40

A disturbance triangle: The case for 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 the suppression of once-widespread disturbance regimes. In recent decades, restoration of the fire-grazing interaction has helped address these declines in the North American Great Plains. Conversely, relatively little attention has been paid to another historically ubiquitous disturbance agent -- the black-tailed prairie dog (*Cynomys ludovicianus*). While some research exists on the interaction between large ungulates and prairie dogs, scant work recognizes the triangle of historical and current interactions among large ungulates, fire, and prairie dogs, and research on interaction between the latter two disturbances is especially rare. Upon reviewing the literature, 34 sources discussed the fire-prairie dog interaction, but only one empirically tested the direct effect of prairie dogs on fire. Despite this research gap, historical fire patterns, current fire management activities, and unpublished data indicate prairie dogs likely reduce wildfire spread and/or intensity.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 further exploration of these more complex disturbance interactions worldwide

Introduction

Most grassland and shrubland ecosystems evolved in the context of various interacting disturbances (Fuhlendorf and Engle 2001). The periodicity, spatial extent, and intensity of disturbances helped shaped the floral and faunal composition of these systems; thus, 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. 2001, Garnett et al. 2010). 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 facilitate encroachment of woody species and homogenized herbaceous structure further contributing to biodiversity reduction (Ratajczak et al. 2016).

Accordingly, restoration of historic disturbances and their interaction has become a major goal of rangeland ecologists and conservation biologists alike (Sayre et al. 2013). While 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 like bison on both public and private rangelands via patch-burn grazing, with evidence that this management approach can support both livestock and biodiversity goals (Fuhlendorf et al. 2009). Despite progress towards the reintegration of fire and grazing as interacting disturbances, most grassland management paradigms continue to ignore another interacting disturbance that was historically ubiquitous across the Great Plains: burrowing mammals, and specifically, the black-tailed prairie dog (*Cynomys ludovicianus*).

As a keystone species, black-tailed prairie dogs are an important prey item for numerous avian and mammalian predators including the endangered black-footed ferret (*Mustela nigripes;* Hoogland 2006). Prairie dogs are also ecosystem engineers, living live in dense colonies with hundreds or thousands of individuals that together consume vegetation and actively clip it to optimize predator visibility (Hoogland 2006). Their digging and shrub clipping helps to aerate soil and reduce the rate of woody encroachment (e.g., Barth et al. 2014), burrows provide habitat for rattlesnakes (*Crotalus* spp.) and burrowing owls (*Athene cunicularia*), and the short, sparse vegetation structure they generate is ideal for the imperiled mountain plover (*Charadrius montanus;* Duchardt et al. 2019). This same engineering that provides so many ecosystem benefits can also reduce forage availability for livestock in certain contexts (Augustine and Derner 2021). This conflict is largely responsible for eradication programs that have reduced current prairie dog populations sizes to 5% of historical estimates (Miller et al. 1994). While there is evidence that prairie dogs can negatively affect livestock production, recent research indicates that this conflict may be contingent on factors like interannual precipitation variability (Connell et al. 2019, Augustine and Derner 2021). Moreover, forage *quality* is often greater on colonies because prairie dogs maintain vegetation at an early phenological state and can shift species composition towards more nutritious plants (e.g., Connell et al. 2019).

While researchers and managers have acknowledged relationships between fire and grazers (e.g. Fuhlendorf and Engle 2001), and between grazers and prairie dogs (e.g., Augustine and Derner 2021), less consideration has been given to the other side of this triangle: prairie dogs and fire; few studies exist on impacts of fire on prairie dogs, and we are unaware of any experimental studies demonstrating the effects of prairie dog ecosystem engineering on fire behaviour. To address this knowledge gap, we 1) review the literature on influence of fire on prairie dogs and prairie dogs on fire and 2) propose a framework by which to consider the historic role of prairie dogs within the fire-grazing interaction.

Methods and Results

We hypothesized that fire would have a similar influence on prairie dogs as grazing, facilitating expansion of prairie dogs into burned areas (+). Conversely, because prairie dogs not only remove biomass like other grazers but also lead to soil disturbance, we expected a suppressive effect of prairie dogs on fire (-) (Fig. 1). To better understand both sides of the fire-prairie dog interaction, we reviewed the primary literature using Google Scholar and Academic Search Premier. We conducted our Google Scholar search between 20–23 October 2023 using [“prairie dog” OR “Cynomys”] and “fire”, which returned 10,900 hits. We exhausted all 100 pages that Google Scholar generates (1,000 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 titles for relevance then searched for the terms: “fire”, “burn”, and “fuel” within each relevant source. If a source contained any of these keywords, we downloaded the source for a subsequent full review, which yielded 98 documents. Upon review, we deemed 38 of these resources as relevant; 34 addressed the fire → prairie dog interaction either theoretically or empirically. Most of these resources (n = 29, 85.3%) merely discussed the directional effect of fire on prairie dogs; text referencing fire influences on prairie dogs predominantly appeared in introduction, discussion, and management implications. 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 expansion into burned areas (e.g., Milne-Laux and Sweitzer 2006, Augustine et al. 2007).

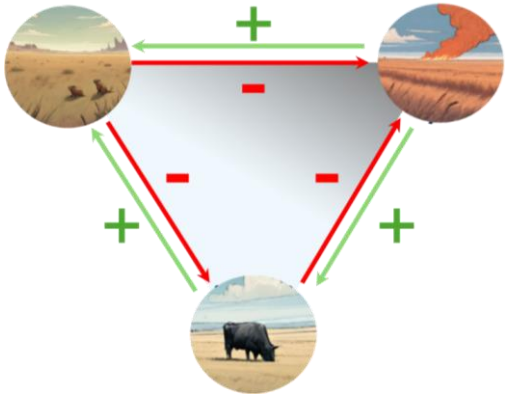

Fig. 1. Proposed disturbance triangle between fire, ungulate grazing, and prairie dogs within the Great Plains of North America.

Few sources discussed, let alone tested, the prairie dog → fire interaction. Only 6 sources 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 which

themselves made statements without supporting research citations). Only one source, a dissertation (Strawn 1995), empirically tested the effects of prairie dogs on fire, and found a 20% reduction in fire coverage on burned prairie dog colony as compared to an adjacent area that was also burned, although this was tested somewhat indirectly with burn tiles and with mixed efficacy (personal communication, S. Strawn). 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 need. Potential evidence for prairie dogs reducing fire intensity or size can first be found in historical fire return intervals. Although we know of no dataset 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 et al. (2018) highlighted the incongruity of fire-intolerant big sagebrush (*Artemisia tridentata*) persisting in portions of northeastern Wyoming, where fire-free intervals were estimated at ~7 years (Perryman and Laycock 2000). Researchers posited several potential factors leading to discontinuity of fuels, including disturbance caused by prairie dogs (Porensky et al. 2018).

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 ha 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 bison survived (Browning and Browning 2016, Magnus McCaffery, Turner Ranches, personal communication). Based on discussions with managers, it also appears that prairie dogs are taken into consideration when crafting burn plans, either as a means of "catching" (helping to limit) fire (David Lucas, Fish and Wildlife Service), or as a hindrance to fire spread in more arid systems (Ana Davidson, Colorado Natural History Program).

Discussion

While potential interactions between fire and prairie dogs appear straightforward, we found little evidence in the literature of previous research focused on this relationship. Little is known about the effect of prairie dogs on fire, barring a few references in the literature, and only one empirically-based dissertation chapter. The lack of research on how prairie dogs influence fire extends to other taxa as well, highlighted by a recent review (Foster et al. 2020). Therein, authors highlight the effect of animals on fire regimes are often overlooked, and studies incorporating the effect of fauna typically focus on mega-herbivores. However, 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 (e.g., 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. Despite a lack of empirical research, anecdotal evidence from numerous fires on the Great Plains supports this hypothesis.

We encourage a paradigm shift towards this multi-disturbance model not only because it appears to be more is 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 address woody encroachment, one of the largest threats to portions of the Great Plains (Morford et al. 2022).

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 in bison herd survival on the Z-bar ranch fire, and more broadly in terms of fire spread on the Marshall, Wildcat Creek, and Gilbert Ranch fires. Nevertheless, these interactions have yet to be empirically tested. A better understanding of these dynamics is crucial, given 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).

Further research is needed on how prairie dogs influence fire behaviour in prescribed burns and wildfires. Further investigation of manager perceptions of prairie dogs in the context of fire may also be informative. 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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