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Forum

A disturbance triangle: The interactive role of prairie dogs with fire and ungulate grazing in the Great Plains

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Abstract

Global biodiversity declines have been hastened by suppression of once-widespread disturbance regimes. In recent decades, the restoration of the fire–grazing interaction has helped address declines in the North American Great Plains. Conversely, another historically ubiquitous disturbance agent, the black-tailed prairie dog (*Cynomys ludovicianus*), has received little attention. Although research exists on the interaction between large ungulates and prairie dogs, scant work recognizes the triangle of interactions among fire, large ungulates, and prairie dogs. On reviewing the literature, 34 sources discussed fire influencing prairie dogs, but only one empirically tested the effect of prairie dogs on fire. Despite this research gap, historical fire patterns, current fire management, and unpublished data indicate that prairie dogs likely reduce wildfire spread or intensity. We advocate for a paradigm shift in Great Plains rangeland management that considers prairie dogs as the third corner of a disturbance triangle and increased research on how prairie dogs influence fire behavior.

Keywords: biodiversity, burrowing mammal, grassland, pyric herbivory, rangeland

Most grassland and shrubland ecosystems evolved in the context of various interacting disturbances (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2017, Wilsey 2018). The periodicity, spatial extent, and intensity of disturbances helped shape the floral and faunal composition of these systems; therefore, systematic suppression or alteration of historical disturbances during the past few centuries has led to decreased biodiversity and ecosystem health in myriad rangelands (Truett et al. 2001b, Garnett et al. 2010, Pfeiffer et al. 2021). In the North American Great Plains, European settlement has coincided with reduced fire frequencies, novel grazing patterns of ungulates, and large-scale conversion of grasslands to row crop agriculture (Fuhlendorf et al. 2012, Augustine et al. 2021). Altered disturbance regimes on remaining grassland patches facilitated encroachment of woody species and homogenized herbaceous structure further contributing to biodiversity reduction (Ratajczak et al. 2016, Capozzelli et al. 2020, Hovick et al. 2023). Accordingly, the restoration of historic disturbances has become a major goal of rangeland ecologists and conservation biologists alike (Fuhlendorf et al. 2012, Sayre et al. 2013, Twidwell et al. 2013, Schowanek et al. 2021).

In the past three decades, researchers have shown that it was not only fire suppression causing this reduction in ecosystem services but the decoupling of the fire–grazing interaction (i.e., pyric herbivory; Fuhlendorf et al. 2009, 2017). Essentially, periodic fires ignited by Indigenous peoples or lightning would have reduced dead vegetation biomass and increased forage quality in patches across the landscape. Large herbivores such as American bison (*Bison bison*) preferentially grazed recently burned patches (Allred et al. 2011), which enabled fuels to accumulate in less used patches, making them more fire prone. Therefore, fire and grazing interacted through positive and negative feedback across landscapes through time to create a shifting mosaic of vegetation composition and structure that promoted biodiversity (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Although the ranges of native large herbivores, including bison and elk (*Cervus canadensis*), have contracted since European settlement and fire has been long suppressed, the fire–grazing interaction has been mimicked using domestic livestock and native grazers such as bison on both public and private rangelands via patch–burn grazing, with evidence that this management approach can support both livestock and biodiversity goals (Coppedge et al. 2008, Fuhlendorf et al. 2010, Augustine and Derner 2014, Duchardt et al. 2016, Scasta et al. 2016, Starns et al. 2020). This fire–grazing interaction has provided a much-needed framework to guide management in these ecosystems in ways that mimic historical disturbance regimes. Despite progress toward the reintegration of fire and grazing as interacting disturbances, most grassland management paradigms continue to ignore another interacting endogenous disturbance that was historically ubiquitous across the Great Plains: burrowing mammals—specifically, the black-tailed prairie dog (*Cynomys ludovicianus*).

Five species of prairie dog occupy North America, but the black-tailed prairie dog (hereafter, *prairie dog*) was historically the most widespread and had the greatest influence on vegetation composition and structure in North American rangelands (Baker et al. 2013). As a keystone species, prairie dogs are an important

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prey item for numerous mammalian carnivores including badgers (*Taxidea taxus*), kit foxes (*Vulpes macrotis*), swift foxes (*Vulpes velox*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and the endangered black-footed ferret (*Mustela nigripes*; Kotliar 2000, Hoogland 2006). Prairie dogs were such a critical food source for ferrets (75%–90% of its diet; Campbell et al. 1987, Brickner et al. 2014) that the near extinction of the ferret was directly linked with prairie dog population declines in the twentieth century (Miller et al. 1990). Large raptors such as ferruginous hawks (*Buteo regalis*) and golden eagles (*Aquila chrysaetos*) also use prairie dogs as a primary prey source during breeding, migration, and winter periods (Jones 1989, Salas et al. 2024), and their abundance has been observed to decline following major prairie dog die-offs (Seery and Matiatos 2000, Duchardt et al. 2023).

In addition to its role as a keystone species, the prairie dog is also an ecosystem engineer; this endogenous disturbance (e.g., Larson 2003) is more prolonged than fire or grazing but often has similar impacts on flora and fauna. Prairie dogs live in dense colonies, with hundreds or thousands of individuals that, together, consume and actively clip vegetation to optimize predator visibility (Hoogland 2006). Their digging and shrub clipping helps to aerate the soil and to reduce the rate of woody encroachment (Barth et al. 2014, Connell et al. 2018). Prairie dog burrows provide habitat for rattlesnakes (*Crotalus* spp.), tiger salamanders (*Ambystoma tigrinum*), and burrowing owls (*Athene cunicularia*), and the short, sparse vegetation structure they generate is ideal for the imperiled mountain plover (*Charadrius montanus*). Many species are found primarily or solely associated with prairie dogs in some parts of their range (Kotliar et al. 1999).

This same engineering that provides so many ecosystem benefits can also reduce forage availability for livestock in certain contexts (Derner et al. 2006, Augustine et al. 2024). This conflict is largely responsible for eradication programs that have reduced current prairie dog populations sizes to less than 5% of historical estimates (Miller et al. 1994). Although there is evidence that prairie dogs can negatively affect livestock production, recent research indicates that this conflict may be contingent on other factors. There is often sufficient forage quantity on prairie dog colonies in all but the driest years (Connell et al. 2019, Augustine and Derner 2021, Augustine et al. 2024). Moreover, forage *quality* is often greater on colonies because prairie dogs maintain vegetation at an early phenological state and can shift species composition toward more nutritious plants (Augustine and Springer 2013, Connell et al. 2019). Bison and other ungulates preferentially graze and loaf on prairie dog colonies (Chipault and Detling 2013, Sierra-Corona et al. 2015, Buehler 2023), leading to a similar interaction between grazers and prairie dogs as that observed between grazers and fire. Similarly, Coppock and Detling (1986) observed that bison preferentially grazed on prairie dog colonies in Wind Cave National Park, and although they shifted to grazing uncolonized burned areas soon after a fire occurred, their grazing shifted back to prairie dog colonies within 2 years of the fire (Detling 2006). Although fire reduced standing dead vegetation and increased overall forage quality, the effect was temporary relative to the forage quality on colonies, highlighting the complementary roles of fire and prairie dogs for grazers. Fire has also been touted as a means to reduce woody encroachment and, therefore, to increase herbaceous forage (Twidwell et al. 2013), but prairie dogs provide this service as well; prairie dogs clip woody vegetation on their colonies, suppressing encroachment (Hale et al. 2020). Over 20 years of research supports the ability of prairie dogs to suppress encroaching shrubs such as mesquite (*Prosopis* sp.) and creosote bush (*Larrea tridentata*), increasing herbaceous forage availability (Weltzin et al. 1997, Ponce-Guevara et al. 2016, Hale et al. 2020).

Although fire and prairie dogs have many similar impacts on vegetation, they respond quite differently to grazing; heavy grazing reduces fire intensity and spread but typically has the opposite effect on prairie dogs (Koford 1958). The reduction of dense vegetation and increased soil disturbance from grazing facilitates the expansion of prairie dog colonies, such that heavily grazed sites, especially those areas near water tanks, are often soon occupied by prairie dogs (Koford 1958). Conversely, a combination of low grazing intensity and high precipitation can lead to the extirpation of prairie dog colonies (Osborn and Allan 1949). Knowledge of this interaction has been applied both to encourage the expansion of colonies using grazing (Hoogland 2006) and to curtail their expansion by creating ungrazed buffer zones of taller grass (Cable and Timm 1987, Terrall et al. 2005).

Although researchers and managers have acknowledged relationships between fire and grazers and between grazers and prairie dogs, less consideration has been given to the other side of this triangle: prairie dogs and fire. In areas where prairie dog conservation is an objective (e.g., regions with reintroduced populations of black-footed ferrets), fire has been identified as a potential tool for aiding prairie dogs' expansion or shifts in their occupancy. Multiple studies have shown that the application of fire on the edge of a colony can facilitate expansion into that area and that the application of fire to potential reintroduction sites increases reintroduction success (e.g., Augustine et al. 2007, Northcott et al. 2007, Breland et al. 2014). One would expect similar support for a suppressing effect of prairie dogs on fire or, at least, a robust body of research exploring this interaction. Unfortunately, we are unaware of any experimental studies demonstrating the effects of prairie dog ecosystem engineering on fire behavior.

In the past 25 years, our understanding of the fire–grazing interaction has vastly increased, improving our ability to manage a large proportion of the Great Plains. More recently, data suggest that a third disturbance, burrowing and herbivory from prairie dogs, has the potential to both positively and negatively interact with grazing herbivores. Given the ample data on certain aspects of disturbance interactions in the Great Plains, it is surprising that relatively little research appears to exist on the interaction between fire and prairie dogs, but to date, there has been no review of this literature. To address this knowledge gap, we review the literature on the influence of fire on prairie dogs and prairie dogs on fire; present evidence for the potential for prairie dogs to mitigate wildfire spread in the Great Plains, leveraging mapped fire perimeters and prairie dog colonies; and propose a framework by which to consider the historical role of prairie dogs within the fire–grazing interaction.

Prairie dog–fire interaction: Literature review

We hypothesized that fire would have an influence on prairie dogs similar to that of grazing, facilitating their expansion into burned areas. Conversely, because prairie dogs not only remove biomass like other grazers do but also disturb the soil, we expected a suppressive effect of prairie dogs on fire. To better understand both sides of the fire–prairie dog interaction, we conducted a systematic review (Centre for Evidence-Based Conservation 2013) of the primary literature using the Google Scholar and Academic Search Premier online databases. We defined a priori search terms (*("prairie dog" OR "Cynomys") and "fire"*) and review criteria (table S1). We conducted our Google Scholar search between 20

Table 1. Citation, source type, and study location of sources returned during literature search containing discussion or empirical data of the fire to prairie dog or prairie dog to fire interaction.

Citation	Source type	Location	Fire to prairie dog	Prairie dog to fire	Empirical data
Archuleta 2014	Thesis	New Mexico	☐		☐
Augustine 2011	Peer reviewed	Colorado	☐		
Augustine and Derner 2012	Peer reviewed	Colorado	☐		
Augustine et al. 2007	Peer reviewed	Colorado	☐		☐
Avila-flores 2009	Thesis	Chihuahua	☐		
Avila-flores et al. 2010	Peer reviewed	Chihuahua	☐		
Beeton et al. 2019	Peer reviewed	South Dakota	☐		
Bidwell et al. 2003	Gray literature	Oklahoma		☐	
Breland 2010	Thesis	Oklahoma	☐		☐
Byington 2011	Gray literature	NA	☐		
Ceballos et al. 2010	Peer reviewed	Chihuahua	☐		
Clippinger 1987	Thesis	Colorado	☐		
Curtis 2012	Thesis	Utah	☐		
Eads 2015	Gray literature	NA	☐		
Hale 2017	Thesis	Arizona		☐	
Jones 2013	Gray literature	NA	☐		
Klukas 1987	Gray literature	South Dakota	☐		
Kotliar et al. 1987	Peer reviewed	NA		☐	
Lloyd et al. 2013	Peer reviewed	Saskatchewan	☐		
Mack et al. 2017	Gray literature	NA	☐		
Milne-Laux and Sweitzer 2006	Peer reviewed	North Dakota	☐		☐
Mit 2008	Thesis	Colorado	☐		
Morrison and Peitz 2011	Peer reviewed	Nebraska	☐		
Northcott et al. 2007	Peer reviewed	New Mexico	☐		☐
Oakes 2000	Thesis	Arizona, Chihuahua, New Mexico, Sonora		☐	
Player and Urness 1982	Peer reviewed	Utah	☐		
Porensky et al. 2018	Peer reviewed	Wyoming	☐		
Roehrs 2004	Thesis	Nebraska	☐		
Singh 2020	Thesis	Saskatchewan	☐		
Strawn 1995	Thesis	Oklahoma	☐	☐	☐
Symstad and Jonas 2011	Peer reviewed	NA	☐		
Truett 2003	Peer reviewed	NA	☐		
Truett and Savage 1998	Peer reviewed	NA	☐		
Truett et al. 2001a	Peer reviewed	NA	☐		
Truett et al. 2001b	Peer reviewed	NA	☐		
Warren et al. 2021	Peer reviewed	NA	☐		
Whicker and Detling 1993	Gray literature	South Dakota	☐		
Youngberg and Panjabi 2014	Gray literature	Colorado	☐		

and 23 October 2023, and it returned 10,900 hits. We exhausted all 100 pages that Google Scholar generates (1000 hits) on 23 October 2023. We completed the Academic Search Premier search on 25 November 2023 using the same search terms, which returned 758 hits. We reviewed all hits for our inclusion criteria by first reviewing the title of each paper and accessing the source if the title seemed relevant (i.e., they included prairie dogs, prairie dog associated species, fire, controlled burning, etc.) and searching for the terms *fire*, *burn*, and *fuel* within each source. Our search revealed 42 sources that met our inclusion criteria. Four of these sources were not focused on prairie dogs but did discuss or test the effects of fire on other burrowing mammals, including the southern brown bandicoot (*Isoodon obesulus*; Ramalho et al. 2018), the yellow ground squirrel (*Spermophilus fulvus*; Koshkina et al. 2022), the bobak marmot (*Marmota bobak*; Koshkina et al. 2019), and several Australian digging mammals (Fleming et al. 2014).

Of the 38 relevant sources on fire and prairie dogs, 34 addressed the fire–prairie dog interaction either theoretically or empirically (table 1). Approximately half of these were peer reviewed ($n = 18$, 53.0%), with the remainder composed of theses and dissertations ($n = 8$, 23.5%) or other gray literature, including extension bulletins and agency reports ($n = 8$, 23.5%; table 1). Most of these resources ($n = 29$, 85.3%) merely discussed the directional effect of fire on prairie dogs (figure 1). The text referencing fire's influences on prairie dogs predominantly appeared in the introduction, discussion, and management implications sections. A small portion ($n = 5$, 14.7%) of the literature empirically explored the effects of fire on prairie dogs, with overwhelming support for a positive effect of fire on prairie dogs, mainly by facilitating their expansion into burned areas (table 1). Although each study evaluated success somewhat differently, precluding a vote-counting approach to summarizing findings, the number of studies is small enough that we can further discuss each of their findings. Milne-Laux and Sweitzer (2006) performed controlled burns and brush removals next to existing prairie dog colonies in western North Dakota. They found that prairie dogs disproportionately expanded into treatment compared with control plots, with greater

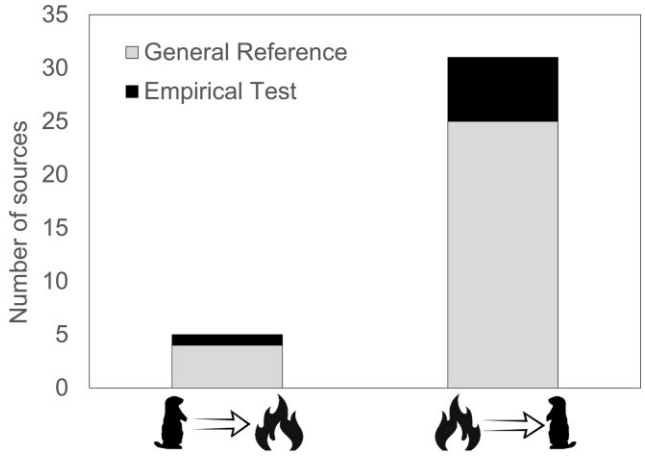

Figure 1. Results of a literature review exploring the effect of prairie dogs on fire (left) and of fire on prairie dogs (right). The black bars represent sources that empirically tested the effect in question. The gray bars represent sources that referred to the given effect but did not test it.

numbers of excavated burrows and more observations of individuals in the treated areas. Similarly, Augustine and colleagues (2007) found that colony expansion into recent burns in southeastern Colorado was double the rate of expansion into adjacent unburned areas. Northcott and colleagues (2007) conducted burning and mowing treatments near existing colonies in southern New Mexico and found that burrow densities were greater on treated areas but there was no difference among treatment type (mow versus burn). The direction and rate of colony expansion was also oriented toward treatments. In her 2010 thesis, Breland explored the effect of burning on dispersal in southern Oklahoma and found an increased number of prairie dogs in burn treatments over that in unburned sites, but the population sizes and the number of burrows within the burn treatments declined after 12 months after the fire. Breland also found no difference in foraging effort between burned and unburned sites. Archuleta (2014) looked at the effect of burn timing and frequency on colony expansion in northeastern New Mexico and found no differences between dormant- and growing-season burns, nor among 3-, 6-, and 9-year burn intervals.

Few sources discussed—let alone tested—the prairie dog–fire interaction. Only six sources (table 1) mentioned this potential interaction, typically by identifying prairie dogs as potential engineers of fire breaks without direct supporting citations (or in some cases, citing resources that, themselves, made statements without supporting research citations). Only one source, a dissertation, empirically tested the effects of prairie dogs on fire; Strawn (1995) found a 20% reduction in fire coverage on burned prairie dog colony as compared with an adjacent area that was also burned, although this was tested somewhat indirectly with burn tiles and with mixed efficacy (S. Strawn, University of Central Oklahoma, Edmond, OK, personal communication, 10 January 2023). Strawn (1995) also indirectly explored the effect of fire on prairie dogs and tested the prairie dog–grazing interaction, finding support for positive interactions between prairie dogs and grazers.

Where the literature is incomplete, scientists often turn to natural history to begin considering mechanisms; such first steps are crucial in identifying future research needs. Below, we describe several site-specific observations addressing how prairie dogs historically interacted with fire, highlighting four recent fires where prairie dogs seem to have influenced fire spread and severity.

Prairie dog–fire interaction: Case studies

Potential evidence for prairie dogs reducing fire intensity or size can first be found in historical fire return intervals. Although we know of no data set that would facilitate modeling these dynamics directly, abnormally small or infrequent fires relative to predicted frequencies could be interpreted as an indication of the role of prairie dogs. For instance, Porensky and colleagues (2018) highlighted the incongruity of fire-intolerant big sagebrush (*Artemisia tridentata*) persisting in portions of northeastern Wyoming, where fire-free intervals were estimated at approximately 7 years (Peryman and Laycock 2000) with average fire-return intervals estimated at 6–18 years at lower elevations (Guyette et al. 2012). Big sagebrush can take more than 100 years to recover after a fire (Cooper et al. 2011), and its persistence in this landscape along with the imperiled greater sage grouse (*Centrocercus urophasianus*) is surprising. Researchers posited several potential factors leading to discontinuity of fuels, including disturbance caused by prairie dogs (Porensky et al. 2018).

Inferences can also be derived from our understanding of fuel loads and fire behavior in grasslands. In eastern Colorado, Augustine and colleagues (2014) examined how variation in fuel loads and weather conditions affect fire spread in shortgrass steppe dominated by blue grama (*Bouteloua gracilis*). They showed a sharp discontinuity in the ability of fires to spread when fuel loads dropped below 350 kilograms (kg) per hectare (ha) regardless of weather conditions, and very low-intensity fires with fuel loads of 350–550 kg per ha when relative humidity was above 20%. Analyses of standing vegetation biomass on prairie dog colonies in semiarid grasslands of eastern Colorado and Montana showed that vegetation biomass fluctuated dramatically within the range of 230–800 kg per ha during the growing season (May–September; Johnson-Nistler et al. 1904, Augustine and Springer 2013). Even in the more mesic mixed-grass prairie on Buffalo Gap National Grassland of South Dakota, prairie dogs maintained standing vegetation biomass in the range of 400–800 kg per ha during a year of above-average precipitation, which was 62% lower than biomass off colonies (Augustine and Springer 2013). Given that standing biomass on colonies would be expected to decline substantially below these levels after the growing season ends, because of year-round plant consumption by prairie dogs (in the absence of plant growth), we can predict that fuel loads on prairie dog colonies during the dormant season, particularly during the window of February–April, when vegetation is fully senescent, would either be too low for fire spread or only capable of low-intensity fire during a narrow range of ideal weather conditions.

In addition to these inferences drawn from fire pattern and fire behavior in the western Great Plains, more direct observations of the role of prairie dogs in influencing fire exist. The Anderson Creek Wildfire was the largest recorded fire in Kansas history, burning across 161,774 hectares in 2016. Many structures were destroyed, and hundreds of livestock were killed, but on one ranch, the losses were not so steep. Free-roaming bison on the Z Bar Ranch were observed moving to prairie dog towns during the fire. The fire did not carry across the colony, and all of the bison survived (Browning and Browning 2016; Magnus McCaffery, Turner Ranches, personal communication, 15 July 2022). On the basis of discussions with managers, it also appears that prairie dogs are taken into consideration when the managers craft their burn plans, either as a means of catching (helping to limit) the fire (David Lucas, Fish and Wildlife Service, personal communication, 10 September 2022) or as a hindrance to the fire's spread in more arid systems (Ana Davidson, Colorado Natural History Program, personal communication, 10 September 2022).

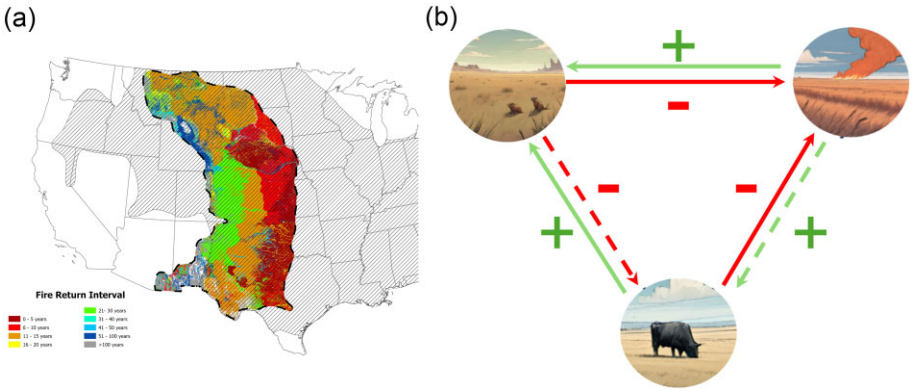

Figure 2. (a) Fire, prairie dogs, and ungulate grazers spatially overlapped within the North American Great Plains, where historical bison distribution is shown by the hatched boundary, with LANDFIRE fire return intervals shown within prairie dog range (the dashed line). (b) We propose a disturbance triangle, depicting the interactions of fire, grazing, and prairie dogs within the Great Plains. The fire–grazing interaction has, by far, received the most attention among the three interactions, with empirical support for a positive effect of fire on forage quality and a negative effect of grazing on fire spread via reduced fine fuels. There is evidence that ungulate grazers facilitate the expansion of prairie dogs into heavily grazed areas, whereas prairie dogs reduce forage quantity but can increase forage quality. The fire–prairie dog interaction is, by comparison, understudied, with a small amount of empirical work supporting a positive effect of fire on prairie dogs, mainly through facilitating colony expansion. The dashed lines indicate interactions that may flip in sign under certain conditions or along an east–west precipitation gradient. For example, in areas of high productivity, where forage is not limiting, the effects of prairie dogs on cattle may be positive overall via increased forage quality. Similarly, if fire is followed by drought, forage availability may be decreased to an extent to negatively affect livestock. Source: The graphics were created by Canva AI.

Recent wildfires across the Great Plains provide further evidence for this interaction; we identified four wildfires within the past 3 years where presence of prairie dogs appears to have mitigated fire intensity or spread (figure 3, box 1). These fires occurred under highly variable weather conditions in both suburban and rural settings across prairie dog range from Montana to Oklahoma. In each case, the fire's spread was patchy on colonies, leaving many areas unburned; in some cases, this indicates alteration of the overall extent and direction of the fire's spread. As was demonstrated in our literature review, potential interactions between fire and prairie dogs are not well known among managers and researchers; as a result, data on the influence of colony size or vegetation biomass on fire behavior were often not collected. However, in the case of the Marshall Fire, in Boulder, Colorado (box 1), researchers did map unburned areas within the fire perimeter and found that, among colonies more than 4 hectares in size, over half of the colony was typically unburned (up to 74%). Despite a lack of experimental rigor, these observations lend further credence to the overlooked impacts of prairie dogs on fire in the Great Plains.

More research needed: The Great Plains disturbance triangle

Although the potential interactions between fire and prairie dogs appear straightforward, we found little research investigating this relationship. Support for a positive effect of fire on prairie dogs was constrained to tests of management applications, but fire was consistently identified as an effective tool in facilitating and directing colony expansion. Even less is known about the effect of prairie dogs on fire, barring a few references in the literature and only one empirical dissertation chapter.

This research gap may be driven in part by sociopolitical perceptions of burrowing rodents and other small mammal ecosystem engineers; most federal funding in the United States for research and management of prairie dogs was focused almost solely on forms of lethal control to combat agricultural losses until relatively late in the twentieth century. Although these priorities have shifted in recent decades, especially with federal listing of the black-footed ferret, research focused on ecosystem services of burrowing rodents is still considered contentious in some regions. However, this issue extends beyond both prairie dogs and North America, as was highlighted by a recent review (Foster et al. 2020). Therein, the authors highlighted that the effect of animals on fire regimes are often overlooked, and studies that incorporate the effect of fauna are typically focused on megaherbivores (also see Karp et al. 2024). Although some studies have begun to dig into the impacts of smaller digging and burrowing mammals, such as bandicoots (e.g., *Isoodon obesulus*), potaroos (*Potourus* sp.), and bettongs (*Bettongia* sp.) in Australia and plains viscacha (*Lagostomus maximus*) in South America on fire (Hierro et al. 2011, Fleming et al. 2014, Hayward et al. 2016), even internationally, the literature is dominated by studies on larger ungulate grazers affecting fuel amounts. However, fuel structure and condition are equally important, and all three factors are influenced by a broad suite of wildlife. In the case of prairie dogs, effects arguably include all three fuel characteristics (figure 2): Prairie dogs consume and clip vegetation, reducing fuel availability and altering vertical structure. Prolonged occupation of a colony is associated with altered vegetation composition favoring annual forbs, often with a drastically reduced shrub component relative to the surrounding area (Whicker and Detling 1988, Baker et al. 2013, Duchardt et al. 2019); as a result, they also influence the composition of fuels, drastically reducing the availability of coarse fuels that would burn hotter and longer. Together with increased annual forb cover, burrowing activities increase bare ground, reducing fuel continuity. Altered air flow associated with burrows and altered chemical composition of shrubs because of persistent clipping could also play a role in fire behavior, but research into these mechanisms does not exist. Despite a lack of empirical research, anecdotal evidence from numerous fires on the Great Plains supports this hypothesis.

Adoption of a disturbance triangle paradigm is useful not only to acknowledge and apply the interactions among these disturbances but also to think critically about similarities and differences among the ecosystem services that each disturbance provides. For example, both fire and prairie dog activity reduce standing dead vegetation, reduce forage quantity, but increase forage quality (Detling 2006), albeit across different temporal

Box 1. Descriptions of fires.

Beaver River Fire

The Beaver River Fire in western Oklahoma was discovered on 5 April 2022, spreading south under strong (sustained 30 miles per hour, 40–45 mile per hour gusts) north winds. The fire burned approximately 7612 hectares (ha) with an estimated cost of $434,932 (figure 3; National Interagency Fire Center 2024). Many small (0.5–1 ha) prairie dog colonies dotted this landscape, with at least two south of the ignition point. The colonies were partially burned, with several unburned locations retaining live vegetation (figure 4). On at least one colony, the fire crews had leveraged the prairie dog–occupied area as an opportunity to create burn lines, as was discussed above.

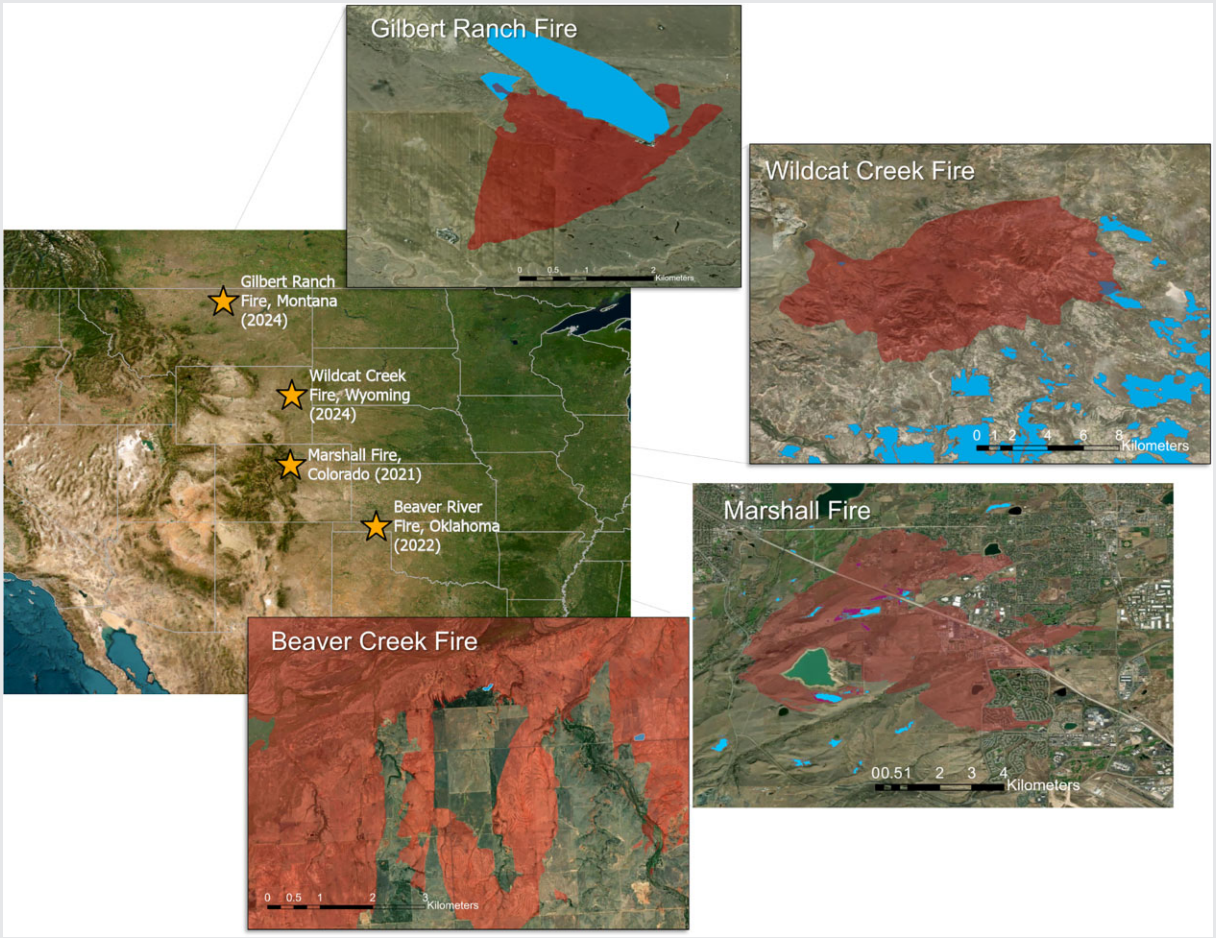

Figure 3. The locations of four recent wildfires in the North American Great Plains where burn severity or spread were altered by black-tailed prairie dog disturbance. The red polygons represent fires, whereas the blue polygons represent prairie dog colonies. On the Marshall fire, the purple shading indicates the portions of prairie dog colonies that were burned during the wildfire, whereas the blue indicates the unburned portions of the colonies.

Gilbert Ranch Fire

The Gilbert Ranch Fire on the Fort Belknap Indian Reservation of northern Montana was detected on 25 July 2024, burning over 280 ha under variable winds. Again, the fire crews had mobilized on the prairie dog colonies to catch fire, but the relatively large size (more than 100 ha) of the colony seem to have played a greater role in influencing the fire's severity and spread. Small portions within the colony were burned but with unburned vegetation distributed patchily (figure 4). In two locations (northeast boundary, northwest edge), the fire perimeter was bounded by these colonies.

(*Continued*)

Box 1. Descriptions of fires.

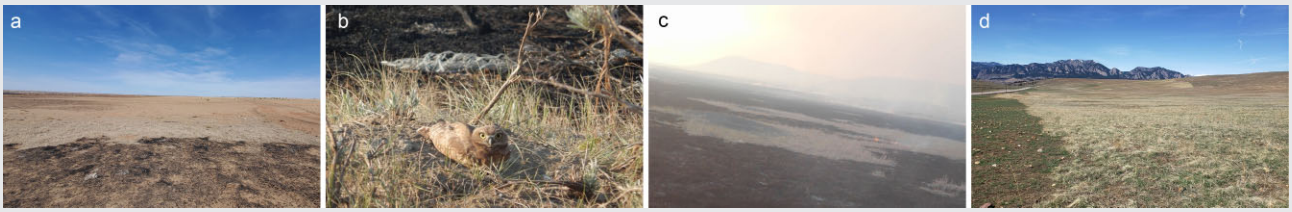

Figure 4. Patchy and incomplete wildfire spread across prairie dog colonies. (a) Patchy fire appeared to cease at the edge of a colony near the Beaver Creek Fire in Oklahoma. (b) A burrowing owl on a prairie dog mound with unburned grass and burn scar in background associated with the Gilbert Ranch Fire in Montana. (c) Fire behavior on a prairie dog colony was captured during the Wildcat Creek Fire in Wyoming, such that a patch around a colony mound remained unburned. (d) A large colony in the center of the Marshall Fire of Colorado was largely unburned, as was shown by burn scar far left, standing dead vegetation and burrows visible to the right and back.

Wildcat Creek Fire

The Wildcat Creek Fire, located in the Thunder Basin National Grassland of northeastern Wyoming, was detected on 2 August 2024 and burned 7357 ha over 2 weeks (National Interagency Fire Center 2024). The fire burned through both timber and grassland. Again, an interesting burn pattern was observed at the southeast corner as the fire encountered a rather large (110 ha) colony; the fire crews initiated a backburn on the southern portion of this colony as a preventative measure, but it appears that the fire slowed and stopped before meeting the fire line (figure 4). The fire scars on smaller colonies were again patchy.

Marshall Fire

The Marshall Fire burned across approximately 2500 ha of suburban and urban Boulder County, Colorado, from 30 to 31 December 2021, driven by extreme winds and fueled by abundant vegetation produced during a wet spring (figure 3; Dougherty and Johnson 2023). In this devastating event, two people were killed, and over 1000 structures were destroyed across this urban–wildland interface, with an estimated cost of $2 billion (RMIIA 2022). The city of Boulder maps prairie dog colonies each year in the fall and later mapped unburned patches within the larger fire polygon during the spring following the fire. Ecologists with the city identified multiple unburned patches up to 13 ha in size either on or near prairie dog colonies (figure 4). A moderate size (20 ha) colony at the south edge of the fire was largely unburned, and it appears that the fire's spread ceased downwind of this colony. Other colonies in the area, ranging in size from 5 to 22 ha, were also associated with unburned patches within and downwind of the colony (figure 4). Although many variables contribute to fire behavior and the resulting damage to property, multiple structures in this area were unburned (figure 3).

scales. Interestingly, although concerns about reduction in forage quantity (especially in dry years) could be leveraged against both fire and prairie dogs, these concerns have led to very different outcomes between these two disturbances; the rangeland community in North America often supports application of fire if it is used in a way that mimics historical return intervals, leading to greater prescribed fire application in the southern and eastern Great Plains than in northern and western locales (Scasta et al. 2016). Despite concerns about negative impacts on forage quantity, fire is often applied for multiple outcomes including improving forage quality (Allred et al. 2011, Everson and Everson 2016) and reducing woody shrub encroachment (Twidwell et al. 2013); although prairie dogs have been shown to provide many similar ecosystem services, acceptance of prairie dogs as a valuable ecosystem component remains lower than the acceptance of fire. Reframing the dominant paradigm from only pyric herbivory to include interactions with burrowing rodents may facilitate greater consideration of similar or complementary ecosystem services of prairie dogs.

We encourage a paradigm shift toward this multidisturbance model not only because it appears to be more ecologically accurate but also because it could be increasingly important for future management of these imperiled systems. Management on remaining rangelands in the Great Plains must necessarily factor in economic considerations; therefore, we do not expect every pasture or property within native prairie dog range to contain prairie dogs. Indeed, this would not have been the case historically and would be infeasible now. However, as our understanding of ecological processes grows, so should our management toolbox. Rangeland biodiversity in the Great Plains was not historically maintained by just fire and bison grazing, and we do managers a disservice by ignoring the unique ecosystem services that prairie dogs can provide. These include a potentially effective approach to addressing woody encroachment, one of the largest threats to portions of the Great Plains (Morford et al. 2022).

Moreover, the fire-suppressive force of prairie dogs may be important for wildfire management in the future. By reducing woody encroachment and fuel availability, prairie dogs have been observed to reduce fire effects locally, as was the case in the bison herd survival rate on the Z Bar Ranch Fire and more broadly in terms of fire spread on the Marshall, Wildcat Creek, and Gilbert Ranch fires (box 1). Nevertheless, these interactions have yet to be empirically tested. A better understanding of these dynamics is crucial, given that fire frequency has nearly quadrupled in the Great Plains in the past decade, relative to the 1980s and 1990s (Iglesias et al. 2022) with more frequent megafires in the southern plains (Shore 2019). Additional research is needed also to understand how the value of fire mitigation may offset potential losses of forage quantity for livestock on prairie dog colonies.

Further research is also needed to better understand how relationships within the disturbance triangle interact via either positive or negative feedback loops and are moderated by the

east–west gradient of precipitation in the Great Plains. For example, disturbances from fire or grazing are especially important for the maintenance of prairie dogs in the more mesic east (e.g., Osborn and Allan 1949), and negative effects of prairie dogs on forage quantity may be negligible in this region given much larger biomass production. The overall effect of prairie dogs on grazers in the Eastern Plains may, in fact, be neutral or even positive, given negligible impacts on quantity and increased forage quality. Although research on the fire–grazing interaction has occurred across the Great Plains, studies describing the relationship of prairie dogs with either fire or grazing are less common at the eastern edge of the prairie dog's range.

Specifically regarding the prairie dog–fire relationship, additional research is needed on how prairie dogs influence fire behavior in prescribed burns and wildfires. The former should be straightforward in landscapes with prairie dogs where fire is already a common management tool; data collection could be as simple as determining the percentage of fuels burned at multiple locations on and off colonies via visual survey or as complex as employing thermocouples to determine fire intensity along a gradient from colony core through colony edge and in adjacent uncolonized areas. Research on wildfire interactions with prairie dogs will necessarily be more opportunistic but could combine fire scars with mapped prairie dog cover to infer influences on fire behavior. Further investigation of manager perceptions of prairie dogs in the context of fire may also be informative. Management recommendations are contingent on the findings of future research but could demonstrate benefits of maintaining colonies especially in fire-prone areas.

We acknowledge that this disturbance triangle does not incorporate all the potential feedback loops among fire, grazing, and prairie dogs, nor does it directly incorporate the effects of local climate or climatic variation, but we argue that it is an improvement on the current paradigm, which is focused solely on fire–grazing interactions. We hope that continued research and discussion may do for the fire–prairie dog interaction and the disturbance triangle as a whole what we have observed with the fire–grazing interaction over the past 25 years. Although the restoration of any historical disturbance is dependent on both ecological and social context, much work has already been done to educate the public on the important ecological services these diverse disturbances can provide in grassland and rangeland ecosystems. Although incorporating prairie dogs into the grassland disturbance paradigm may be an uphill battle, we hope that this is at least a first step in that direction facilitated by a broader understanding of fire dynamics.

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Data availability

Data associated with literature review are located in Table 1 of the manuscript. All data on fire perimeters are publicly available from the National Interagency Fire center. Because spatial data for prairie dog colonies are considered sensitive, these are available upon request.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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