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REVIEW

Small mammal associations with habitat composition, configuration, and management in tallgrass prairies: a review

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ABSTRACT

1. Tallgrass prairie is among the most threatened ecosystems but is often fragmented and surrounded by human-modified landscapes. Small mammals are integral components of tallgrass prairies. However, little is known about how landscape composition, configuration, and management impact small mammals in tallgrass prairies.
2. We conducted a systematic literature review to identify species-specific and community associations with three broad topics: landscape composition, landscape configuration, and management practices.
3. We identified 61 studies that assessed our variables of interest. We categorised the location, species assessed, variables monitored, and results by species and for the community.
4. The majority of studies (64%) were conducted in two states, Illinois and Kansas. Deer mice (*Peromyscus maniculatus*), prairie voles (*Microtus ochrogaster*), and white-footed mice (*Peromyscus leucopus*) showed specific associations with landscape variables, with deer mice preferring bare ground and recently burned plots, and prairie voles preferring thatch and negatively associated with prescribed fire. White-footed mice were frequently associated with wooded areas.
5. Small mammal biodiversity was positively associated with patchy habitats containing greater diversity in vegetative composition and management regime. Management and land composition were both relatively well studied for several species; habitat configuration was understudied.
6. We identified significant gaps in our understanding of small mammal landscape ecology in tallgrass prairies. With tallgrass prairie restoration a growing trend in this region, a greater understanding of drivers of small mammal populations will be crucial to successful restoration efforts. Future research should focus on understudied areas and species, and examine how habitat heterogeneity impacts small mammal biodiversity.

INTRODUCTION

Small mammals (here defined as any mammal weighing less than 400 g) are some of the most abundant taxa across ecosystems and play critical ecological roles in the ecosystems they inhabit. In addition to filling specific dietary niches and providing critical prey resources to mesocarnivores and other predators, small mammals provide

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numerous ecosystem services. Given their central role in food webs, small mammals can be used as an indicator species for broad ecosystem health or function (Avenant 2000, Leis et al. 2008). Many species of small mammals burrow, creating soil disturbances that can aid in aeration and topsoil formation (Martin 2003). They are significant consumers of invertebrates and seeds and have been shown to have an impact on diversity of both invertebrates and plants (Churchfield et al. 1991, Poe et al. 2019). They may consume plants and invertebrates that are species of interest or conservation targets in these systems (Gibson et al. 1990, Tschumi et al. 2018), making a clear understanding of the drivers of their populations critical for ecosystem management. Finally, many small mammals are vectors for diseases such as lyme disease and hantavirus (Mills 2006, Ostfeld et al. 2018). Increased threats from these diseases have been associated with biodiversity losses and landscape structure changes (Langlois et al. 2001, Allan et al. 2003, Mills 2006), so a greater understanding of small mammals in threatened and fragmented ecosystems is key.

Small mammals play important roles in grassland ecosystems (Laidlaw et al. 2013) such as prairies but are understudied in these systems, with much of the existing literature focusing on small mammals in forests. A Web of Science search of "small mammal*" AND forest yielded 3858 results, while "small mammal*" AND grassland yielded only 1224. Even more seldom studied are the ways small mammals respond to landscape-scale variables (land cover/composition, landscape configuration, and landscape-scale management) in these systems. Tallgrass prairies are one of the most globally threatened ecosystems, with less than 5% of historical extent remaining (Howe 1994, Sampson & Knopf 1994, Hoekstra et al. 2005). This significant decline in habitat has led to tallgrass prairie being a common target for ecological restoration efforts. Today, most of the remnant (i.e. never ploughed) and restored tallgrass prairie exists as small, fragmented patches, often within vast agricultural networks. While these relationships are not well studied in North American grasslands, small mammals have broad and species-specific responses to changes in land cover (Wegner et al. 1999, Méro et al. 2015) or habitat connectivity in other ecosystems (Mulligan et al. 2013, Downing et al. 2015). As habitat loss continues and restoration efforts grow, it will only become more important to understand the dynamics of small mammals in fragmented habitats with variable land cover such as tallgrass prairies. It is also important to conduct studies in both remnant and restored habitats, as they have been shown to differ in plant communities (Polley et al. 2005, Barak et al. 2017), and therefore small mammal response to landscape-scale variables may vary between them.

Small mammals are sensitive to variation in land cover, at both local and landscape scales. Variation in cover can drive community assembly (Michel et al. 2007), dispersal and population genetics (Howell et al. 2017), and population cycling (Birney et al. 1976). In remnant and restored prairies, there may be a mosaic of land cover types in close proximity, including agricultural or grazing fields, developed land, and savannas or woodlands. Small mammals often have species-specific associations with particular habitat types and variations in connectivity or fragmentation (Delattre et al. 1996, Nupp & Swihart 2000). Research into these patterns can support a greater understanding of the drivers of small mammal populations and community composition. Furthermore, many of the current studies examine specific populations and contexts, meaning that drawing generalizable trends from the data can be difficult.

While composition deals with the cover type and structure of a landscape, configuration refers to the connectedness or position of different cover types in relation to one another. In highly fragmented areas, there is increased exposure to edge areas bordering on less suitable habitat such as agricultural or urbanised land. Some taxa like birds vary with proximity to habitat edge over other landscape factors in tallgrass prairie systems (Winter et al. 2000). However, mammals are considerably less well studied, with much of the work being conducted in urban or forested systems (Bayne & Hobson 1998, Allan et al. 2003, Gomes et al. 2011, Delciellos et al. 2018). It is critical to understand how fragmentation impacts small mammals in tallgrass prairies, which are generally highly fragmented habitats in matrices of agriculture or human development.

Land management drives tallgrass prairie plant and animal populations (Guiden et al. 2021) and can have significant impacts on habitat structure. Management practices like prescribed fire and grazing are common practices that impact a variety of taxa (Hartnett et al. 1996, Eom et al. 2001, Boyce et al. 2021). These management activities can have significant direct and indirect impacts on small mammal communities (Vinton et al. 1993, Matlack et al. 2001, Burke et al. 2020, Guiden et al. 2023), which can in turn create a ripple effect on the vast spectrum of taxa connected to these species through food webs. Given their central roles in tallgrass prairie food webs, understanding the drivers of their populations and the potential impacts of management activities outside of their intended purpose is key.

While landscape context and management are important in shaping small mammal communities, studies thus far have largely focused on single sites or single species, meaning that it is difficult to glean generalities across sites or species. Further work is necessary to study small mammals

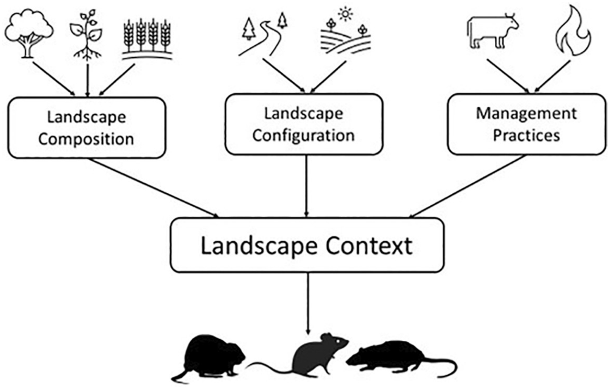

Fig. 1. A conceptual figure representing the three topics assessed in this literature review. Landscape composition includes the land cover type and structure of an area (agriculture, tall grass, woodlands). Landscape configuration includes the connectivity or fragmentation of an area, as well as responses to edge. Finally, management practices here include grazing herbivores and prescribed fire.

across a wider scope of landscape contexts, as well as to examine patterns across larger spatial scales (Fahrig et al. 2011). Here, we present a review of the literature examining the relationships between small mammals and landscape composition, landscape configuration, and management within tallgrass prairies in North America (Fig. 1).

We seek to highlight trends in both species-specific and community-wide relationships, as well as to identify gaps in the literature in locations and concepts, and suggest future directions for research that will support the successful management of these key organisms in grassland ecosystems.

METHODS

We obtained original published studies through a literature search in the Web of Science database in the spring of 2020 (Science Citation Index Expanded database). We used keywords “small mammal*” AND prairie OR “tallgrass prairie”, yielding 339 results. We examined the manuscripts for relevance using the criteria of location and topic or focus of the study. Location was limited to sites in the tallgrass prairie region, including parts of Illinois, Iowa, Kansas, Oklahoma, Ohio, Indiana, Texas, Nebraska, Missouri, South Dakota, North Dakota, Wisconsin, and Minnesota, as well as parts of Saskatchewan, Manitoba, and Ontario. We narrowed the focal studies to 90 by including studies only if small mammals were the focus and if the study considered any variable associated with landscape composition, configuration, or management. We excluded a further 39 studies after full review using the same criteria as above, resulting in 51 studies included in the review. We repeated the search in spring of 2022 to collect any recent publications that met the criteria, adding an additional five studies. Additionally, we utilised backward snowball sampling by searching the references sections of included papers for relevant studies, identifying an additional 5 studies for inclusion in the review for a total of 61 studies included in the final review.

We extracted information from each paper according to three categories: land use and land cover, referred to as habitat composition, habitat fragmentation and connectivity, referred to as habitat configuration, and management application (Appendix S1). Studies with habitat composition data ($n=46$) focused on how differences in vegetative structure, type of vegetation, plant species diversity, and other factors related to the land or ground cover makeup of the study site. It is important to note that these studies almost exclusively considered ground cover at local scales and that we found very few studies addressing the impacts of landscape-scale cover variation on small mammals. Studies with habitat configuration information ($n=17$) covered research that incorporated concepts of patch size, edge effects, and other measures that examine the connectivity of habitat patches. Several studies addressed multiple subtopics. Finally, studies with management application data ($n=28$) contained information examining the effects of management techniques such as prescribed fire and grazing on small mammal species. We also collected data on the location of study sites, the species included in each study, and the year of publication.

RESULTS AND DISCUSSION

Study locations and organisms

Research locations across 11 states and provinces in the tallgrass prairie region of North America were represented in the literature. Of the 61 publications reviewed for this study, 23 (38%) took place in Kansas, with 15 (65% of Kansas studies) of those conducted by Kansas State University and taking place at Konza Prairie Biological Station, a long-term ecological research site (25% of the reviewed studies overall). Another 16 (26% of all studies) studies took place in Illinois, nearly half of which were conducted by the University of Illinois – Urbana-Champaign (12% of all studies). This split distribution of research highlights the uneven coverage of this topic across the tallgrass prairie region. Furthermore, with over 35% of the reviewed studies coming from only two research sites, there is a lack of replication across space and observed patterns may not be representative of patterns in small mammals as a whole, but instead skewed to impacts in those two locations. Five studies were conducted in Texas and seven in Oklahoma, with only nine studies total between Iowa, Nebraska,

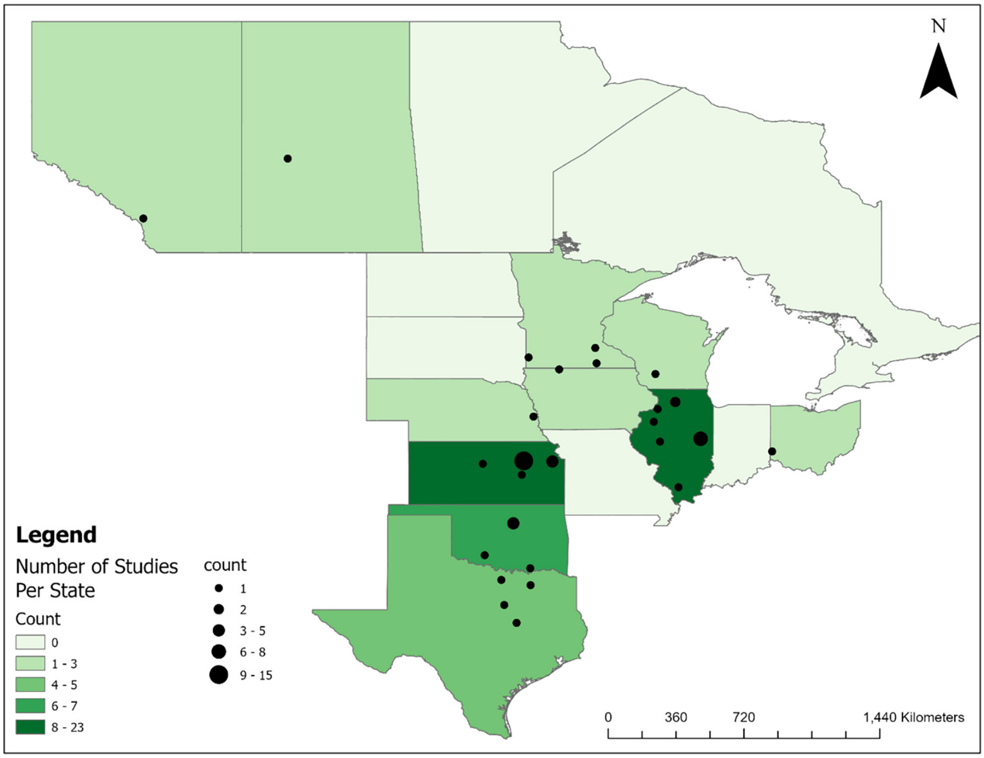

Fig. 2. A map representing the distribution of the reviewed studies. Kansas and Illinois had the most studies, with 23 in Kansas and 17 in Illinois. Ontario, Manitoba, Missouri, Indiana, North Dakota, and South Dakota all had zero studies included in the review.

Minnesota, and Wisconsin. Missouri, North and South Dakota, and Indiana were not represented at all. This reflects a major gap in the literature focusing on small mammals of the north-central tallgrass prairie region. Finally, only three studies addressed Canadian tallgrass prairie sites, reflecting the need for more work in the far north tallgrass prairies (Fig. 2). Furthermore, only one study assessed patterns across a range of states within the region (Reed et al. 2006).

In total, 47 species were reported across the reviewed studies (Appendix S2, Fig. 3). Of those 47, 30 appeared in more than two studies and 15 appeared in 10 or more. Furthermore, some species appeared in the methods or results section only briefly, with capture numbers being too low for inclusion in analysis. The most commonly studied species was the deer mouse (*Peromyscus maniculatus*), represented in 44 studies (72%), followed by the prairie vole (*Microtus ochrogaster*) in 42 studies (69%). These species were also not represented evenly geographically. Deer mice were reported in every state or province included, while white-footed mice (*Peromyscus leucopus*) and prairie voles were reported in almost every location, with white-footed mice absent from the two Canadian provinces and prairie voles not reported in Canada or Texas. All species included in more than 10 studies occurred in at least three states except for the Elliot's short-tailed shrew (*Blarina hylophaga*) and the fulvous harvest mouse (*Reithrodontomys fulvescens*), which were each only reported in two states (Kansas and Oklahoma, Oklahoma and Texas, respectively). This reflects the smaller overlap between the ranges of these two species and the tallgrass prairie region. Fifteen species were only reported in one state or province, with the majority of these from studies in Saskatchewan, Oklahoma, and Texas. These three states/provinces have less of their area in the tallgrass prairie region and were also less well represented in the studies overall.

Landscape composition

The majority of studies ($n=25$ of 46, 54%) that addressed land use and cover specifically addressed the impacts of variation in ground cover types (e.g. bare ground, grasses, forbs, woods) on small mammal populations and communities. These studies primarily used local metrics of ground cover, rarely considering broader trends in landscape-level cover. While the majority of studies described species-specific interactions, 15 also reported patterns in diversity and community composition. Deer mouse associations with land cover type were reported in 30 studies

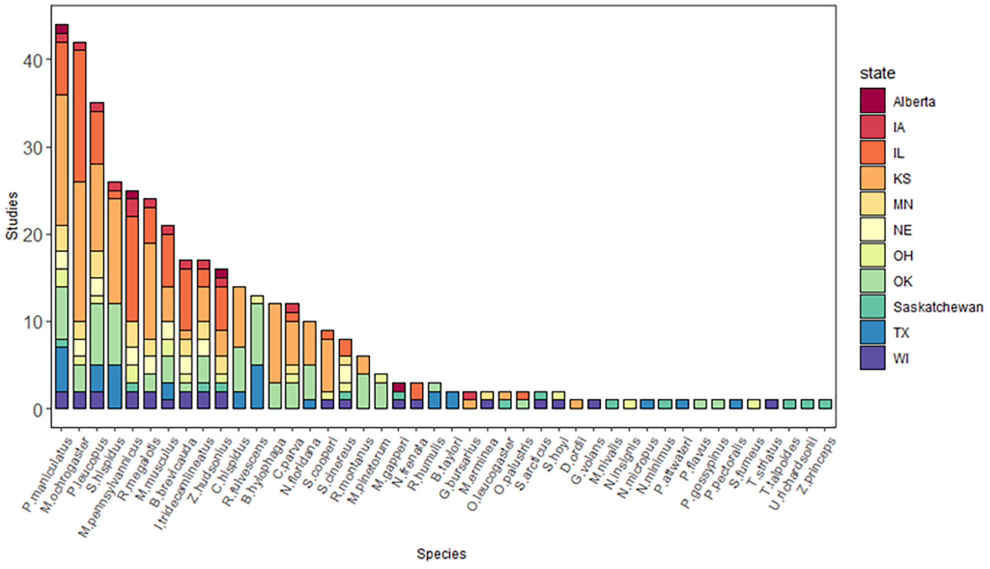

Fig. 3. A bar chart representing the distribution of species studied by state. Deer mice (*Peromyscus maniculatus*) are well distributed across the states, while meadow voles (*Microtus pennsylvanicus*) are heavily weighted in Illinois and hispid cotton mice (*Sigmodon hispidus*) are weighted towards the western tallgrass prairies. Several species were only mentioned in one or two studies, with the majority of these being from Saskatchewan, Oklahoma, Texas, and Wisconsin. Two studies are excluded as they took place in multiple states/provinces and did not report which species occurred in which location. For full names of species listed by study, see Appendix S2.

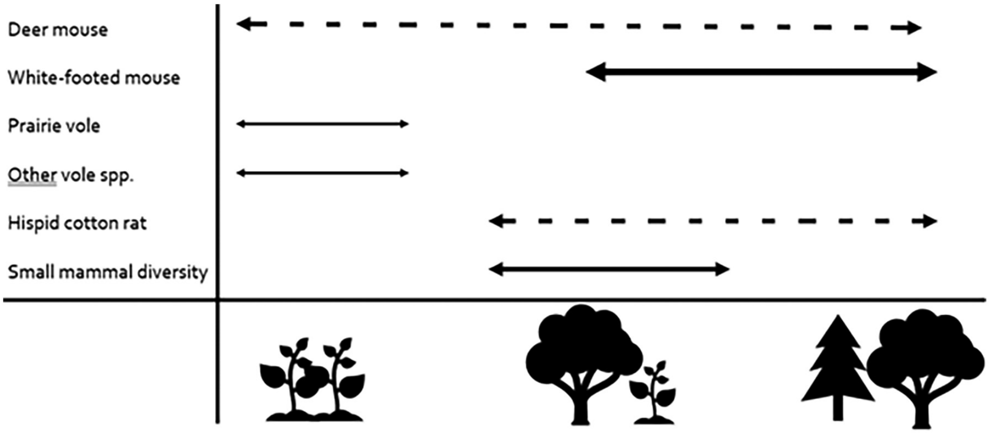

Fig. 4. A figure representing the species-specific and community diversity associated with differences in land cover type. The icons on the left represent grass and forb dominant cover, while those on the right represent forests. The boldness of the line represents the amount and strength of the evidence of an association between the species and the vegetative condition represented (boldest line >5 studies, medium line 3–5 studies, thinnest line 1–2 studies). Dashed lines represent relationships with conflicting evidence.

(65% of landscape composition studies). Six studies reported positive associations between deer mice with bare ground (Kaufman et al. 1988, Snyder & Best 1988, Fuhlendorf et al. 2010, Richardson 2010, Kirchner et al. 2011, Green & Wilkins 2014), but only one study specifically compared the two dominant subspecies (*P. m. gracilis* and *P. m. bairdii*) and reported differential responses to bare ground and woody debris (Stephens & Anderson 2014). Deer mice also showed varied associations with habitats. While previous research has suggested that deer mice prefer open, xeric habitats and are negatively associated with other habitat types (Kaufman & Fleharty 1974, Morris 1996), many studies posited that deer mice are broad habitat generalists (Peles et al. 1997). Snyder and Best (1988) found that deer mice could be found across a spectrum of grassland and woodland habitat (Fig. 4) but only had strong positive associations with bare ground (Fig. 5), not with specific cover types.

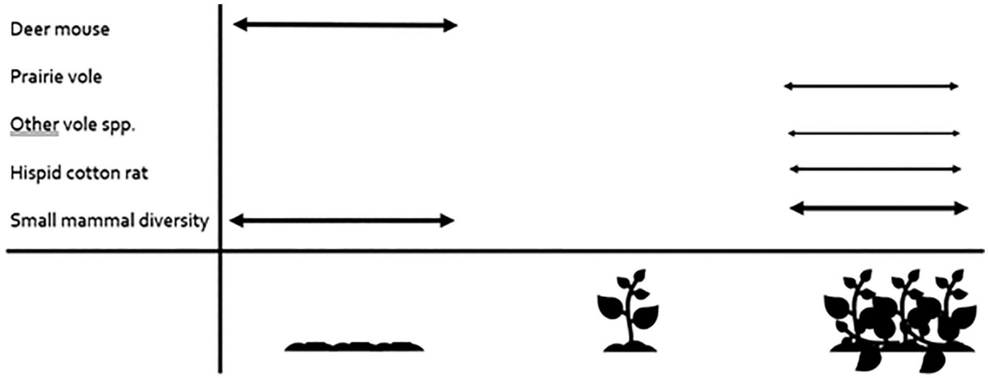

Fig. 5. A figure representing the species-specific and community diversity associated with differences in habitat structure. The icon on the left represents bare ground, while the icons on the right indicate dense vegetation and thatch cover. The boldness of the line represents the amount and strength of the evidence of an association between each species and the vegetative density represented (boldest line >5 studies, medium line 3–5 studies, thinnest line 1–2 studies).

Three studies presented a negative association between deer mice and prairie grasses or forbs (Horncastle et al. 2005, Fuhlendorf et al. 2010, Kirchner et al. 2011). Still others found a positive association between deer mice and proportion of nearby croplands (Kirsch 1997, Heisler et al. 2013), lowland woods (Hanchey & Wilkins 1998), upland prairies (Clark et al. 1998), and ditches (Kaufman et al. 2000). Part of the contrasting information on this species can be attributed to subspecies-specific habitat associations. Much of the literature does not identify deer mice to subspecies or only reports on a single and more dominant subspecies to the locality. However, given the ubiquitous nature of this species in North America and generally weaker habitat associations, it is likely that deer mice fill a more generalist role in whatever system they are in.

A close relative of the deer mouse, the white-footed mouse (*Peromyscus leucopus*) was also commonly reported in land cover studies ($n = 27$, 59% of landscape composition studies). This species is widely reported in woodland habitats across North America (Raymond 1922, Kaufman & Fleharty 1974), and when studied in prairies, it was almost always in close association with nearby woodland or savanna habitat (Fig. 4; Clark et al. 1987). Ten studies reported a positive association between white-footed mice and woody structure (Wilkins 1995, Matlack et al. 2008, Harder et al. 2014, Stephens & Anderson 2014) or invasion by woody invasives like red cedar (Horncastle et al. 2005), including four studies that suggested that white-footed mice are limited to wooded areas or land in close proximity to woodlands (Schramm & Willcutts 1983, Snyder & Best 1988), where they tend to dominate and may be nearly ubiquitous (Wilkins 1995, Stephens & Anderson 2014). Finally, one study reported that while total captures did not change, the number of white-footed mice declined with increased cover of the invasive reed canary grass, which may relate to reduced food availability (Spyreas et al. 2010).

Prairie voles had much less straightforward habitat associations through the 29 studies that examined their associations with landscape composition (63% of landscape composition studies). The most frequently reported trend was a positive association with plant litter or thatch and a negative association with bare ground (Fig. 4), but this was only examined directly in two studies (Fuhlendorf et al. 2010, Burke et al. 2020). One study also reported a negative association with woody vegetation (Fig. 4) (Horncastle et al. 2005). Two others reported positive associations with denser vegetation (Snyder & Best 1988, Kaufman et al. 2000) which could be a precursor to more thatch. While prairie voles are largely considered prairie specialists, Kirsch (1997) found that prairie voles were most common in ditches alongside prairie and cornfields compared to prairie. It is unclear without replication whether this reflects a habitat preference or the influence of confounding factors such as competitive dynamics. Other work has suggested a more general habitat preference, and that availability of material for aboveground runways is the most important feature (Kaufman & Fleharty 1974).

Close relatives of the prairie vole, such as meadow voles (*M. pennsylvanicus*) and sagebrush voles (*Lemmiscus curtatus*), were slightly less well studied ($n = 17$). Even when they were included in studies that analysed community composition, few ($n = 8$) examined these species specifically, typically due to low capture numbers. Meadow voles showed similar habitat preferences to prairie voles, such as a preference for grassland habitat (Heisler et al. 2013) with negative associations with trees (Fig. 5; Stephens & Anderson 2014). Six studies examined dynamics between meadow voles and prairie voles in shared habitat (Klatt et al. 2015), but the majority of these studies ($n = 5$) are from the same location and dataset, the University of

Illinois Biological Research Area (Getz et al. 2001, 2005a, b, 2006, 2007). These studies document that habitat preferences and spatial niche partitioning between prairie and meadow voles may relate to both preferences for cover and food availability and that the strength of these preferences may differ per species (Getz et al. 2005a). While some trends have been repeatedly demonstrated, such as a preference for thatch, others warrant further study to tease apart species habitat preferences. Future work should also target the understudied vole species (meadow voles, sagebrush voles, etc.) to identify habitat preferences, especially where these species co-occur.

Fourteen studies examined hispid cotton rat (*Sigmodon hispidus*) habitat associations. However, these studies were relatively geographically limited. Two studies reported positive associations between hispid cotton rats and grass cover (Kaufman et al. 2000, Green & Wilkins 2014) and two identified them as among the dominant species in tallgrass systems (Wilkins 1995, Hanchey & Wilkins 1998). However, there is some disagreement in trends relating to non-grass plant cover. Kaufman et al. (2000) reported a positive association between hispid cotton rats and cover of yellow clover and plum or cedar, and Clark et al. (1998) described greater abundance in prairie with forbs and shrubs, but other studies reported negative associations with forbs (Wilkins 1995) and woody cover (Fig. 4; Hanchey & Wilkins 1998). Another repeated trend was a positive association with leaf litter (Fig. 5; Hanchey & Wilkins 1998, Kirchner et al. 2011). These conclusions are drawn from only five studies, of which three share an author and are limited to central Texas, so more research is necessary to understand this species' habitat associations.

Trends in community composition studies ($n=10$) showed increases in small mammal diversity and abundance with increased plant species or functional diversity (Alford et al. 2012, Glass & Eichholz 2021) or declines in diversity in relationship to an invasion by a plant species that may become dominant (Horncastle et al. 2005), though one study identified a negative correlation between small mammal phylogenetic diversity and plant phylogenetic diversity (Guiden et al. 2023). This may be due to increasing plant diversity creating more microhabitats that support different mammal species, or due to increased diversity in food availability contributing additional niches that mammal species may occupy. This pattern was also demonstrated in ungrazed buffer edges along streams within agricultural fields, where abundance and richness were greatest, possibly because the community is a combination of the two bordering areas (Chapman & Ribic 2002). While some showed increased thatch or nesting cover yielded increased diversity, others indicated that bare ground was positively associated with diversity. This seemingly paradoxical relationship is also explored by Burke et al. (2020), which identifies positive relationships between diversity and both bare ground and thatch cover. This pattern may relate to shifts in the dominant member of the assemblage changing between these two plant covers, while an intermediate between the two may lead to absence of both rather than co-occurrence. This relationship is likely highly localised and relates closely to the habitat preferences of the dominant species within a landscape. Future work should also seek to identify whether habitat preferences are driven by cover or food availability, building on current work assessing dietary preferences of small mammal species (DeJaco & Batzli 2013).

Community assemblages/occupancies ($n=6$ studies) overall differed according to dominant cover type (Heisler et al. 2013, Stephens & Anderson 2014). Deer mice were much more dominant in assemblages where there were high proportions of cropland and significantly lower in native grassland regions, while the opposite was true for sagebrush voles (Heisler et al. 2013). These relationships may be due to species associations with specific cover types, as well as differences in trophic niches between species (Hope et al. 2021). However, four studies showed that these relationships are weak at the local scale and that other drivers, such as climate or management, may be more significant (Sietman et al. 1994, Bruckerhoff et al. 2020, Glass & Eichholz 2021, Guiden et al. 2023). Furthermore, another study showed that species richness did not differ between dominant cover type (Port et al. 2019).

Seven studies examined associations between species or communities and vegetative structure and density. However, many come from the same study sites and authors ($n=3$ from Konza Prairie, $n=2$ including Wilkins as an author). In general, prairie voles and meadow voles seem positively correlated with dense vegetative cover (Stokes 1995, Kaufman et al. 2000, Getz et al. 2005a). Where these two species co-occur, one study identified that meadow voles showed a stronger preference for dense cover, while prairie voles had a stronger relationship with food availability. Four studies also reported positive associations between dense cover and the populations of harvest mice (Kaufman et al. 2000, Kirchner et al. 2011) and both northern short-tailed shrews (*B. brevicauda*) and Elliot's short-tailed shrews (Snyder & Best 1988, Matlack et al. 2002), and three showed negative associations with cover density for deer mice (Wilkins 1995, Kirchner et al. 2011) and hispid cotton rats (Stokes 1995). However, the hispid cotton rats had a positive relationship with tall vegetation and leaf litter at 5 cm from the ground, which may be related to predation. Overall, this component of land cover is understudied in tallgrass prairie small mammals, and more work should be done to tease apart preferences for vegetative diversity and composition vs. cover density. Finally, there is abundant room for work examining small mammal associations with abiotic landscape factors and how these may in turn impact cover associations (Reed & Slade 2009).

Landscape configuration

Landscape configuration, encapsulating studies of connectivity and fragmentation as well as relationships to edge, was highly understudied (*n* = 17, 28% of all studies). These concepts are better studied in other habitats (Wolff et al. 1997, Allan et al. 2003, Downing et al. 2015) but should be studied in tallgrass prairies, especially given that habitat loss and restoration efforts have led to highly fragmented prairie ecosystems. Furthermore, previous work has hinted at species-specific relationships and unexpected patterns in small mammal responses to fragmentation, and this work should be expanded upon (Wolff et al. 1997, Downing et al. 2015).

In a study assessing how distribution of species differed in space, small mammals showed a bimodal distribution, with most species occupying either more than 90% or fewer than 10% of sites. This may illustrate the differences in how generalist and specialist species respond to varied and fragmented habitats (Collins & Glenn 1997).

The studies that examined small mammal relationships to habitat fragmentation were primarily concerned with the effects of fragmentation on dispersal. Few species-specific relationships were examined repeatedly across studies. Mowed edges between habitat patches presented a barrier to dispersal for prairie voles, deer mice, and hispid cotton rats, though the relationship was weaker for deer mice (Diffendorfer et al. 1995). Prairie voles showed increased mortality as distance between patches increased and that dispersal occurred primarily between closer patches (Smith & Batzli 2006). This pattern seems to relate to the habitat and cover preferences of these species. For example, prairie voles had greater sensitivity to recreational trails than mice (camera traps were used and mice were not identified to species, but local species included deer mice, white-footed mice, western harvest mice (*R. megalotis*), and meadow jumping mice (*Zapus hudsonius*)) and 13-lined ground squirrels (Shorb et al. 2020). In contrast, since deer mice are more generalist species and can often be found in areas of shorter vegetation, these mowed edges may be less of a barrier and may still be viewed as usable habitat (Slade & Crain 2006). However, even these relationships may not be universal, as Leis et al. (2008) found that deer mice were less common in areas where vehicle track density was highest compared to areas with lower track density. Additionally, meadow voles dispersed more frequently in fragmented landscapes, though prairie voles rarely dispersed beyond their patch (Getz & Hofmann 1999). This is critical context for land managers working in highly fragmented ecosystems, who may not recognise that mowed areas for firebreaks or vehicle use may present a significant barrier to dispersal for some species.

When multiple species are considered, patterns differ when examining patches by their own size or as archipelagos of good habitat within a larger region. Population densities were high for several species on small patches, though this reversed when smaller patches were lumped into larger clusters (Foster & Gaines 1991). While prairie vole captures were higher in patches with a greater amount of optimal habitat, high population densities in small patches may suggest that the voles may still use marginal mowed habitat (Batzli 2016). Another study identified that unmowed ditches and creek areas may present a corridor for dispersal of voles in more fragmented systems (Mulligan et al. 2013). The single study that examined long-range dispersal showed that long-range dispersal was uncommon and occurred at low population densities among deer mice (Rehmeier et al. 2004). Finally, in the only study that directly compared edge and interior, small mammal abundance was not different between edge and interior within patches (Pasitschniak-Arts & Messier 1998). In that study, any edge effects that were present were lower in the summer than in the spring when vegetation along the ecotone may have been the densest. Contrasting other findings, deer mice were most common in the interior, meadow voles were most common on the edge, and species richness was greatest on the edges. These variable results may be reflective of limited replication and differing study design among the few studies reporting these findings. We encourage greater study of the impacts of habitat configuration on small mammals in tallgrass prairies to support greater efficacy in manager efforts and a greater understanding of the impacts of increasing habitat loss and fragmentation.

Prescribed fire

Prescribed fire was the best-studied form of management in our review (*n* = 18, 30% of total studies, 64% of studies on management). Overall, studies identified species-specific responses to prescribed fire (Fig. 6). Deer mice showed one of the strongest associations with fire, and this relationship was the most well studied (*n* = 5). Deer mice were more common after burns than before burns (Snyder & Best 1988), in one case showing a 40-fold increase post-burn (Kirchner et al. 2011), which may relate to their preference for bare ground cover post burn reported above and could also be due to other species who may be stronger competitors being detrimentally impacted by fire (see below). Deer mouse populations peaked six months after a burn and then steeply declined after that point, showing a strong preference for recent burns (Kirchner

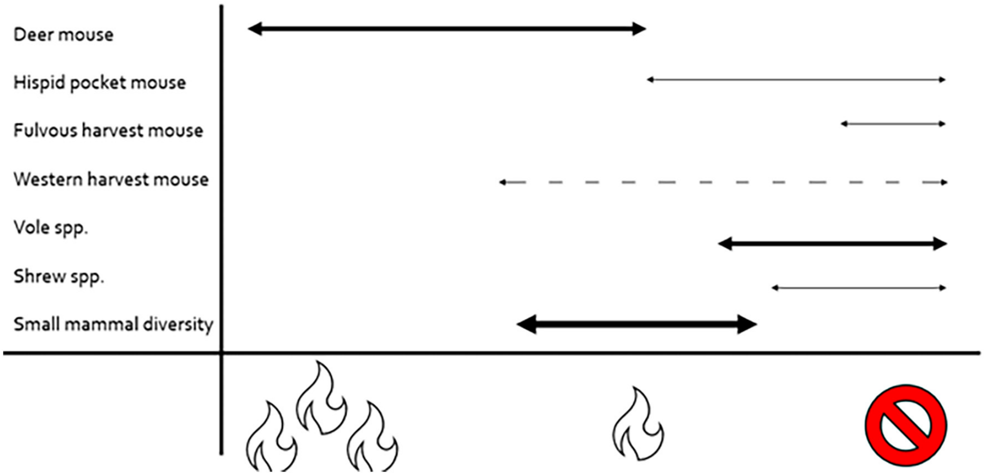

Fig. 6. A figure representing the species-specific and community diversity associated with differences in prescribed fire management. The left of the figure represents recent or frequent fire, while the left represents no fire. The boldness of the line represents the amount and strength of the evidence of associations between each species and the prescribed fire regime (boldest line >5 studies, medium line 3–5 studies, thinnest line <3 studies). Dashed lines represent relationships with conflicting evidence.

et al. 2011). However, two studies found burns did not affect deer mouse movement, with no evidence of deer mice leaving or entering burned areas (Clark & Kaufman 1990, Rehmeier et al. 2004), which may imply a neutral relationship with fire rather than a strong preference. In contrast to deer mice, prairie and meadow voles were reported to respond negatively to prescribed fire, likely associated with their preference for landscapes with a layer of thatch, often eliminated by burns (Schramm & Willcutts 1983, Clark & Kaufman 1990, Getz et al. 2001, Burke et al. 2020). Additionally, fulvous harvest mouse, hispid pocket mice (*Chaetodipus hispidus*), pygmy mice (*Baiomys taylori*), western harvest mice, masked shrew (*Sorex cinereus*), and Northern short-tailed shrews showed negative associations with fire (Schramm & Willcutts 1983, Snyder & Best 1988, Clark & Kaufman 1990, Matlack et al. 2008, Kirchner et al. 2011, Kaufman et al. 2012a, b). Given that all these species were rarely captured in sufficient numbers to be analysed, these relationships are largely understudied. It is also important to note that the majority of these reports for more cryptic species are derived from Konza Prairie Biological Station, further demonstrating the need for more work in other locations. Additional work from this location has described differential habitat use by these cryptic species given both topographical and management contexts, but statistical analysis was limited due to low capture numbers (McMillan et al. 1998). Other effects of prescribed fire, such as disease or parasite risk for small mammals, are also understudied, with only one report of increased infestation of larval bot flies (*Cuterebra* sp.) in unburned plots (Boggs et al. 1991).

Fewer studies ($n = 7$) considered the impacts of prescribed fire, as well as fire return interval, on small mammal diversity. In general, species richness tended to decline immediately following prescribed fire and increase afterwards, though where this increase peaked varied between studies (Richardson 2010, Burke et al. 2020, Guiden et al. 2021). However, one study reported significant but not directional differences in community composition between burned and unburned sites (Jones et al. 2017). When landscapes receive fire at different intervals of time, this can shape the vegetative structure over time, and in turn shape the small mammal communities (Jones et al. 2017, Bruckerhoff et al. 2020, Guiden et al. 2021). In general, studies found that frequent fire (return intervals between one and four years) led to reduced landscape heterogeneity, and with it, reduced species richness of plants (Collins 1992). While two studies reported lower species richness at frequently or recently burned sites (Collins 2000, Richardson 2010), Collins (2000) reported that the changes in richness did not appear to be in synchrony with changes in the vegetative community, which counters the hypothesis that a reduction in vegetative heterogeneity and diversity with frequent fire is what drives decreases in small mammal diversity. One potential explanation for this could be that in the immediate aftermath of a fire, there is very limited cover or food available, leading to dispersal or mortality for many species. As plants regrow, species that prefer bare ground or are less fire-sensitive begin to recolonize the landscape. Over time, as the plant litter builds back up, the most litter-dependent species can return, but the species that prefer bare ground may be able to persist due to habitat variability creating pockets of ideal habitat for them. Finally, as time since fire increases beyond a few years, the landscape becomes dominated by the litter-dependent species and others are not able to persist. This hypothesis is supported by the literature, but more research is necessary to specifically examine these relationships and develop predictive models.

Grazing

Only seven studies researched impacts of grazing on small mammals. Two studies focused on bison specifically, three more on only cattle, and two studies examined the impacts of both bison and cattle. Bison presence had no effect on small mammal abundance and diversity (Burke et al. 2020), although that study was done in the first couple of years post bison reintroduction. Similarly, in a review of varied drivers of species richness on prairie taxa, bison grazing explained most of the variation in species richness for all taxa except small mammals (Bruckerhoff et al. 2020). Conversely, high grazing pressure from cattle resulted in increased populations of deer mice but lower populations of meadow voles (Bueno et al. 2012). Similarly, deer mice dominated both cattle-grazed and ungrazed grasslands, while white-footed mice occurred but were rare (Kaufman et al. 2000). Comparing ungrazed buffer area to cattle-grazed pastures, small mammal diversity and abundance were higher on buffer sites. Meadow voles were the most common species in pastures, while deer mice and white-footed mice were dominant in buffer sites. Furthermore, there was no difference in small mammal populations between regular and rotation-grazed pastures, which may indicate that the rest period of rotation is insufficient to impact small mammal communities (Chapman & Ribic 2002).

It is critical to examine the differential impacts of bison and cattle grazing. Bison selectively graze on grasses, allowing for less competitive forbs to grow and increasing vegetative diversity (Knapp et al. 1999, Truett et al. 2001, Fuhlendorf & Engle 2006, Collins & Calabrese 2012). Cattle often selectively graze forbs and select areas in closer proximity to water or woodlands (Allred et al. 2011). Because of these different grazing preferences, the impacts of these species on vegetation can differ significantly (Towne et al. 2005, Ratajczak et al. 2022). These impacts on vegetation are often hypothesised to be the mediator through which grazing impacts small mammals, but this may not be the only interaction. Bison are also ecosystem engineers, altering habitat structure through their movement and behaviours like wallowing (Fox et al. 2012, Nickell et al. 2018). The changes driven by bison activity have been shown to alter small mammal activity timing (Guiden et al. 2023), but more work is necessary to understand both the direct and indirect impacts of grazers on small mammals.

Another important consideration is the interaction between grazing and other management activities, such as prescribed fire. Pyric herbivory is the spatiotemporal interaction between fire and grazing, where grazing activity is driven by fire. We only identified three studies specifically examining pyric herbivory, which each had slightly different parameters. Deer mice were more abundant in sites grazed by bison or cattle before a fire, but there was no difference in abundance between grazed and ungrazed sites after a fire (Matlack et al. 2001). Small mammal species richness and diversity were highest at sites that were patch-burned and grazed than at sites that were burned only, where richness and diversity were still higher than at sites that were grazed only (Ricketts & Sandercock 2016). One of the suspected drivers of this diversity increase is increasing landscape heterogeneity with patchy burns and grazing. Vegetative heterogeneity was as much as three times greater in landscapes that were burned and grazed compared to sites that were just grazed alone (Fuhlendorf et al. 2010). In this heterogeneous landscape, small mammal capture rates declined slightly with time since burn, with this trend potentially being driven by reduced deer mice captures, but species richness increased to a maximum point 30 months following a burn. This may reflect a shift in dominance as deer mice populations decline with reduced bare ground as time since fire increases, allowing other species to move in and increasing species richness.

CONCLUSIONS AND FUTURE DIRECTIONS

With tallgrass prairie a key priority for conservation and restoration in North America, it is increasingly important to better understand the complex dynamics of how the interconnected landscape dynamics of landscape composition, landscape configuration, and landscape management interplay and how these factors impact taxa at all levels. This study revealed trends in not only what has been studied but where we have studied it and which organisms have been studied. Tallgrass prairie studies focusing on small mammals are primarily in Kansas and Illinois, with many of those studies coming from the same site. This means that the basis of many of our assumptions may not be universally applicable. Additionally, a large portion of the literature on small mammal habitat associations in tallgrass systems comes from remnant prairie sites. These results may not be consistent with restored prairie sites. More work must be done, especially in regions not well covered by current literature, such as Missouri, Iowa, and Nebraska, as well as in restored tallgrass prairies.

Much of our understanding of small mammal populations is driven by knowledge of the most dominant species. Because deer mice, white-footed mice, prairie voles, meadow voles, and hispid cotton rats are caught in larger numbers and in more studies, they are much better understood. Rarer species, which may be of more significant conservation interest, are far less studied and therefore not as well understood. It is hard to target management for conservation of these species when so little is known about their habitat preferences or responses to management. Studies of these species could be conducted through meta-analysis since few sites capture them frequently enough to conduct their own analysis.

Of the three topics we examined, ground cover associations are the most well studied. There are distinct trends in both species-specific and community-based patterns across space and time. Less well studied are the impacts of landscape configuration variables. However, very little work considered the impacts of broader land cover change on small mammals, instead focusing on local-scale variations in ground cover. Future work should target teasing apart the impacts of landscape composition and configuration through methods such as those described in the landscape ecology literature (Fahrig 2003, 2013). Furthermore, as land management through prescribed fire and grazing become increasingly important in the preservation and restoration of this highly vulnerable ecosystem, more work is necessary to understand the direct and indirect effects of these interventions on mammals, as well as interactions between these interventions that alter their impacts.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

A full spreadsheet of the studies included in this review is available in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. A PRISMA flowchart representing the literature search and exclusion process for this review.
Appendix S2. Summary of reviewed publications.