromyscus leucopus*.

of these species to a narrow summer isotopic niche localized rather than centralized within isotopic niche space, we assume they are feeding on only a few seasonally abundant resources. For *P. leucopus*, these likely include common invertebrates. *S. hispidus* are likely feeding on early C₃ grasses and subsequently forbs that become abundant by late spring (Randolph and Cameron 2001). In contrast, summer diets of *P. maniculatus* and *M. ochrogaster* within grassland treatments were more diverse (larger areas). These species are therefore facultative generalists, compared with woodland rodents. Contrary to our prediction of greater temporal variability within grasslands due to frequent fire and more exposed habitats compared with woody encroached areas, species from grassland treatments did not exhibit significant seasonal or inter-annual shifts, although spring ellipses were larger. This is again reflective of centralized isotopic niches indicating feeding on more limited abundances of a broad resource pool in spring and feeding on a broad pool of more plentiful resources in summer (resulting in a smaller ellipse). The broad overlap in ellipses between *P. maniculatus* (granivore/omnivore) and *M. ochrogaster* (folivore) is likely

possible due to differing trophic guild, although consistently low densities of rodents within grassland treatments may preclude significant direct competition for resources.

This study illustrates that trophic niches of small mammal assemblages from different habitats are offset isotopically (Fig. 2). As such, small mammals in woodland habitat are effectively non-interacting with resources in grassland habitat during the summer. This result illustrates a turnover in consumer roles and resource use as this ecosystem transitions from grassland to woodland. In support of our prediction, the mammals from woody habitats had a greater reliance on C₃ plant species, whereas mammals from grasslands had greater use of C₄ plant species. Although it is likely that C₄ plants are being used by woodland rodent species at least seasonally (particularly through overwinter seed bank), the isotopic data suggest an increasing disconnect of these species from their potential roles as dispersers of prairie seed (Jayadevan et al. 2018). This is also accompanied by increased potential for enhancing woody encroachment through the same mechanisms (Archer et al. 2017). A spring-time shift to more diverse food resources might

maintain functional linkages between woodland mammals and prairie flora, but if woody encroachment progresses to more climax and widespread woodland conditions, a trend of reduced mammalian richness and dietary breadth is likely (Matlack et al. 2008). This dynamic will also depend on rodent home range size and location within experimental watersheds. For instance, *S. hispidus* generally occupies lowland areas within watersheds; regions that tend to be impacted first, and most heavily, by woody encroachment and are also furthest from watershed boundaries (Rehmeier et al. 2005). As such use of non-woody resources through time will decrease more quickly than for species occupying upland and peripheral areas.

Our results have strong bottom-up implications for how small mammal diets are influenced by major landscape change through variable disturbance regimes. In addition, our data provide insight for future investigations of the top-down role of small mammals as consumers. As stated, it is possible that increased woody encroachment may generate a positive feedback through small mammal resource consumption that influences the relative interactions of these mammals with native prairies vs. woody habitats. Our data indicate that seasonal and inter-annual changes in weather impact isotopic niche, including position and size of isotopic ellipses, respectively, of small mammals across all habitats, as has been shown statistically through alternative multivariate community analyses (Bruckerhoff et al. 2020). Frequent wildfire is known to temporarily reduce populations of certain grassland small mammal species. For instance, *R. megalotis* is known to respond negatively to fire (Clark and Kaufman 1990) and was rarely sampled from annually burned habitats including the recovering grassland. Given that home range size of this species is ~60 m (considerably less than the size of watershed treatments; Clark et al. 1988), use of annually burned grasslands by this species is likely restricted to peripheral regions bordering non-burned treatments, or wet lowland areas that are more protected from fire disturbance, providing species-specific occupancy buffers depending on home range, dispersal capability, and treatment regime. In general however, all of these grassland mammals are at least somewhat resilient to periodic wildfire (Clark and Kaufman

1990). The primary impact of fire appears instead to be maintenance of consistently broad resource use by mammals, independent of season. Evidence of scatter hoarding and caching of diverse prairie seeds may consequently impact prairie plant regeneration (Rusch et al. 2014), an ecosystem service that is therefore reduced with woody encroachment. While American bison and cattle impact prairie floral diversity and biomass, our study did not assess the impacts of these mega-herbivores on small mammal trophic ecology, and interactions among these and other major consumer groups warrants further study (e.g., Joern 2005). Plant productivity in tallgrass prairie is generally nutrient limited (Fay et al. 2015), and as such, rodent waste likely contributes to nutrient availability within this system, particularly given periodic eruptions of species such as *S. hispidus* that are considered to have a potentially significant impact on nutrient cycling (Clark et al. 2005). In this scenario, consistently higher rodent carrying capacity in woody habitats might cause greater nutrient deposition to further promote associated woodland plant communities.

We have demonstrated the novel insight provided using multiple tissue types for inferring trophic variability across multiple fire frequency treatment regimes through time. It is unlikely this variability is a consequence of error in sample preparation, as our designated duplicate samples provided consistent isotopic signatures, and broader spring diet than summer has been noted previously across multiple rodent species from a semi-arid assemblage in the southwestern USA (Hope and Parmenter 2007). However, sampling error may still impact interpretation of stable isotope values from fur. Although we sampled fur from the same body region and age class, the timing and pattern of molt both within and among species is variable (Mares et al. 1982) and may impact comparisons of isotopic composition. This is further complicated by a presumption of equal enrichment factors among species and between tissue types, where discrepancies may also influence isotopic variation (Ben-David and Flaherty 2012), and may account in part for both observed seasonal shifts, and intra-specific differences between habitats in isotopic niche space. Given that position of the ellipse did not consistently change between tissue types in all

habitats or with all species, the likelihood of error associated with these presumptions is minimal. However, further experimentation would establish actual molt times and enrichment factors within this system for different tissue types (Caut et al. 2009). Given that much of the trophic ecology literature based on stable isotopes of small mammals has used fur through non-lethal sampling, we suggest that greater resolution of trophic dynamics is achievable through analysis of alternative tissue types such as liver (Caut et al. 2009), or if non-lethal methods are prerequisite, using feces (short turnover) or blood collection (for more extended dietary timeframes). Full specimen vouchering and permanent archive in biorepositories with at least a subset of the sampled individuals, as was conducted here for half of the specimens, can greatly enhance their value for isotopic analysis of multiple tissue types, and in general for other future research avenues (Galbreath et al. 2019).

Speculations for future research

Changes in mammalian trophic ecology across habitats may be reflected by cascading biodiversity changes through ecosystems undergoing state change dynamics. If dietary turnover could be established through analysis of rigorous reference materials or through molecular metabarcoding techniques (Welti et al. 2019), future integrated biodiversity investigations that incorporate stable isotope methods will become feasible. An example would be investigation of small mammal hosts and their parasites and pathogens (Bordes et al. 2015). The two most numerous Konza small mammals, *P. maniculatus* and *P. leucopus*, host a wide range of zoonotic diseases (Larson et al. 2018) and fulfill complex parasite lifecycles that enable spread of disease and increased potential for emergence of new pathogens (Mendoza et al. 2020). Our results clearly demonstrate that woody encroachment leads to dietary turnover as these two dominant species change (with methodological caveats; Appendix S1: Fig. S2). Less certain is how host turnover and differing resource use translates to altered ecology of local vectors (e.g., ticks) and rodent-borne diseases (Roy-Dufresne et al. 2013). Stable isotope analyses in combination with molecular and co-evolutionary investigations have potential for resolution of connections

between small mammals, other vertebrate hosts, and shared vectors of disease (Xu et al. 2015).

Conclusions

Our results provide a first stable isotope assessment of how small mammal trophic ecology may contribute to ongoing woody encroachment within threatened grasslands of North America and a basis for generating future long-term experiments to further resolve the relative importance of consumers for affecting ecosystem change. Importantly, we found that small mammal trophic dynamics provided predictable patterns of resource use within a region experiencing marked habitat change and associated faunal community turnover. Small mammals as an assemblage within native grasslands consume a consistently broad diet that varied dramatically among individuals (broad isotopic niche within the same species and habitat). Conversely, woody habitats supported higher densities of small mammals that focused more narrowly on relatively few resources that were displaced within isotopic niche space from those resources available in open grasslands. For the woodland assemblage, dietary specialization varied among species, but also varied by season, most likely as preferred resources fluctuate in their availability. Conversely, in grasslands, our results reflect generalist feeding across seasons with variation in abundance of the available pool of resources the main limiting factor. Our data have effectively established a dichotomy in functional resource use by small mammals associated with different habitats, that will feed back to decreasing interactions between small mammals and native prairies and increasing associations with woody habitats. Given the observed changes in both species composition and abundance of small mammals as habitat turnover progresses, our findings of different trophic dynamics among these small mammal assemblages will also enhance efforts aimed at maintaining or restoring native faunal communities.

DATA

All mammal specimens sampled for analysis are archived in the Museum of Southwestern Biology, University of New Mexico. Associated museum specimen numbers are provided with the full isotopic dataset available from the

figshare digital repository <https://doi.org/10.6084/m9.figshare.13325903.v1>. Isotopic values for dietary reference categories for plants were retrieved from Craine et al. (2012).

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SUPPORTING INFORMATION

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