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COMPETITIVE RELEASE DURING FIRE SUCCESSION DRIVES ECOLOGICAL TURNOVER IN A SMALL MAMMAL COMMUNITY

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COMPETITIVE RELEASE DURING FIRE SUCCESSION DRIVES ECOLOGICAL TURNOVER IN A SMALL MAMMAL COMMUNITY

A THESIS APPROVED FOR

THE DEPARTMENT OF BIOLOGY

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ABSTRACT As fire seasons increase in severity and length, understanding the drivers of ecological responses to fire may help us predict community resilience. In western North America, post-fire succession in small-mammal communities is marked by a transition between two species: old-growth forests are predominated by southern red-backed voles (*Myodes gapperi*) which are largely replaced after wildfire disturbance by North American deermice (*Peromyscus maniculatus*). While this shift has been frequently documented, the processes that mediate this turnover are debated. One possibility is competitive release, which predicts a reduction in vole competition should result in niche expansion in deermice. Alternatively, optimum foraging theory predicts that turnover in both species is shaped by differences in their preferred resource base. We evaluated these hypotheses using stable isotopes and spatial mark-recapture histories taken from deermice and vole populations prior to and following a fire as part of a longitudinal study in the Greater Yellowstone Ecosystem. Fire disturbance was associated with a 94% decrease in voles and a 102% increase in deermice. Even after accounting for microhabitat, vole and deermice populations were negatively correlated spatially and temporally, and models incorporating competitors were a better fit for pre-fire abundance. Pre-fire, when vole abundance was high, deermouse dietary niche was small and marginal to that of voles. Post-fire, deermouse dietary niche nearly tripled and was enriched in ^{13}C (i.e., more C4 plants), while voles occupied a similar dietary niche throughout. The results suggest deermice are experiencing ecological release due to a reduction in vole competition. This research provides important insights into how small mammals are impacted by fire succession and competition for similar foods.

KEY WORDS competition, deermice, dietary niche, disturbance, fire, greater Yellowstone ecosystem, *Myodes*, *Peromyscus*, red-backed voles, stable isotopes

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INTRODUCTION

Over the last three decades, the duration of wildfire season has increased dramatically in Western North America (Abatzoglou and Williams 2016, Riley and Loehman 2016). Human-caused conditions such as global climate change, land-use practices, and species range shifts lead to changes in fuels, ignition sources, fire weather, and ultimately fire regimes (Turner et al. 2003, Romme et al. 2011, Kelly et al. 2020). As fires become more prevalent, it is essential to understand their impact on ecologically important species, as well as overall community structure (Abatzoglou and Williams 2016). Previous fire-disturbance research has largely focused on the role of abiotic changes, vegetation community shifts, and the responses of large mammals to these changing habitats during succession (Turner et al. 2003, Romme et al. 2011). However, far less is known about the impacts on biotic interactions, such as competition, that shape small mammal communities during this process (Griffiths and Brook 2014).

Evaluating possible mechanisms for how post-fire succession influences small-mammal abundance is important for predicting ecosystem changes in a world with more extreme and frequent fires (Romme et al. 2011, Abatzoglou and Williams 2016, Riley and Loehman 2016). Small mammals provide a trophic link between producers and higher-level predators, they are an important guild of plant predators, fungal dispersers, and prey for mesocarnivores (Lacher et al. 2019). Small mammals also influence important ecological functions through seed dispersal, and their burrowing contributes to soil nutrients and moisture (Brehme et al. 2011, Wilson and Smith 2015). Thus, studying the factors driving the relative abundance of small mammals in fire-prone ecosystems will allow us to better understand community dynamics during fire succession.

In western North America, fire succession in small mammal communities is often marked by a transition between two dominant species. Southern red-backed voles (*Myodes gapperi*;

hereafter red-backed voles) are abundant in old-growth forests but are largely replaced after a fire by North American deermice (*Peromyscus maniculatus*; hereafter deermice; Krefting and Ahlgren 1974). As vegetation matures 3–4 years into fire succession, red-backed voles gradually begin to replace deermice (Stanton et al. 1991, Lanier et al. 2014). Although this transition has been well documented, the underlying drivers are still under debate: e.g., source–sink dynamics, decreased predation, increased food resources, and increased foraging efficiency (Krefting and Ahlgren 1974, Morris 1996). Some evidence supports habitat preference and foraging efficiency as key factors driving deermouse increases post-fire (Zwolak 2009, Zwolak et al. 2012; Fig. 1a); however, the role of competition from voles in shaping deermouse population shifts during fire succession is untested. Evaluating the role of dietary competition, with pressure from voles limiting the dietary niches of deermice pre-fire and subsequent competitive release driving deermouse increases post-fire, may provide important insights into community change during fire succession.

Evidence for competition between deermice and red-backed voles is mixed, with support for either vole (Crowell and Pimm 1976) or deermouse (Lemaître et al. 2010) dominance, depending on the ecological context in which competition is measured. Both species eat seeds, grains, nuts, fruit, and flowers, but red-backed voles consume more mosses and fungi (Merritt 1981, Orrock and Pagels 2002), where deermice shift resource selection depending on what is locally available. Under the ecological release hypothesis (Wilson 1961), dietary breadth and population density of deermice is diminished due to competition from voles in old-growth habitats. We hypothesize that fire, by reducing competitive pressure from voles, leads to ecological release of deermice allowing them to expand their dietary niche and increase in abundance (Fig. 1b; Fig. 2; Herrmann et al. 2021). Under the competitive release hypothesis, we

predict greater pre-fire competitive pressure from voles on deermice in a semi-shared dietary niche, with deermice excluded from a portion of their fundamental niche by the voles (Hutchinson 1957). We contrast these predictions with dietary and habitat shifts expected under optimal foraging theory (MacArthur and Pianka 1966), which suggests species turnover will reflect changes in resource availability. Under this scenario (Fig. 1a) we predict little niche overlap between species either pre- or post-fire, narrow dietary niches in habitats with preferred food resources, and dietary niche expansion when a species forages in suboptimal habitat in order to compensate for decreases in resource quality, quantity, or accessibility (Stephens et al. 2019). Fire-associated shifts in deermice and red-backed voles under this hypothesis would represent responses to dietary and habitat specialization (Morris 1996, Boonstra and Krebs 2012), not competition. Understanding resource partitioning within the community requires simultaneously considering that multiple mechanistic models, such as competition and niche differentiation, may be driving the observed abundance shifts (Schoener 1974).

Here we investigate shifting food resources and interspecific dietary competition in a fire-prone system to better understand community turnover between two dominant species (voles and deermice) after fire disturbance in a boreal forest. Using longitudinal sampling from a fire-prone ecosystem (Lanier et al. 2017), we evaluated how dietary breath and geographic space use by voles and deermice shifted following a fire. We apply stable isotope analysis of vole and deermouse hair to evaluate plant types and resources consumed in terms of total carbon and nitrogen contributions, which allowed us to examine changes in dietary niche breadth and overlap. Nitrogen stable isotopes ($\delta\ ^{15}N$) are useful for assessing consumer diets as they are usually enriched by 3–4‰ with each increase in trophic level (Newsome et al. 2012). Carbon stable isotopes ($\delta\ ^{13}C$) tell us the ultimate carbon sources a consumer uses (i.e., C3 vs. C4 plants

use different carbon photosynthetic pathways and therefore have different isotopic signatures; Flaherty and Ben-David 2010, Newsome et al. 2012). To evaluate space use by deermice and voles, we analyzed microhabitat variables and spatial capture history, testing whether habitat shifts may explain variation in small mammal abundance during fire succession. Our goal was to evaluate the effects of competition and resource availability on variation in small mammal abundances across different seral stages following fire. Overall, this work provides important insights into fire succession and the role of small mammal competition in community dynamics of western ecosystems.

MATERIALS AND METHODS

Field Methods

Study area.—The study area consisted of four 1-ha sampling grids along the John D. Rockefeller, Jr. Memorial Parkway, between Yellowstone and Grand Teton National Parks (Fig. 3; Lanier et al. 2017). This lodgepole pine-dominated ecosystem has been the subject of decades of influential research in fire and disturbance ecology (Turner et al. 1997, Romme et al. 2011). All four grids (two on east-facing and two on west-facing slopes) were initially established after the 1988 Yellowstone wildfires in order to compare fire succession on two burned grids with nearby, unburned habitats (Fig. 3; Stanton et al. 1991). Continued work on these sites has provided a long-term, vouchered dataset that our research builds on. A new set of wildfires burned all four grids in 2016 (Lanier et al. 2017), providing the opportunity to directly test the role of pre- and post-fire dietary competition and space use in shaping population dynamics in this system.

Trapping and sampling.—Each 1-ha grid consisted of 100 Sherman trap stations, each 10 m apart, baited with peanut butter and oats (Lanier et al. 2017). Small mammals were sampled in

four overnight trapping sessions per month, repeated during the months of June, July, and August surveyed during 2009, 2014, 2015, 2017, and 2018. Live-captured small mammals were sexed, and measurements were taken for total length, tail length, ear width, and weight. Captures were singly (2009) or doubly (2014) marked with ear tags, or one ear tag and one Passive Integrated Transponder tag (2015, 2017, 2018) for mark-recapture abundance estimates. "Total captures" in our dataset reflect both the new (i.e., unique) small mammal individuals captured as well as recaptures to encompass the intensity of individual activity, whereas "unique captures" refer to the number of new individuals captured (i.e., excluding recaptures). A quarter of the Sherman traps (25 of the 100 trap stations for each grid; 100 per session) were paired with a pitfall trap, filled with propylene glycol, during the consecutive 4-night trapping session in order to better sample shrew species. These traps also provided an important voucher specimen record, facilitating the dietary aspects of this study. All trapping and mammal handling was conducted following the ASM Guidelines for Wildlife (Sikes 2016) and handled in accordance with IACUC protocols 20140520ZR00105 and 20170517ZR0071. Museum catalog numbers for all voucher specimens associated with this paper can be accessed in Table 1.

Vegetation sampling.—To understand the baseline plant communities, vegetation and habitat data were collected from 25 trap stations per grid once per year, during the July trapping session. Around each trap we evaluated microhabitat characteristics, such as ground and canopy cover, distance to nearest seedling and shrub, and characteristics of the coarse woody debris. Ground-dwelling small mammals rely heavily on microhabitat for food and protection, so vegetation measurements of ground cover and shrubs and seedling density provide insights into the resources small mammals have available at those trap stations. Canopy cover, estimated with a spherical densiometer, is important in fire succession, altering plant communities and abiotic

conditions as well as providing small mammals with cover from predators. We estimated percentage of ground cover using a Daubenmire frame at the trap station to quantify percentages of bare ground, grass, herbaceous plant, leaf litter, shrub, and woody plant, each to the nearest 25% (i.e., 0%, 1–25%, 26–50%, 51–75%, 76–100%; Daubenmire 1959, Deuser and Shugart 1978). We assessed coarse woody debris (i.e., downed logs >7.5 cm in diameter) occurring along a transect in each cardinal direction within a 5-meter distance from the trap site and for each we measured: distance to the trap; debris diameter; height from the ground; and a categorical decay class (0–5, from most to least decayed). When no seedling or shrub was found during search efforts within the 10 meters surrounding the trap station, the distances for those two variables were set to 15 meters. For 4 traps (out of 400 total) missing percent canopy and ground cover data were imputed as the means from the 4–6 physically closest traps from the same year.

Isotopic Analysis

Stable isotope analysis.—To assess dietary differences within and among species we used nitrogen and carbon isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) from the hair of 61 deermouse and 58 red-backed vole specimens collected in 2009, 2014, 2015, 2017, and 2018 (Table 1). We measured ($\delta^{13}C$ and $\delta^{15}N$) with a Flash EA Isolink Elemental Analyzer (Thermo Fisher Scientific, Inc., Waltham, MA, USA) connected to a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Inc., Waltham, MA, USA). We adjusted $\delta^{13}C$ and $\delta^{15}N$ and elemental compositions (%C and %N) with in-house standards and reference materials USGS42 and USGS40 (Reston Stable Isotope Laboratory, U.S. Geological Survey, Reston, VA, USA). These materials have known elemental compositions and were run alongside our samples for quality assurance. We report results as $\delta^{13}C$ and $\delta^{15}N$ ratios in parts per thousand (‰) in relation to the international standards Vienna-Peedee Belemnite (VPDB; $\delta^{13}C$) and atmospheric

nitrogen (AIR; $\delta^{15}N$; Manlick et al. 2017). We confirmed the precision, accuracy, and repeatability of isotope runs with control tests on the standard and reference materials. Across all runs, the average standard deviations for $\delta^{13}C$ and $\delta^{15}N$ measurements of USGS42 and USGS40 were 1.198 and 0.703, respectively. The measured values for $\delta^{13}C$ and $\delta^{15}N$ for machine drift and linearity were corrected when needed.

Data Analysis

Estimating dietary niche shifts.—We used $\delta^{13}C$ and $\delta^{15}N$ of individual deermice and red-backed voles to evaluate dietary niche breath and overlap. In order to interpret and graph the magnitude of dietary shifts relative to the 2016 fire, we analyzed the isotope signatures using a Bayesian model implemented in the R packages `SIAR` version 4.2 and `SIBER` version 2.1.4 (Jackson et al. 2011, Parnell and Jackson 2013, Jackson and Parnell 2020). To evaluate the dietary niche breadth of a population, we used standard ellipses corrected for small sample size (SEAc) in `SIBER` and enclosed species distributions of isotopic values with dash-lined convex hulls within a given year. To test for differences among species and within species among years, we ran MANOVAs on species' carbon and nitrogen isotope signatures (the dependent variable) using the base functions in R version 3.6.0 (R Core Team 2019).

Capture-based estimates of competition.—To further evaluate competition, we assessed the signal for competitive interactions as reflected in the spatial distribution of animals. First, to test whether deermice and voles were unlikely to co-occur among trap stations, we used a randomization analysis, where we compared the observed species overlap within a month against a randomized, simulated overlap matrix. We ran this co-occurrence analysis using the binary presence-absence capture history of deermice and red-backed voles from each monthly sampling session over the 5 sampling years (for a total of 15 comparisons). We compared this to simulated

datasets where the two species occurrences were randomized among the trap stations during the same sampling period. Simulated datasets were constructed with the R package `EcoSimR` v. 0.1.0 (Gotelli et al. 2015) using 1,000 randomizations with the "Sim2" metric. We compared our observed data to simulations using the C-score index (Stone and Roberts 1990), which evaluates the average covariance between each species pair in capture occurrences among the trap stations. Large values of the C-score index indicate strong species segregation among traps.

Although randomization allows us to evaluate co-occurrence, it does not consider vegetation or distance between traps. In order to better control for these factors we evaluated the spatial dynamics of resource availability and putative competitor abundance using a simultaneous autoregressive (SAR) model (Kissling and Carl 2008). The SAR model is a regression approach that accounts for structural spatial autocorrelation, allowing us to simultaneously examine the influence of competitor abundance (i.e., the number of captures of deermice or voles at a trap) and vegetation communities at a trap station while accounting for spatial distance. Analyses were run in the R packages `spdep` v. 1.1-5 (Bivand and Wong 2018) and `sars` v. 1.2.3 (Matthews et al. 2021) for each year, focusing on the trap stations per grid with vegetation and capture data (25 stations/grid; 100 stations/year), and were run separately with either deermice or redback vole abundance as the response variable. To control for the effect of correlated vegetation characteristics, we reduced our microhabitat variables to the top 3 principal components across all four years (contributions shown in Table 2). Microhabitat differences based on PC1 most strongly captured fire succession trends, with more herbaceous plants, grasses, downed logs, and space below logs in pre-fire years and a shift to fewer decaying logs but more open canopy and bare ground in post-fire years (Fig. 4). We regressed target-species captures against models containing only microhabitat characteristics (PC1, PC2, and

PC3; Table 2), models including microhabitat and competitor capture, and models including those variables while also accounting for spatial autocorrelation with a distance matrix component based on coordinate data (Douglas and Endler 1982, Kissling and Carl 2008, Bivand and Wong 2018). To test the role of competition, we compared model fit using the Akaike Information Criterion (Sakamoto et al. 1986) in the R packages: `ncf` v. 1.2-9 (Bjornstad and Cai 2020), `spatialreg` v. 1.1-5 (Bivand et al. 2013), and `MASS` v. 7.3-51.4 (Ripley et al. 2020).

RESULTS

Species abundances.—Over the 5 sampling years (2009, 2014, 2015, 2017, and 2018) we captured a total of 2,721 small mammals, including 1,130 red-backed voles and 827 deermice. Prior to the 2016 fire, red-backed voles dominated small mammal communities, but after the fire deermice comprised the majority of the captures (Table 3; Fig. 2). The average number of voles captured per grid (i.e., per ha) per year transitioned from 179 pre-fire to 12 post-fire, whereas deermice transitioned from 63 pre-fire to 189 post-fire (Table 3). Across grids and years, vole and deermouse captures were negatively correlated ($R = -0.447$; $R^2 = 0.199$); with 35 fewer deermice captures for every additional 100 voles captured (Fig. 5).

Capture-based estimates for competition.—Randomization results indicated deermice and voles were significantly more segregated among trap stations than expected by chance for all months and years ($P < 0.001$; Table 4). The SAR analyses confirmed a negative relationship between the two species (e.g., pre-fire $ß_{voles\text{-}effect\text{-}on\text{-}deermice}$ ranged from -0.37 to -0.11 and $ß_{deermice\text{-}effect\text{-}on\text{-}voles}$ ranged from -0.25 to -0.12), even when accounting for spatial autocorrelation and microhabitat (Table 5). None of the model comparisons that included spatial autocorrelation between traps performed better than aspatial models (Table 6). Pre-fire, models that incorporated competitor abundance were better than those that did not, although vegetation-only models were

within ΔAIC < 2 in 2015 (Tables 5 and 6). After the 2016 fire, models that only included vegetation characteristics had the lowest AIC scores, but models with competitor abundance also received substantial support (i.e., ΔAIC < 2; Table 6).

Dietary niche shifts.—Before the 2016 fire, vole dietary niche space was nearly 7x as broad as deermouse niche space, particularly with respect to nitrogen content (Fig. 6). After the 2016 fire, deermice expanded in niche space and experienced more year-to-year shifts. When vole populations were reduced post-fire, the dietary niche of deermice increased by 2.8x ($SEAc_{pre\text{-}fire\ mean}$=0.94; $SEAc_{post\text{-}fire\ mean}$=2.66) whereas vole dietary niche decreased by 0.79x ($SEAc_{pre\text{-}fire\ mean}$=6.56; $SEAc_{post\text{-}fire\ mean}$=5.18). In two of the three years prior to the 2016 fire, the two species differed significantly in nitrogen content but not carbon (Table 7). One year after the fire (2017), species did not significantly differ (Fig. 6; Table 7); however, two years post-fire (2018) overlap decreased and the species significantly differed in carbon (P = 0.01; Table 7). MANOVAs by year indicated that deermice significantly shifted in both dietary axes across years (P = 9.791e-13 for $\delta^{13}C$ and P = 0.0005 for $\delta^{15}N$; Table 8) whereas vole dietary space shifted very little in carbon but significantly in nitrogen (P < 0.05; Table 8).

DISCUSSION

Our results suggest that competition is shaping post-fire community turnover from red-backed voles to deermice. Red-backed vole and deermouse populations are negatively correlated spatially and temporally and non-random differences in spatial capture data suggest strong dispersion even after accounting for habitat, particularly pre-fire. In old-growth habitats, where voles are abundant, deermouse dietary breadth is extremely reduced. However, when vole populations diminished post-fire, deermouse dietary niche breadth nearly tripled. Together, these results support the hypothesis that voles are competitively excluding deermice in older growth

habitats, and deermice are experiencing competitive release when voles diminish following a fire (Herrmann et al. 2021). In contrast, support for reciprocal competitive pressure experienced by red-backed voles from deermice was mixed. Voles exhibited a broad dietary niche across all years and experienced fewer year-to-year shifts in isotopic space, but competitor abundance was an important predictor of vole abundance at a trap station.

Competitive interactions between deermice and red-backed vole populations are supported by capture histories across our study sites. Both spatial and randomization results indicate deermice and voles are non-randomly segregating on the landscape. Models including competitor abundance better explain variation in deermice and voles captured pre-fire than vegetation-only models or those including spatial distances. This fits expectations from behavioral lab experiments where interactions between red-backed voles and deermice (and within deermice) were mostly aggressive (Grant 1970). Red-backed voles often have rigid habitat preferences, which may restrict their habitat selection but increase the competitive pressure for foods in their preferred 'high-quality' old-growth habitat, where they might out-compete or exclude deermice (Crowell and Pimm 1976). Together, this suggests red-backed voles might drive community turnover associated with fires by competitively excluding deermice spatially and restricting access to certain food resources in old-growth habitats, but competitive release drives deermouse abundance after fires. Although support for competitive pressure contrasts with previous studies (Galindo and Krebs 1985, Morris 1996), this may reflect regional and temporal shifts driving differing competitive pressure (similar to the findings of Smith and Fox 2017). Overall, we found a strong, negative influence of voles on deermice, with less impact of deermice on voles, which is similar to other findings regarding habitat use in the two species (Crowell and Pimm 1976).

As an alternative to competition theory, we evaluated the possibility that community turnover associated with fire disturbance may reflect resource-driven habitat preferences (optimal foraging theory). Under this hypothesis (Fig. 1a) each species would experience a greater population density and smaller dietary niche in preferred habitats, where food resources are abundant, with little niche overlap between species. Similar resource-based dietary and niche shifts have been described in white-footed deermice (*P. leucopus*) and North American deermice, with both species exhibiting narrower niche breaths during masting seasons (i.e., when consuming a high-quality food resource) and expanded dietary niches in non-masting seasons when food resources are reduced (Stephens et al. 2019). However, our results run counter to these predictions. Pre-fire, when vole abundance was high, deermouse dietary breadth was extremely reduced and marginal to vole dietary niche space. Instead of niche reduction post-fire, the dietary niche of deermice increased nearly threefold. If post-fire niche expansion in the deermice from our study was solely due to consuming more low-quality food resources in newly burned habitats, we would expect niche expansion and population decreases (similar to Stephens et al. 2019), which is also not the case. Instead our results fit expectations under the ecological release hypothesis (Herrmann et al. 2021), and contrast with alternative niche expansion expectations related to resource-driven habitat preferences.

In contrast to deermice, red-backed voles maintained a large dietary breadth in carbon and nitrogen space across all years, with fewer year-to-year shifts, despite widespread habitat changes (Lanier et al. 2017). Based on stable isotopes, voles consume a broad range of nitrogen food resources pre-fire (Fig. 6), but shift to a more restricted and δ^{15}N-enriched niche after a fire. This may indicate they incorporate more insects in their diet post-fire or it may reflect post-fire nitrogen release from above ground plant matter into soil (Neary et al. 2005). While voles

outcompete deermice in older-growth habitats, supporting competition and competitive release, voles do not seem to receive a lot of reciprocal pressure from deermice based on our isotopic data. This suggests the post-fire vole population crash and dietary shift seem to be driven by resource shifts (and, thus, support for resource tracking/optimal foraging). This finding also may explain their slower expansion into marginal habitat after a disturbance and the lack of evidence for displacing other species after a disturbance (Crowell and Pimm 1976).

Beyond competitive release from red-backed voles, dietary flexibility exhibited by deermice may also contribute to their post-fire success. Both species shifted their dietary niche post-fire, transitioning to a diet enriched in ^{13}C, which coincided with increased grass abundance in burned habitats, as is common in fire succession (Lanier et al. 2017). However, deermouse dietary shifts were greater than those observed in red-back voles (Fig. 6; Table 8). Deermice have also been found to be more efficient foragers than voles, especially in altered habitats (Lemaître et al. 2010, Zwolak et al. 2012), which may allow deermice to be more successful after the fire. Overall, burned areas are high quality habitat for deermice, with similar survival rates and higher reproduction rates compared to unburned habitats (Zwolak and Foresman 2008, Zwolak et al. 2012).

The presence of a deermouse- or vole-dominated small mammal community has important ecological consequences. For example, deermice are important predators on songbird nests (Hethcoat and Chalfoun 2015), whereas red-backed voles are important dispersers of fungal spores (Orrock and Pagels 2002). Moreover, these two species differ with respect to seed choice (Lobo 2014); with deermice exhibiting a greater ability to tolerate plant secondary compounds from pine seeds which impacts their roles as seed predators and dispersers (Lobo and Millar 2011). Deermice and red-backed voles also differ with respect to boldness, seed-predation

and seed caching, and microhabitat preference. For example, seed dispersal differs based upon mouse and vole personalities; specifically, anxiety (time spent grooming) in mice and boldness (time spent in the center of an open-field test) in voles (Brehm et al. 2019). Dispersal distance decreased in anxious deermice while bold red-backed voles dispersed seeds twice the distance of timid voles. Vole cache locations were also predicted by docility, with docile voles more likely to cache seeds in coarse woody debris. These links between species preferences, individual personality and seed selection, dispersal, and caching in different habitats (Brehm et al. 2019) shape the characteristics of the surrounding plant community (Zwolak 2018). Finally, evidence suggests voles and deermice are differentially important as prey items for mammalian and avian predators such as weasels and spotted owls (Wywialowski 1987, Rosenberg et al. 2003). Thus, an abundance of deermice or voles can have both top-down and bottom-up impacts on the surrounding ecological community.

This research provides unique insights into the drivers of community structure during fire succession by evaluating evidence for competitive shifts and resource availability between two regionally dominant small mammals. We found evidence that competition is an important factor influencing community turnover from voles to deermice during succession. Population density, community diversity, and habitat recovery have been suggested as factors that contribute to the community turnover among small mammals during disturbances (Eckrich et al. 2018). Our results suggest competitive release is also important in community turnover during fire succession. Competitive dynamics shift in disturbed habitats, as voles are removed and deermice become abundant, and understanding these dynamics provides important predictions regarding responses to disturbance. As small mammals are a trophic link between producers and higher-level predators, understanding mechanisms that structure diet and abundance shifts in small

mammal communities could help us better predict ecosystem changes. With climate projections suggesting that large, severe fires will become more frequent in coming decades (Romme et al. 2011, Abatzoglou and Williams 2016, Riley and Loehman 2016), these mechanistic insights are vital for predicting community responses and ecosystem resilience.

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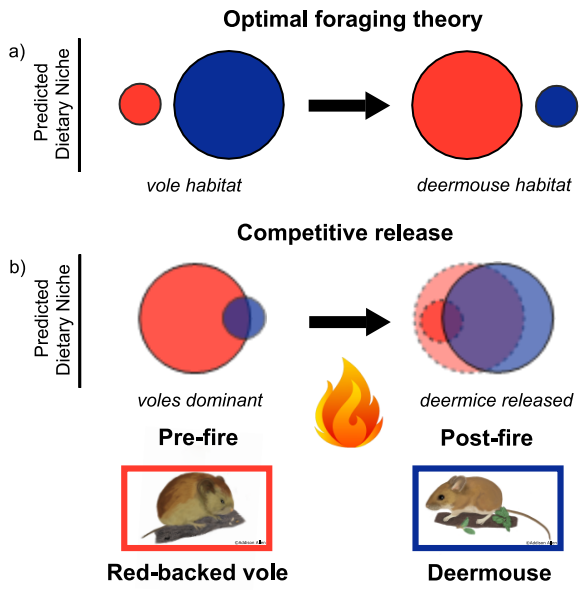


Figure 1. Predicted pre-/post-fire shifts in dietary niche space of red-backed voles and deermice under (a) optimal foraging theory, where each species exhibits a narrow dietary niche in its preferred habitat, and (b) competitive release, where post-fire release from competitive pressure from voles permits deermouse niche expansion. Under competitive release vole dietary niche breadth may be reduced if large deermouse populations exert competitive pressure on the remaining voles, limiting dietary niche space, or maintained, if there is no significant dietary exclusion. Species illustrations © Addison Allen.

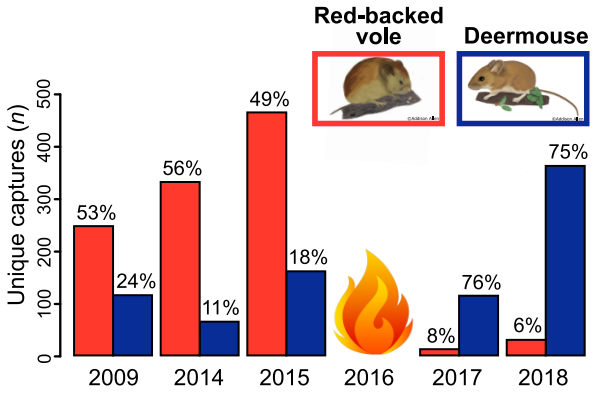


Figure 2. Abundance shifts of each species before and after the 2016 fire, with percentage of total captures above the bar. The remaining unique captures represent other species (*Microtus* spp., *Neotamias amoenus*, *Sorex* spp., *Thomomys talpoides*, *Phenacomys intermedius*, *Zapus princeps*, and *Neotoma cinerea*). Species illustrations © Addison Allen.

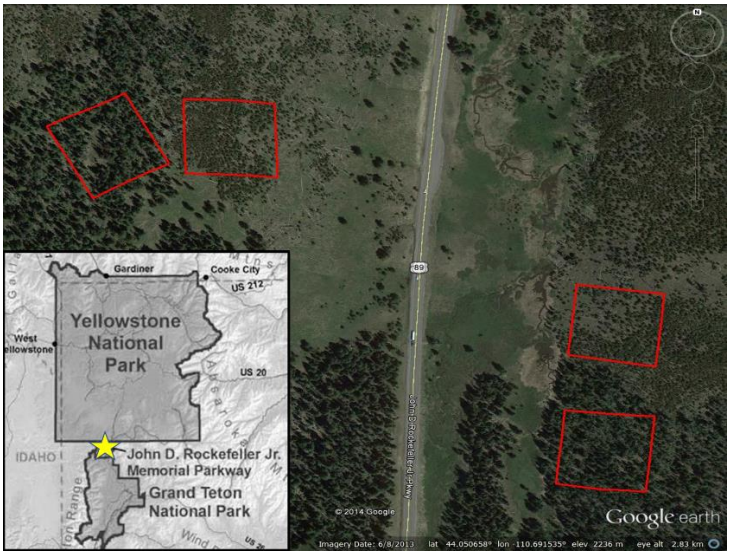


Figure 3.—The 4 grids (1-ha each) were established after the 1988 Yellowstone fires (Stanton et al. 1990), which burned 2 of the grids. In 2016, the Berry fire burned all 4 grids.

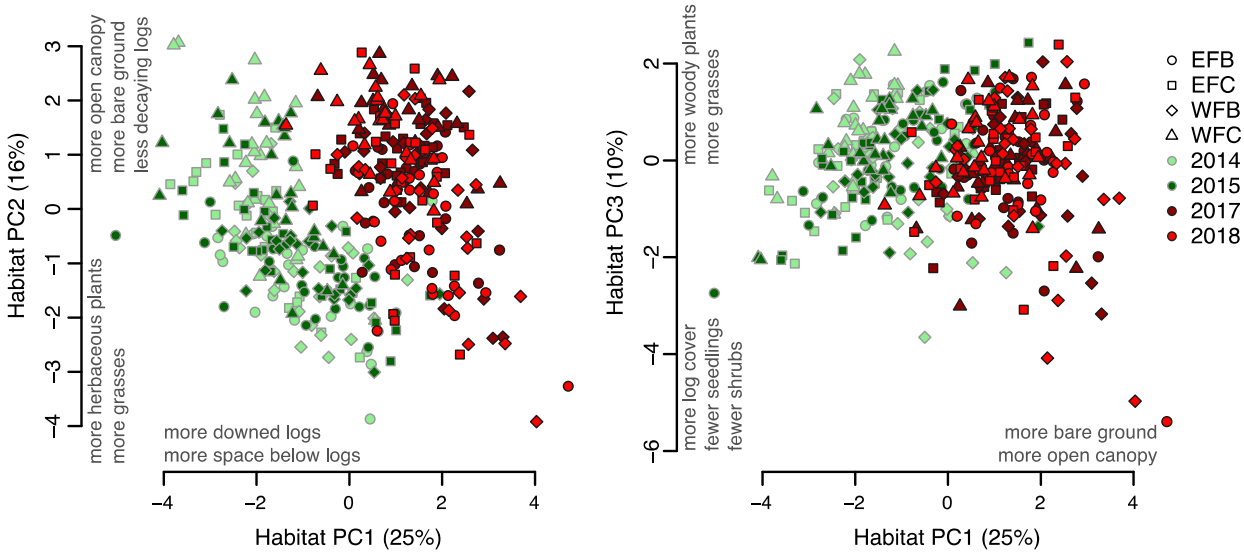


Figure 4.—Microhabitat differences among traps on principal components across all four years (2014, 2015, 2017, 2018; green shaded points for pre-fire years and red shaded points for post-fire years relative to the 2016 fire). Points are shaped according to which grid that vegetation sampling station belonged (4 grids: east-facing burn, east-facing control, west-facing burn, west-facing control; "control" and "burn" in grid acronyms refer to original naming of the grids affected by the 1988 Berry fires). Microhabitat differences with greater contributions to specific axes are shown on those axes.

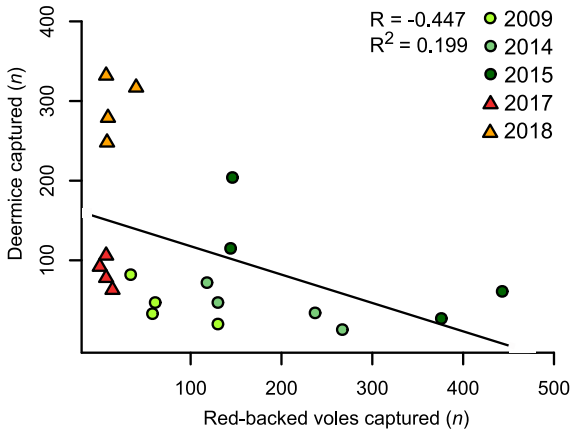


Figure 5. Red-backed vole captures are negatively correlated to deermouse captures during both pre- (circles) and post-fire (triangles) years (regression line shown for context). Red-backed vole captures were negatively correlated to deermice captures, with 35 fewer deermice captures for every additional 100 vole captures.

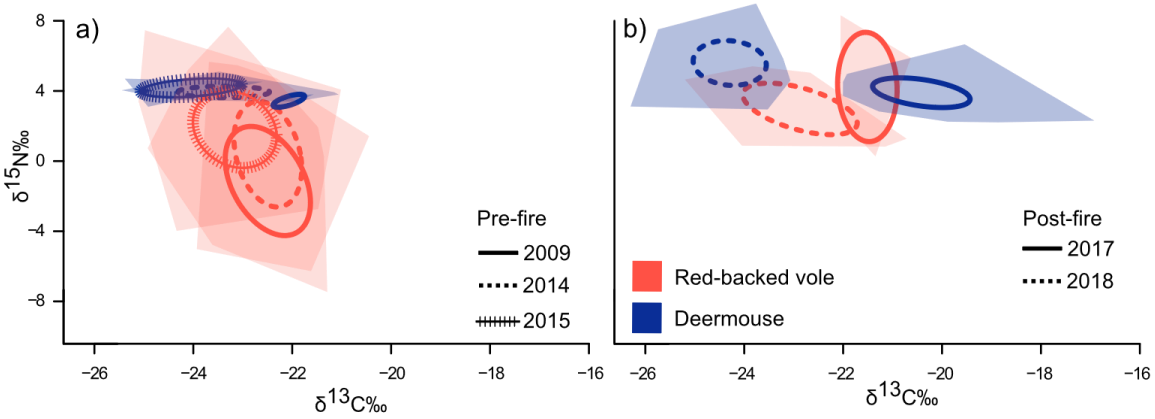


Figure 6. Carbon and nitrogen isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of deermice and red-backed voles shift from (a) pre-fire to (b) post-fire (both axes are the same). Standard ellipses corrected for small sample size (SEAc; lines) illustrate dietary niche breadth and convex hulls (shaded) enclose a species isotopic values within a given year. The post-fire reduction in vole population is associated with a nearly 3x increase in deermouse dietary niche.

Table 1.—Small mammal voucher specimens used for carbon and nitrogen isotope analysis to assess dietary differences. We used hair from 121 deermouse and red-backed vole specimens collected in 2009, 2014, 2015, 2017, and 2018, all of which are vouchered at the Sam Noble Museum of Natural History (OMNH catalog numbers below). Grids refer to four trapping grids: EFB = east-facing burn (burned in 1988 and 2016), EFC = east-facing control (burned in 2016), WFB = west-facing burn (burned in 1988 and 2016), WFC = west-facing control (burned in 2016).

OMNH Catalog No.	Year	Grid	Trap Station	Species	Sex	dC	dN
67013	2009	NA	NA	*Myodes gapperi*	NA	-22.0142	-0.55113
67017	2009	NA	NA	*Myodes gapperi*	NA	-23.2953	7.665053
67009	2009	NA	NA	*Myodes gapperi*	NA	-24.9243	0.731126
67016	2009	NA	NA	*Myodes gapperi*	NA	-24.1128	5.195675
67019	2009	NA	NA	*Myodes gapperi*	NA	-21.4789	1.940109
67007	2009	NA	NA	*Myodes gapperi*	NA	-23.3508	-3.57622
67015	2009	NA	NA	*Myodes gapperi*	NA	-21.7178	-3.2699
67010	2009	NA	NA	*Myodes gapperi*	NA	-21.2914	-7.46614
67014	2009	NA	NA	*Myodes gapperi*	NA	-21.7309	-5.114
67011	2009	NA	NA	*Myodes gapperi*	NA	-22.5404	-1.83187
67008	2009	NA	NA	*Myodes gapperi*	NA	-21.7602	-5.0403
67018	2009	NA	NA	*Myodes gapperi*	NA	-23.6139	-4.77558
67012	2009	NA	NA	*Myodes gapperi*	NA	-21.9366	0.019479
67020	2009	NA	NA	*Myodes gapperi*	NA	-21.359	0.247955
66827	2014	EFC	EFC_7-50	*Myodes gapperi*	M	-23.9284	-5.00774
66928	2014	WFC	WFC_5-80	*Myodes gapperi*	M	-21.6746	-3.78142
66896	2014	WFB	WFB_1-20	*Myodes gapperi*	F	-23.2279	1.66424
66804	2014	EFB	EFB_9-0	*Myodes gapperi*	M	-21.6171	-6.26331
66805	2014	EFB	EFB_1-80	*Myodes gapperi*	F	-22.3114	-0.76801
66898	2014	WFB	WFB_2-20	*Myodes gapperi*	M	-23.1132	5.479173
66835	2014	EFC	EFC_4-80	*Myodes gapperi*	M	-21.8917	-5.07856
66811	2014	EFB	EFB_6-20	*Myodes gapperi*	M	-22.4141	3.769592
66840	2014	EFC	EFC_9-30	*Myodes gapperi*	F	-22.7077	0.246931

66907	2014	WFB	WFB_10-60	*Myodes gapperi*	F	-23.6816	5.672969
66946	2014	WFC	WFC_7-0	*Myodes gapperi*	M	-22.3236	4.74426
66947	2014	WFC	WFC_6-60	*Myodes gapperi*	F	-23.001	2.849413
66842	2014	EFC	EFC_8-20	*Myodes gapperi*	F	-22.7127	0.818717
66817	2014	EFB	EFB_9-40	*Myodes gapperi*	F	-20.4439	1.439641
66818	2015	EFB	EFB_2-0	*Myodes gapperi*	F	-22.3105	-0.57752
66909	2015	WFB	WFB_5-0	*Myodes gapperi*	M	-24.3336	-3.96707
66955	2015	WFC	WFC_8-90	*Myodes gapperi*	M	-22.6734	-1.93223
66910	2015	WFB	WFB_2-20	*Myodes gapperi*	F	-21.4709	-2.72096
66958	2015	WFC	WFC_10-20	*Myodes gapperi*	M	-24.0362	0.139818
66847	2015	EFC	EFC_2-80	*Myodes gapperi*	M	-23.8669	-0.8914
66912	2015	WFB	WFB_6-20	*Myodes gapperi*	M	-24.9747	7.473961
66850	2015	EFC	EFC_4-0	*Myodes gapperi*	F	-23.9334	3.886583
66819	2015	EFB	EFB_5-0	*Myodes gapperi*	M	-21.0122	4.089282
66819	2015	EFB	EFB_5-0	*Myodes gapperi*	M	-21.0122	4.089282
66853	2015	EFC	WFB_8-20	*Myodes gapperi*	M	-25.1047	3.415731
66857	2015	EFC	EFC_6-80	*Myodes gapperi*	M	-22.9819	0.953365
66859	2015	EFC	EFC_2-80	*Myodes gapperi*	M	-22.4466	1.85321
66973	2015	WFC	WFC_1-40	*Myodes gapperi*	F	-23.4506	4.681498
66973	2015	WFC	WFC_1-40	*Myodes gapperi*	F	-23.4506	4.681498
66861	2015	EFC	EFC_6-80	*Myodes gapperi*	F	-22.3912	1.725385
66974	2015	WFC	WFC_1-80	*Myodes gapperi*	F	-23.0796	0.355294
66914	2015	WFB	WFB_5-80	*Myodes gapperi*	NA	-23.9536	4.655653
66915	2015	WFB	WFB_10-20	*Myodes gapperi*	F	-23.3447	2.61451
66981	2017	WFC	WFC_3-0	*Myodes gapperi*	M	-21.3469	0.275105
66984	2017	WFC	WFC_10-20	*Myodes gapperi*	M	-22.0525	8.322922
66821	2017	EFB	EFB_2-60	*Myodes gapperi*	M	-20.6302	5.896888
66916	2017	WFB	WFB_1-10	*Myodes gapperi*	M	-22.0545	2.446926
66987	2018	WFC	WFC_6-20	*Myodes gapperi*	M	-22.5131	2.296345
66988	2018	WFC	WFC_6-20	*Myodes gapperi*	F	-23.8326	5.386263
66989	2018	WFC	WFC_6-20	*Myodes gapperi*	M	-22.6684	5.022552
66822	2018	EFB	EFB_10-40	*Myodes gapperi*	M	-21.1493	0.804478

66990	2018	WFC	WFC_8-90	*Myodes gapperi*	M	-20.7189	1.253738
66918	2018	WFB	WFB_7-0	*Myodes gapperi*	NA	-24.0493	0.854989
66991	2018	WFC	WFC_8-20	*Myodes gapperi*	F	-25.2045	4.629328
66992	2018	WFC	WFC_8-20	*Myodes gapperi*	NA	-23.005	3.392799
66797	2009	NA	NA	*Peromyscus maniculatus*	M	-22.2606	2.875396
66798	2009	NA	NA	*Peromyscus maniculatus*	F	-22.4006	3.36205
66799	2009	NA	NA	*Peromyscus maniculatus*	M	-22.0699	3.715713
66800	2009	NA	NA	*Peromyscus maniculatus*	F	-21.5668	3.811733
66707	2014	WFB	WFB_2-40	*Peromyscus maniculatus*	M	-24.4799	3.647907
66708	2014	WFB	WFB_2-20	*Peromyscus maniculatus*	F	-25.4455	4.050871
66622	2014	EFB	EFB_5-80	*Peromyscus maniculatus*	M	-22.5263	4.520913
66764	2014	WFC	WFC_4-20	*Peromyscus maniculatus*	F	-21.0597	3.809141
66709	2014	NA	WFB_4-20	*Peromyscus maniculatus*	F	-23.5234	3.903116
66710	2014	WFB	WFB_2-20	*Peromyscus maniculatus*	F	-23.7577	3.605248
66711	2014	WFB	WFB_2-20	*Peromyscus maniculatus*	F	-21.152	3.943761
66712	2014	WFB	WFB_2-20	*Peromyscus maniculatus*	M	-24.3947	3.485403
66713	2014	WFB	WFB_2-20	*Peromyscus maniculatus*	M	-23.2688	3.895441
66714	2014	WFB	WFB_5-40	*Peromyscus maniculatus*	M	-24.0163	3.789869
66715	2014	WFB	WFB_5-40	*Peromyscus maniculatus*	F	-24.0711	3.868039
66715	2014	WFB	WFB_5-40	*Peromyscus maniculatus*	F	-24.0711	3.868039
66765	2014	WFC	WFC_2-20	*Peromyscus maniculatus*	F	-23.4818	5.117904
66675	2014	EFB	EFC_7-60	*Peromyscus maniculatus*	F	-21.938	3.403384
66623	2014	EFB	EFB_9-40	*Peromyscus maniculatus*	F	-23.8429	4.39997
66624	2015	EFB	EFB_7-40	*Peromyscus maniculatus*	M	-22.5923	4.541885
66716	2015	WFB	WFB_5-60	*Peromyscus maniculatus*	F	-24.9099	3.111855
66625	2015	EFB	EFB_1-80	*Peromyscus maniculatus*	F	-24.4809	4.051308
66626	2015	EFB	EFB_3-0	*Peromyscus maniculatus*	M	-25.3826	4.716986
66853	2017	WFB	WFB_8-20	*Peromyscus maniculatus*	M	-25.1047	3.415731
66627	2015	EFB	EFB_9-40	*Peromyscus maniculatus*	F	-22.925	4.515722
66718	2017	WFB	WFB_6-20	*Peromyscus maniculatus*	M	-18.9033	3.527118
66628	2017	EFB	EFB_9-0	*Peromyscus maniculatus*	M	-19.5798	3.521829
66676	2017	EFC	EFC_6-80	*Peromyscus maniculatus*	F	-20.8274	5.612175

66982	2017	WFB	WFB_5-80	*Peromyscus maniculatus*	F	-21.3376	4.069227
66720	2017	WFB	WFB_1-40	*Peromyscus maniculatus*	F	-21.6368	4.776318
66997	2017	WFB	WFB_6-20	*Peromyscus maniculatus*	M	-22.005	3.730212
66677	2017	EFC	EFC_1-20	*Peromyscus maniculatus*	F	-21.7981	4.59691
66678	2017	EFC	EFC_1-20	*Peromyscus maniculatus*	F	-19.5412	6.666524
66766	2017	WFC	WFC_5-0	*Peromyscus maniculatus*	M	-19.3962	2.432359
66722	2017	WFB	WFB_10-60	*Peromyscus maniculatus*	F	-16.9183	2.309766
66679	2017	EFC	EFC_6-80	*Peromyscus maniculatus*	F	-20.6408	4.568363
66723	2017	WFB	WFB_6-30	*Peromyscus maniculatus*	M	-21.2777	2.835098
66796	2017	WFC	WFC_5-80	*Peromyscus maniculatus*	F	-19.2917	3.587182
66680	2017	EFC	EFC_2-80	*Peromyscus maniculatus*	M	-22.003	4.528385
66767	2017	WFC	WFC_8-20	*Peromyscus maniculatus*	F	-21.72	3.741714
66629	2017	EFC	EFC_10-0	*Peromyscus maniculatus*	M	-19.8861	2.249797
66630	2017	WFC	EFB_9-80	*Peromyscus maniculatus*	M	-21.9238	4.974965
66681	2017	EFC	EFC_1-20	*Peromyscus maniculatus*	F	-20.0514	4.36343
66724	2017	WFB	WFB_10-50	*Peromyscus maniculatus*	M	-20.7249	3.160152
66631	2017	EFB	EFB_1-80	*Peromyscus maniculatus*	M	-20.8314	4.536692
66725	2018	WFB	WFB_7-0	*Peromyscus maniculatus*	F	-23.887	3.405848
66726	2018	WFB	WFB_10-20	*Peromyscus maniculatus*	F	-26.3022	3.087099
66733	2018	WFB	WFB_8-20	*Peromyscus maniculatus*	M	-23.5282	2.920719
66635	2018	EFB	EFB_9-80	*Peromyscus maniculatus*	M	-23.2137	5.824361
66636	2018	EFB	EFB_2-0	*Peromyscus maniculatus*	F	-24.0483	6.344323
66637	2018	EFB	EFB_10-60	*Peromyscus maniculatus*	F	-24.5443	6.140276
66769	2018	WFC	WFC_4-20	*Peromyscus maniculatus*	M	-23.2006	4.398959
66737	2018	WFB	WFB_4-60	*Peromyscus maniculatus*	F	-24.2792	7.367502
66739	2018	WFB	WFB_5-80	*Peromyscus maniculatus*	M	-25.7428	7.49342
66771	2018	WFC	WFC_5-0	*Peromyscus maniculatus*	M	-23.8235	5.883755
66639	2018	EFB	EFB_8-20	*Peromyscus maniculatus*	NA	-25.2912	6.316674
66773	2018	WFC	WFC_2-20	*Peromyscus maniculatus*	M	-23.761	8.962202
66775	2018	WFC	WFC_4-20	*Peromyscus maniculatus*	M	-24.5644	4.576181
66640	2018	EFB	EFB_9-40	*Peromyscus maniculatus*	F	-25.3869	6.306577
66780	2018	WFC	WFC_2-60	*Peromyscus maniculatus*	NA	-23.0675	4.56692

Table 2.—Principal component axes (PCA) of microhabitat across four years (2014, 2015, 2017, 2018) from 25 trap stations per grid; 100 stations per year (400 stations total). Contributions of each microhabitat variable to each component are shown below. CWD = coarse woody debris (downed logs and branches >7.5 cm in diameter).

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**
Proportion of variance	0.24	0.16	0.10	0.09	0.08	0.075	0.072	0.051	0.045	0.037	0.031	0.017
Cumulative proportion	0.24	0.4	0.5	0.59	0.67	0.75	0.82	0.87	0.91	0.95	0.98	1.0
Standard deviation	1.7	1.4	1.1	1.0	0.98	0.95	0.93	0.79	0.74	0.67	0.61	0.45
Microhabitat Variable Contributions												
% herbaceous plants	0.21	19	0.42	0.4	33	4.9	20	1.6	1.2	2.3	9.5	7
% woody plants	9.4	8.9	6.4	13	19	1	1.1	3.3	7.6	1.5	11	19
% grass	0.0007	19	4.8	0.04	0.02	46	13	0.79	1.7	4.1	0.6	10
% log	5.1	0.14	29	24	1.1	0.43	7.5	2.8	17	8.4	0.97	3.8
% bare ground	19	12	0.98	2.4	1.4	0.05	0.5	0.25	11	0.28	2	50
% leaf litter	6.1	0.72	0.00008	5.1	3.2	30	50	1.3	1.2	0.14	0.98	1.1
CWD count	16	1.1	6.2	8.3	1.3	4.8	0.03	0.29	19	35	7.9	0.1
Mean CWD height	15	2.8	4.8	10	7	0.43	0.04	0.45	19	35	5.9	0.13
Mean CWD decay state	3.5	12	5.2	11	25	8	3.1	0.03	12	13	7	0.073
Canopy cover	13	15	0.001	5.8	2.1	3.2	0.88	2	2.4	0.1	48	7.4
Distance to seedling	7	3.6	19	12	3.1	0.16	1.4	51	2.8	0.41	0.02	0.51
Distance to shrub	5.7	5.3	24	9	3.7	0.71	2.3	37	5.1	0.14	6.8	0.85

Table 3.—Red-backed voles (*Myodes gapperi*), deermice (*Peromyscus maniculatus*), and total small mammal captures by year, and the number of voucher specimens used for isotope analysis.

	Red-backed voles		Deermice		Small mammals	
Year	*n* unique (n_{total} = 1,115)	*n* isotope samples	*n* unique (n_{total} = 824)	*n* isotope samples	*n* unique (n_{total} = 2716)	*n* captures (n_{total} = 5493)
2009	256	14	116	4	486	607
2014	349	16	65	16	650	1197
2015	468	16	162	5	936	1901
2017	12	4	116	21	153	404
2018	30	8	365	15	491	1384

Table 4.—Randomization results from a co-occurrence analysis using binary presence-absence capture history of deermice and red-backed voles from each monthly sampling session over the 5 sampling years. This tested whether species were unlikely to co-occur among trap stations by comparing the observed species overlap within a month (obs) against with a randomized, simulated overlap matrix (sim). Simulations were run 1000 times under the "sim2" algorithm which preserves species rarity in the matrix, but assumes all sites are equally likely to be colonized with no variation in habitat quality.

Year	Month	N_{traps}	N_{voles}	N_{mice}	Mean_sim	SD_sim	Obs	p-value
2009	June	71	54	19	182	72	884	< **0.001**
	July	112	73	47	692	151	2535	< **0.001**
	August	137	84	63	1109	200	3922	< **0.001**
2014	June	73	63	10	73	54	630	< **0.001**
	July	215	179	54	1215	338	5796	< **0.001**
	August	257	221	63	1469	410	6984	< **0.001**
2015	June	138	116	29	429	171	2398	< **0.001**
	July	266	227	76	1804	460	7410	< **0.001**
	August	308	226	146	4611	609	13284	< **0.001**
2017	June	63	10	54	69	49	477	< **0.001**
	July	89	5	86	13	32	252	< **0.001**
	August	103	7	100	19	41	288	**0.001**
2018	June	137	8	132	37	67	645	< **0.001**
	July	242	29	227	357	253	3195	< **0.001**
	August	281	16	273	116	167	2120	< **0.001**

Table 5.—Coefficients and AIC values from the top generalized linear models indicate the influence of competitor abundance (i.e., number of deermouse or vole captures at a trap station) and vegetation on target species abundance. Simultaneous autoregressive (SAR) model accounting for spatial distance (a distance matrix component based on coordinate data) were uniformly worse, based on AIC values (Table 6). Analyses were run by year, focusing on 25 trap stations per grid where vegetation data were collected (100 traps stations/year), and were run separately with either deermice or redback vole abundance in a given year as the response variable.

Year	Model	Intercept	Veg PC1	Veg PC2	Veg PC3	Competitor	AIC
Deermice (*Peromyscus maniculatus*)							
2014	PC1+PC2+PC3+voles	0.07	0.16	-0.06	-0.01	-0.37	198.17
2015	PC1+PC2+PC3+voles	0.10	0.02	-0.32	-0.30	-0.11	289.18
2017	PC1+PC2+PC3	-0.85	0.05	0.23	-0.08	*NA*	214.02
2018	PC1+PC2+PC3	1.09	0.002	0.06	-0.06	*NA*	438.71
Red-backed voles (*Myodes gapperi*)							
2014	PC1+PC2+PC3+deermice	0.23	-0.27	-0.05	0.27	-0.25	350.53
2015	PC1+PC2+PC3+deermice	0.75	-0.26	0.10	0.14	-0.12	416.89
2017	PC1+PC2+PC3	-1.91	-0.54	-0.06	0.05	*NA*	59.59
2018	PC1+PC2+PC3	-1.03	-0.81	-0.01	-0.17	*NA*	95.99

Table 6.—Differences in AIC values between generalized linear models based upon inclusion of competitor abundance and those including a spatial component (simultaneous autoregressive [SAR] models). Before the 2016 fire, models that include the presence of a competitor are a better fit, which fits expectations under the competitive release hypothesis. After 2016, models with a competitor are equivalent to models without a competitor, which suggests a reduction in competitive pressure between species associated with fire disturbance. The comparisons with significant Lambda values (bolded) indicate spatial autocorrelation, which might be due to other unaccounted variables, but accounting for spatial autocorrelation did not affect inferred competition.

Year	Response species	Model	AIC	ΔAIC	$Lambda_{spatial}$	*Lambda p-value*
2014	Deermice	PC1+PC2+PC3+voles	198.17	0.00		
		PC1+PC2+PC3	202.96	4.79		
		PC1+PC2+PC3+voles+spatial correction	313.59	115.42	0.13	0.40
		PC1+PC2+PC3+spatial correction	315.53	117.36	0.14	0.39
	Voles	PC1+PC2+PC3+deermice	350.53	0.00		
		PC1+PC2+PC3	354.19	3.66		
		PC1+PC2+PC3+deermice+spatial correction	388.11	37.58	0.17	0.38
		PC1+PC2+PC3+spatial correction	390.03	39.50	0.19	0.35
2015	Deermice	PC1+PC2+PC3+voles	289.18	0.00		
		PC1+PC2+PC3	289.41	0.23		
		PC1+PC2+PC3+spatial correction	383.39	94.21	0.33	**0.01**
		PC1+PC2+PC3+voles+spatial correction	383.95	94.77	0.31	**0.02**
	Voles	PC1+PC2+PC3+deermice	416.89	0.00		
		PC1+PC2+PC3	418.37	1.48		
		PC1+PC2+PC3+spatial correction	443.26	26.37	0.49	**0.0001**
		PC1+PC2+PC3+deermice+spatial correction	444.54	27.65	0.47	**0.0002**

2017	Deermice	PC1+PC2+PC3	214.02	0.00		
		PC1+PC2+PC3+voles	215.30	1.28		
		PC1+PC2+PC3+spatial correction	293.94	79.92	0.33	**0.02**
		PC1+PC2+PC3+voles+spatial correction	295.64	81.62	0.33	**0.03**
	Voles	PC1+PC2+PC3	59.59	0.00		
		PC1+PC2+PC3+deermice	60.79	1.20		
		PC1+PC2+PC3+spatial correction	106.73	47.14	-0.05	0.74
		PC1+PC2+PC3+deermice+spatial correction	108.26	48.67	-0.06	0.70
2018	Deermice	PC1+PC2+PC3	438.71	0.00		
		PC1+PC2+PC3+voles	440.70	1.99		
		PC1+PC2+PC3+spatial correction	462.9	24.19	0.21	0.17
		PC1+PC2+PC3+voles+spatial correction	464.83	26.12	0.21	0.16
	Voles	PC1+PC2+PC3	95.99	0.00		
		PC1+PC2+PC3+deermice	97.97	1.97		
		PC1+PC2+PC3+spatial correction	162.57	66.58	-0.05	0.75
		PC1+PC2+PC3+deermice+spatial correction	164.55	68.56	-0.05	0.75

Table 7.—Differences in carbon and nitrogen isotopes between species shown as p-values based upon a MANOVA analysis for each of the 5 years.

	2009	**2014**	**2015**	**2017**	**2018**
C Pr(>F)	0.4752	0.1118	0.1855	0.1305	**0.01212 ***
N Pr(>F)	**0.04935 ***	**0.003458 ****	0.0686	0.7222	0.3122

Table 8.—Differences in carbon and nitrogen isotope values across 5 years (2009, 2014, 2015, 2017, 2018), shown as *p*-values based upon a MANOVA analysis for each of the 2 species independently. While deermice show significant niche shifts in both isotopic values, red-back voles only shift in nitrogen use.

	Red-backed voles	Deermice
C Pr(>F)	0.07	**9.791e-13 *** **
N Pr(>F)	**0.03 ***	**0.0005 *** **