Rangeland Ecology & Management xxx (xxxx) xxx

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Thinking Like a Grassland: Challenges and Opportunities for Biodiversity Conservation in the Great Plains of North America☆

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ARTICLE INFO

Article history:
Received 18 March 2019
Received in revised form
5 August 2019
Accepted 9 September 2019

Key Words:
Conservation Reserve Program
fire
fragmentation
grazing
landscape connectivity

ABSTRACT

Fauna of North America's Great Plains evolved strategies to contend with the region's extreme spatio-temporal variability in weather and low annual primary productivity. The capacity for large-scale movement (migration and/or nomadism) enables many species, from bison to lark buntings, to track pulses of productivity at broad spatial scales (> 1 000 km^2). Furthermore, even sedentary species often rely on metapopulation dynamics over extensive landscapes for long-term population viability. The current complex pattern of land ownership and use of Great Plains grasslands challenges native species conservation. Approaches to managing both public and private grasslands, frequently focused at the scale of individual pastures or ranches, limit opportunities to conserve landscape-scale processes such as fire, animal movement, and metapopulation dynamics. Using the US National Land Cover Database and Cropland Data Layers for 2011–2017, we analyzed land cover patterns for 12 historical grassland and savanna communities (regions) within the US Great Plains. On the basis of the results of these analyses, we highlight the critical contribution of restored grasslands to the future conservation of Great Plains biodiversity, such as those enrolled in the Conservation Reserve Program. Managing disturbance regimes at larger spatial scales will require acknowledging that, where native large herbivores are absent, domestic livestock grazing can function as a central component of Great Plains disturbance regimes if they are able move at large spatial scales and coexist with a diverse array of native flora and fauna. Opportunities to increase the scale of grassland management include 1) spatial prioritization of grassland restoration and reintroduction of grazing and fire, 2) finding creative approaches to increase the spatial scale at which fire and grazing can be applied to address watershed to landscape-scale objectives, and 3) developing partnerships among government agencies, landowners, businesses, and conservation organizations that enhance cross-jurisdiction management and address biodiversity conservation in grassland landscapes, rather than pastures.

Introduction

In his eloquent essay "Thinking Like a Mountain," Aldo Leopold discussed his experiences in the mountains of the southwestern United States, where he had "watched the face of many a newly wolf-less mountain, and seen the south facing slopes wrinkle with a maze of new deer trails …," leading him to "suspect that just as a deer herd lives in mortal fear of its wolves, so does a mountain live in mortal fear of its deer" (Leopold 1949). Here, we apply a similar perspective to the grasslands of central North America, arguing that "thinking like a grassland" entails recognition that grasslands live in mortal fear of anthropogenic activities that eliminate the disturbance regimes essential to sustaining grassland ecosystems. The loss of these disturbances, such as fire and grazers, ultimately leads to landscape-scale homogenization and loss of biodiversity. We examine challenges and opportunities for biodiversity conservation across the Great Plains that center on the capacity for fire and fauna to move across broad, spatially diverse landscapes and for prairie dogs to

☆ Research was funded by the USDA–ARS and the Natural Resources Program award 2015-67019-23009, accession 1005543 of the USDA National Institute of Food and Agriculture. The USDA-ARS, Plains Area, is an equal opportunity/affirmative action employer, and all agency services are available without discrimination. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

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https://doi.org/10.1016/j.rama.2019.09.001

play their keystone role (Fuhlendorf et al. 2009; Davidson et al. 2012; Fuhlendorf et al. 2017). In this paper, we first review the paleoecology of Great Plains flora and fauna since the last ice age and discuss how large-scale movements of some species, as well as metapopulation dynamics of others, contribute to their persistence in the Great Plains. We then present an analysis of the contemporary degree of grassland fragmentation across the Great Plains, to illustrate the scale, distribution, and extent of grassland alteration by croplands, woody plant encroachment, and urban expansion. Finally, we conclude with a discussion of recent successes and potential opportunities for defragmentation of these grasslands. Large, connected landscapes are critical to restoring ecosystem integrity, natural disturbance regimes, and biodiversity of the Great Plains; here we aim to illuminate both the current magnitude of Great Plains grassland fragmentation and ways forward to reconnect these grasslands.

Great Plains Paleoecology

The central grasslands of North America emerged from the last glacial period ~12 000 yr ago (Walker et al. 2009), as glaciers that covered modern-day Canada and portions of the northern United States retreated and substantial shifts in climatic conditions began to shape the flora and fauna of the region. Before this glacial retreat, today's southern Great Plains supported hardwood forests in the east and coniferous parklands in the west, intermingled in a patchy mosaic with sagebrush shrublands (Porter 1983). During the glacial retreat, many North American large mammals became extinct for reasons we do not debate here and extensive grasslands supporting lower-quality forage replaced the former mosaic of plant communities. The shift from the Pleistocene to the Holocene (~14 000−10 000 yr ago) entailed dramatic climatic changes that reorganized ecosystems and gave rise to floral and associated faunal communities that coevolved over the next 12 000 yr. These communities experienced another dramatic change in ecosystem organization initiated by the Homestead Act in 1862, which encouraged the first large-scale conversion of grasslands and landscape fragmentation.

From ~12 000 to 8 000 yr ago, drought-resistant grasslands expanded and lake levels declined across the Great Plains, favoring C_4-dominated grasslands in the south and mixed C3/C4 grasslands farther north (Baker et al. 2000; Woodburn et al. 2017). Drier conditions 9 000−8 500 yr before present (BP) eliminated upland and riparian forests in the eastern Plains and increased C_4 grass dominance, with the driest conditions likely occurring 8 500 to 5 800 yr BP (Baker et al. 2000; Mandel et al. 2014). Bison *(Bison bison)* evolved as the primary large grazer in the region and declined in body size during the early Holocene, ultimately reaching their modern form in the Great Plains ~6 500 yr ago (Hill et al. 2008; Lewis et al. 2010). Black-tailed prairie dogs (*Cynomys ludovicianus;* hereafter, BTPDs) occupied the nonglaciated portions of the Great Plains throughout the last glacial maximum and expanded into the northern Great Plains as the glaciers receded ~12 000 yr ago, at which time they had already reached their modern body size (Goodwin 1995). Genetic analyses of the mountain plover *(Charadrius montanus),* which nests on BTPD colonies, indicate their population underwent a significant expansion during this period of glacial retreat (Oyler-McCance et al. 2005), coincident with the northward expansion of BTPD. Fossil remains show other grassland birds currently endemic to the Great Plains including lark buntings *(Calamospiza melanocytes),* longspurs (*Calcarius* spp.), western meadowlark *(Sturnella neglecta),* and upland sandpipers *(Bartramia longicauda)* already occurred in their modern form in the central Great Plains ~26 000 yr BP (Downs 1954; Emslie 2007). Over the past 2 700 yr, plant communities of the Great Plains have resembled those present at the time of European settlement but experienced periodic extreme droughts that were likely similar to or more severe than the drought of the 1930s (Baker et al. 2000). Collectively, these paleoecological studies indicate the flora, fauna, and associated disturbance regimes that are the focus of conservation efforts in the Great Plains have been present and interacting for thousands of years. As we move into a new era of climate changes (USGCRP 2017) layered on all of the other anthropogenic alterations that Great Plains grasslands have experienced since European settlement, conserving the region's flora and fauna is clearly a major challenge.

Movement and Metapopulations

North America's Great Plains once rivaled Africa's Serengeti. Large, migratory herds of herbivores, including bison, elk *(Cervus elaphus),* deer (*Odocoileus* spp.), and pronghorn *(Antilocapra americana),* moved at varying and largely unquantified spatial scales across North America's prairies in the millions (Samson et al. 2004; Sanderson et al. 2008). Through grazing, browsing, trampling, wallowing, and defecating, large herbivores altered vegetation composition, habitat structure, soils, nutrient cycling, and fire regimes, creating heterogeneous landscapes that included suites of grassland species that associate with open and intensively grazed habitats (Knapp 1999; Fuhlendorf and Engle 2001; Sanderson et al. 2008; Derner et al. 2009). Opportunities exist for livestock to continue to provide the ecological functions that sustain heterogeneity and many components of Great Plains biodiversity, although domestic livestock in the Great Plains are typically constrained to move over far smaller spatial scales than native herbivores did in the past (Towne et al. 2005; Derner et al. 2009; Allred et al. 2011). In addition, bison have been restored to limited portions of their historic range (Sanderson et al. 2008). Efforts to restore native wildlife populations are unlikely to be successful from an ecological and functional perspective without providing large, connected landscapes that support migratory movements so that animals can track resource availability (Berger 2004; Samson 2004; Fuhlendorf et al. 2017a).

Movements of Great Plains fauna occur at a wide range of spatial scales in response to spatiotemporal variation in weather, seasons, fire patterns, and vegetation dynamics. The Great Plains encompass a temperature gradient extending across nearly 3 000 km from north to south and a precipitation gradient extending nearly 1 500 km from northwest to southeast (Lauenroth et al. 1999). In any given location, precipitation and temperature fluctuate dramatically over temporal scales from days to seasons, years, and decades (Knapp and Smith 2001; Chen et al. 2018). This large geographic area and extreme temporal variability combined with the limited vertical structure of the vegetation create a challenging environment shaping the regions' fauna over ecological and evolutionary time scales. As a result, many species depend on the capacity for large-scale movements (over hundreds to thousands of kilometers) to track resources and avoid inclement weather. Bison, elk, and pronghorn, the historically most abundant large herbivores on the Great Plains, are all well known for their ability to undertake long-distance migrations to track forage resources (Lott 2002; Berger 2004).

For many bird species, multiple scales and patterns of mobility are an important component of their strategies for survival in the Great Plans. Birds of conservation concern that migrate from breeding grounds in the Great Plains to overwintering locations farther south include passerines such as McCown's and chestnut-collared longspurs, Sprague's Pipit *(Anthus spragueii),* grasshopper, Henslow's and Baird's sparrows (*Ammodramus savannarum, A. bairdii,* and *A. henslowii*), and lark buntings (Rosenberg et al. 2016), grassland-breeding shorebirds such as mountain plovers, upland sandpipers and long-billed curlews *(Numenius americanus)* (Page et al. 2014; Pierce et al. 2017), and raptors such as burrowing owls *(Athene cunicularia),* ferruginous hawks *(Buteo regalis),* and golden eagles (*Aquila chrysaeitos;* Watson et al. 2018). Individuals of some migratory species may return to consistent locations within their breeding grounds year after year, but recent studies show substantial capacity for within- and among-year movements in response to spatially variable resources or habitats. For example, dense concentrations of breeding lark buntings track those portions of the Great Plains with recent high precipitation (Wilson et al. 2018). Mountain plovers may move > 2 km in just the first 2 d after a brood hatches (Knopf and Rupert 1996) and > 20 km between two successive nesting attempts in a given breeding season (Skrade and Dinsmore 2010). Once brood rearing is complete, they migrate long distances from breeding grounds to late-summer staging grounds in the southern Great Plains (Pierce et al. 2017). Other migratory shorebirds move opportunistically to recently burned areas during migration (Hovick et al. 2017). Similarly, individual ferruginous hawks exhibit long-distance, post-breeding movements within the Great Plains to track availability of prey resources (Watson et al. 2018). All of these examples emphasize the importance of large-scale mobility for survival and persistence of many Great Plains organisms.

Even for sedentary species that both breed and overwinter within year-round territories (e.g., < 10 km^2), extensive, connected landscapes can be critical for maintaining populations. Local extirpations of a species can occur as a result of multiple factors, including shifting habitat conditions as vegetation responds to disturbances (e.g., wildfires or woody plant encroachment locally eliminating nesting habitat for prairie grouse; Fuhlendorf et al. 2017), disease outbreaks (e.g., epizootic plague affecting local BTPD populations; Cully et al. 2010), or extreme weather events (e.g., hail and ice storms or heat waves killing local breeding bird populations; Ross et al. 2016; Carver et al. 2017). Recolonization of an area that experienced a local extirpation depends on metapopulation dynamics, which require connectivity and dispersal among portions of the landscape operating as population sinks versus sources (Hanski 1994).

One keystone species that has experienced dramatic declines throughout its range and relies strongly on metapopulation dynamics for persistence in the western Great Plains is the BTPD. BTPDs occur in complexes of spatially distinct colonies that typically support hundreds to thousands of individuals, and these colonies are interconnected via occasional dispersal (Hoogland 2006; Davidson et al. 2012). BTPD colonies are well-known to create habitat for numerous associated species, such as burrowing owls and mountain plovers, and they attract large herbivores, such as bison and cattle, that prefer the higher quality forage found on their colonies during periods of rapid plant growth (Kotliar et al. 2006; Bayless and Beier 2011; Augustine and Baker 2013). A diverse array of predators also rely on prairie dogs as a primary food source, including multiple raptor species, American badgers *(Taxidea taxus),* coyotes *(Canis latrans),* and the endangered black-footed ferret *(Mustela nigripes)* (Goodrich and Buskirk 1998, Cook et al. 2003; Biggins and Eads 2018). Since the introduction of sylvatic plague to North America in the early 1900s, BTPD populations have been regulated by periodic plague outbreaks that cause dramatic (> 95%) local population collapses (Cully et al. 2010). Field research linked with population modeling analyses reveal how BTPD persistence over broad landscapes depends on metapopulation dynamics, as populations in varying phases of collapse or recovery from plague exchange individuals and genetic diversity (Antolin et al 2006; Snall et al. 2008; Savage et al. 2011; George et al. 2013). As a result, associated species that rely on prairie dog colonies for habitat also depend on the metapopulation dynamics that sustain prairie dogs over broad spatial and long temporal scales.

Metapopulation dynamics are also increasingly recognized as essential to the persistence of sedentary bird species, such as the Lesser Prairie-Chicken *(Tympanuchus pallidicinctus),* which has experienced dramatic population declines and range contraction within the increasingly fragmented landscapes of the southern Great Plains. For example, prairie chicken populations can undergo steep declines in response to extreme drought (Ross et al. 2016) or woody plant encroachment (Fuhlendorf et al. 2017b), while landscapes containing more connected patches of grasslands, including those restored through the Conservation Reserve Program (CRP), can serve as population sources (Spencer et al. 2017). Although Prairie-Chickens are frequently sedentary, occupying year-round home ranges, Global Positioning System telemetry reveals they undertake occasional long-distance movements, which can connect populations across distances of ~5–25 km (Earl et al. 2016). Analyses to project long-term persistence of Lesser Prairie-Chickens rely on metapopulation models and emphasize the need to sustain connectivity among regions and core areas containing source populations in order to conserve the species (Hagen et al. 2017). These examples illustrate that even for birds and mammals, in which long-distance movement is not central to their strategy for living in the Great Plains, population dynamics occur across broad landscapes and extend far beyond the typical size of individual pastures or ranching operations.

Grassland Loss and Fragmentation

Today, extensive portions of the US Great Plains have been converted into some of the most productive croplands in the world. Conversion of native grassland to cropland combined with additional losses to woody plant encroachment, urban expansion, and energy extraction are widely recognized as major challenges for grassland species conservation (Samson et al. 2004; Williams et al. 2011). Widespread grassland to cropland conversion was precipitated by the Homestead Acts beginning in 1862 and new technologies like central pivot irrigation, with varying economic forces and national policies driving continued conversion for more than a century (Wright and Wimberly 2013). Samson et al. (2004) estimated that by 2003, tallgrass, mixedgrass, and shortgrass provinces of the Great Plains were reduced to 13%, 29%, and 52% of their historic extent, respectively. More recent analyses suggest that 22.1 million ha (54.7 million acres) of grassland were converted to cropland in the northern Great Plains during 2009–2017 (2018 Plowprint Report). At the same time, beginning in the 1980s, extensive amounts of cropland have been restored back to grasslands of varying composition through the Conservation Reserve Program in the United States and the National Soil Conservation Program in Canada. Although these restored grasslands can in some cases provide valuable wildlife habitat and serve to reestablish grassland connectivity, their value is often limited due to the dominance of non-native grasses and lack of diverse forb communities. Here, we use recent data layers compiled by the National Agricultural Statistics Service (NASS) on cropland distribution (2011–2017) combined with the 2011 National Land Cover Database (NLCD) to quantify the current status of Great Plains grasslands in terms of amount and distribution.

Methods

Quantifying Rangeland Loss and Fragmentation in the Great Plains

To define subregions of the Great Plains, we used a revised version of Kuchler's (1964) map of the potential natural vegetation of the United States. The map was digitized from the 1979 physiographic regions map produced by the Bureau of Land Management, which added 10 physiognomic types. All analyses are based on data sources specific to the United States; hence, we only analyze the portion of the Great Plains occurring in the United States. Similar contemporary analyses are needed for the Canadian

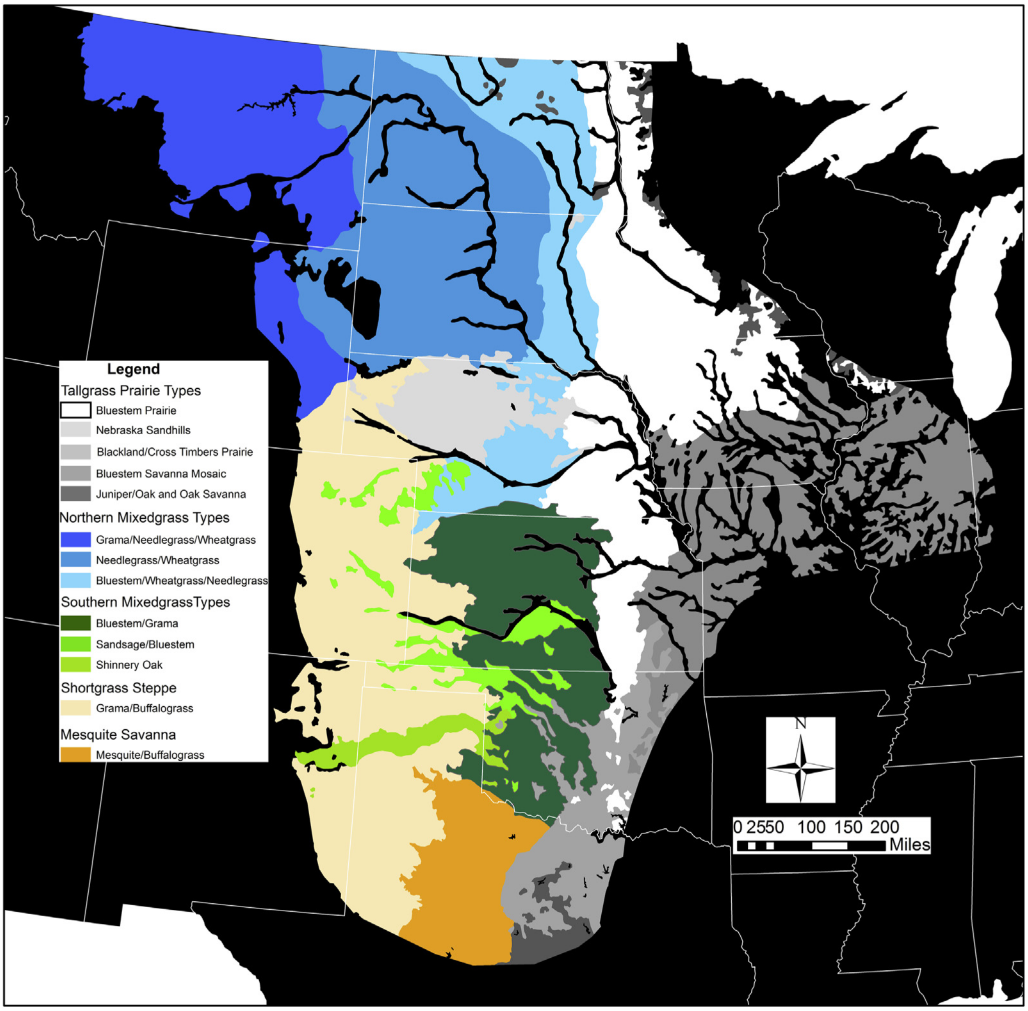

Figure 1. Potential natural vegetation of US portion of the North American Great Plains, adapted from Kuchler (1964).

portion of the Great Plains, but for a relatively recent and comprehensive overview of anthropogenic alterations to the Canadian Great Plains, see Williams et al. (2011). We extracted all of the grassland, shrubland, savanna, and forest communities in the US Great Plains from the revised Kuchler natural vegetation map (Fig. 1). Following Lauenroth et al. (1999), we refer to the northern portion of Kuchler's "Shortgrass Prairie" region (the grama/needlegrass/wheatgrass community) as "Northern Mixed Grass" types and the southern portion (the grama/buffalograss community) as "Shortgrass Steppe."

We sought to quantify the current amount of rangeland in the US Great Plains converted due to 1) woody plant encroachment; 2) urban, exurban, and other forms of development (e.g., energy infrastructure); and 3) cultivation of cropland. At the time of this analysis, the most contemporary measure of land cover across the United States was the 2011 NLCD (Homer et al. 2015). One limitation of the NLCD is that some grasslands with high rates of productivity, such as herbaceous wetlands or grasslands along riparian zones, are misclassified as cropland. A second limitation is the inability to capture cropland conversion occurring after 2011 (Lark et al. 2015). Beginning in 2009 (and retroactively for 2008), the US Department of Agriculture−NASS has annually produced a Cropland Data Layer (CDL) for the United States from satellite imagery, which maps individual crop types at a 30-m spatial resolution. Since 2009, methods were refined and improved, such that caution is recommended in using early years of CDLs for any analysis of land cover change (Lark et al. 2015, 2017). At the same time, using as many years of CDL data as possible can assist in identifying classification errors and delineating individual field boundaries (Lark et al. 2017). We used the annual CDLs from 2011 to 2017 to map the distribution of cropland in the Great Plains as follows. After constraining each layer to the boundaries of the Great Plains (see Fig. 1), we generated a layer with all cropland types (excluding grassland, grass-based pasture, and hay) in one class and all noncropland as a second class for each of the 7 yr. For each pixel, we calculated the number of years (out of 7) that it was classified as cropland. Pixels classified as cropland for $\geq$ 2 yr were classified as cropland in our final 7-yr integrated CDL layer (iCDL). This procedure eliminated pixels that likely were misclassified in 1 yr due to factors such as variable phenology of grasslands but still retained pixels with crop rotations that may result in classification as noncropland in some years. As a final step, we applied a minimum area filter, where any contiguous cluster of $\leq$ 10 cropland pixels (i.e., 0.9 ha) was reclassified as noncropland. This step was important for screening out small strips of productive grassland along pond edges or lowlands that were misclassified in the CDL as cropland, common in certain landscapes such as the Sandhills of Nebraska. Note that our approach seeks to quantify the amount and distribution of all grasslands, regardless of whether or not they have a history of being plowed and then restored, and hence differ from the approach of Olimb et al. (2018) and the Plowprint Report produced by the World Wildlife Fund (2019).

Please cite this article as: Augustine, D et al., Thinking Like a Grassland: Challenges and Opportunities for Biodiversity Conservation in the Great Plains of North America, Rangeland Ecology & Management, https://doi.org/10.1016/j.rama.2019.09.001

Table 1
Estimated extent of 5 major ecoregions of the US Great Plains, subdivided into 14 vegetation communities as mapped by Kuchler (1964; see Fig. 1). For each community, we present the estimated percent of the landscape in each of 10 land cover types based on an integration of cropland data layers (2011−2017) with the 2011 National Land Cover Database (see Fig. 2).

	Potential natural vegetation (km^2)	Percent of potential natural vegetation occurring as:								
		Cropland	Forest	Water	Developed	Barren	Grassland	Shrubland	Pasture/ Hay	Developed open space	Uncertain grass/crop
Tallgrass prairie types											
Bluestem Prairie	259 802	68.5	3.5	1.7	1.4	0.0	14.1	0.0	2.8	4.2	3.8
Bluestem Savanna Mosaic	186 969	11.0	21.4	1.7	3.3	0.2	41.3	5.1	8.1	5.6	2.3
Blackland and Cross Timbers Prairie	83 275	9.1	1.1	1.1	0.2	0.1	86.5	0.0	0.3	0.9	0.7
Juniper/Oak and Oak Savanna	31 581	58.8	10.9	0.8	3.7	0.1	4.0	0.2	13.6	4.2	3.7
Nebraska Sandhills	58 439	29.4	16.2	3.2	1.3	0.1	24.2	13.1	3.6	4.6	4.3
Northern mixed-grass types											
Grama/Needlegrass/Wheatgrass	202 299	22.4	4.3	0.4	0.2	0.3	53.9	14.7	0.2	0.8	2.7
Needlegrass/Wheatgrass	246 531	32.5	2.0	1.5	0.4	0.9	53.2	4.4	1.2	1.9	2.0
Bluestem/Needlegrass/Wheatgrass	134 408	62.7	1.4	2.0	0.6	0.0	23.6	0.0	3.7	3.4	2.6
Southern mixed-grass types											
Bluestem/Grama	150 323	46.4	2.6	0.8	1.2	0.1	37.4	3.1	0.5	3.5	4.3
Sandsage/Bluestem	42 569	35.9	1.1	0.6	0.5	0.2	49.5	4.2	0.9	3.2	4.0
Shinnery	22 061	5.8	0.9	0.3	0.6	0.3	48.7	40.8	0.0	1.5	1.1
Shortgrass steppe											
Grama/Buffalograss	299 951	34.9	1.1	0.2	1.2	0.1	46.8	9.5	0.5	2.7	3.2
Desert savanna											
Mesquite/Buffalograss	68 800	23.6	2.8	0.4	0.7	0.4	20.4	47.2	0.1	3.1	1.3
Mesquite savanna	10 578	7.9	2.8	0.3	0.9	0.0	7.7	76.8	0.0	3.3	0.2
Total	1 797 586	40.6	4.4	1.0	1.2	0.2	36.3	7.5	2.9	3.0	3.0

We merged the iCDL layer with the 2011 NLCD, using NLCD to classify all "noncropland" pixels in the iCDL layer into one of nine land cover types (Table 1): 1) Forest (a combination of Deciduous, Evergreen, and Mixed Forest and Wooded Wetlands); 2) Open Water; 3) Developed Land (a combination of Low-, Medium-, and High-Intensity Developed land from NLCD); 4) Barren Land; 5) Grassland; 6) Shrubland; 7) Improved Pasture/Hay; 8) Developed Open Space (primarily rural roads); and 9) Uncertain Grass/Cropland (hereafter UGC). The UGC category consisted of lands classified as cropland in the NLCD, but as noncropland in the iCDL, and represented 3% of the total area of the Great Plains (Table 1). Given the more contemporary methods used to create the 2011−2017 CDLs, as well as their reliance on methods designed to specifically identify croplands, the UGC category likely represents lands misclassified as cropland by NLCD, including productive and/or restored grasslands, such as lands enrolled in the CRP. We refer to this fusion of NLCD and iCDL as fNLCD-CDL.

We used the fNLCD-CDL product to analyze rangeland fragmentation in the Great Plains based on two sets of assumptions concerning which land cover categories constitute "rangelands" and which cover types fragment rangelands. For each analysis, we used the fNLCD-CDL to calculate the distance from each rangeland pixel to the nearest fragmenting land cover type, with all nonrangeland pixels set to a value of zero. We then calculated the total area within each of the 14 vegetation subregions (see Fig. 1) consisting of rangeland occurring at varying distances from fragmenting land cover types.

In the first analysis (the "best case scenario"), we assumed that 1) rangelands consist of grasslands, shrublands, improved pasture/hay, and the UGC category; 2) fragmenting land cover types consist of cropland, forest, and developed land; and 3) the remaining land cover types (developed open space, open water, and barren lands) are not rangeland but also do not fragment rangelands. In the second analysis (the "worst case scenario") we assumed that 1) rangelands consist only of grasslands and shrublands; 2) fragmenting land cover types consist of cropland, forest, developed land, developed open space, improved pasture/hay, and UGC; and 3) open water and barren lands are not rangeland but do not fragment rangelands. The "best case" scenario was intended to provide an index of current rangeland fragmentation for organisms that may be capable of inhabiting land cover types dominated by any type of grass and are not strongly impacted by rural roads (e.g., pronghorn antelope) and optimistically assumes that discrepancies in cropland mapping by NLCD versus iCDL represent primarily restored grassland (e.g., CRP fields) or simply grasslands misclassified as cropland. The "worst case" scenario is intended to provide an index of rangeland fragmentation for organisms that do not inhabit grasslands dominated by non-native plant species and pessimistically assumes the additional lands classified as cropland by NLCD are indeed croplands.

Results

The fNLCD-CDL product estimates that 43.7% of the Great Plains still consists of grasslands and shrublands, with the remainder consisting of 40.6% cropland, 4.4% forests, 3.0% UGC, 3.0% developed open space, 2.9% improved pasture or hay fields, 1.2% developed land, 1.0% water, and 0.2% barren land, with important regional and subregional variation in the extent of rangeland loss to cropland, forests, and developed land (Table 1; Fig. 2; maps accessible at https://gpsr.ars.usda.gov/greatplainslandcover/).

Tallgrass prairie vegetation types have undergone the most extensive losses, particularly in the bluestem prairie and oak savanna mosaic types, where only 4.2−14.1% remain as grassland and shrubland. As much as 46% of the blackland and cross timbers prairie types and 37.3% of juniper and oak savannas remain as grassland or shrubland. At the same time, these types are highly fragmented by a combination of cropland conversion and forest encroachment, with < 1% of their total area occurring > 800 m (0.5 mi) from fragmenting land cover types. Similarly, only 1% of original bluestem prairie and none of the bluestem savanna mosaic occurs > 800 m from fragmenting land cover. A notable amount (2.3−4.3%) of all tallgrass prairie types other than the Nebraska Sandhills is classified as cropland by NLCD but not by iCDL, suggesting much of this could be restored grasslands. These landscapes also contain the greatest amount of developed open

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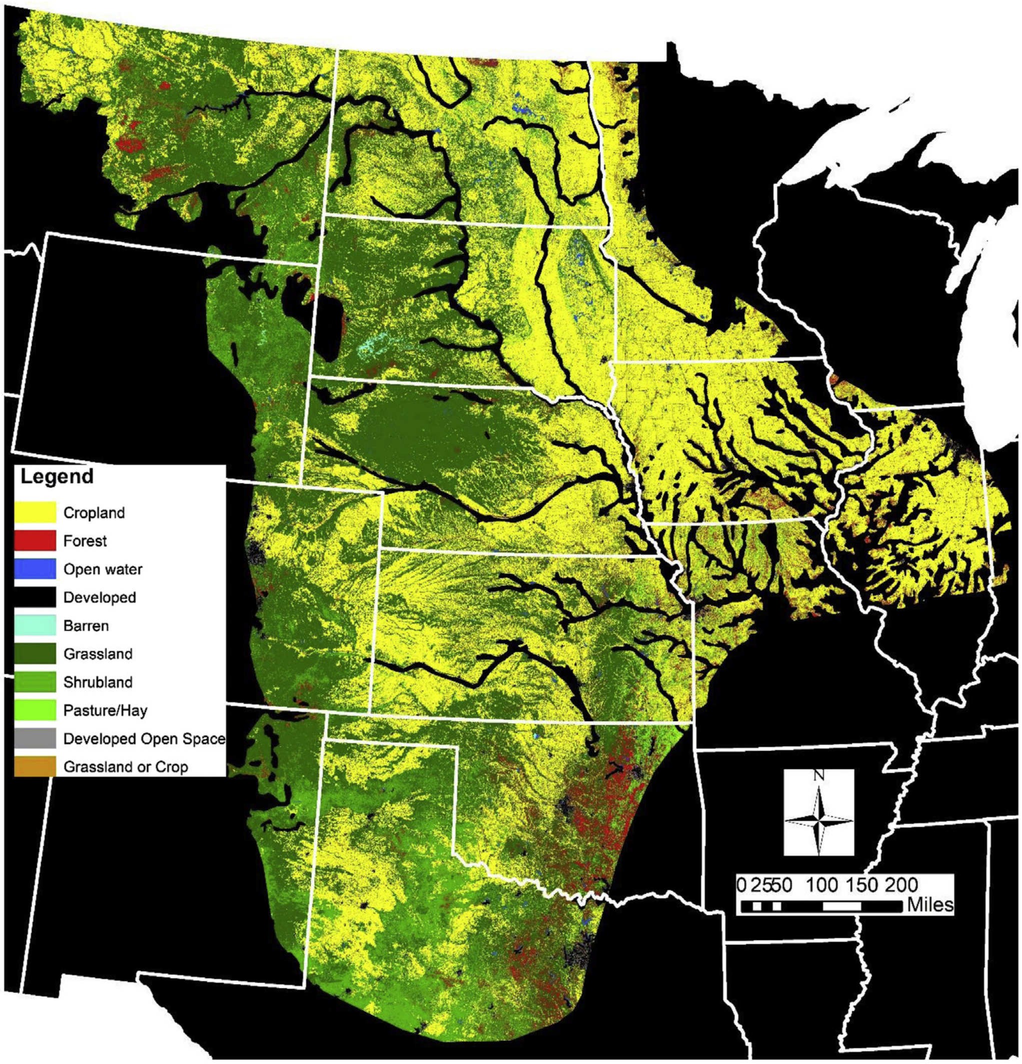

Figure 2. Land cover of the US portion of the North American Great Plains derived from a combination of the 2011 National Land Cov4.er Database (NLCD; Homer et al. 2015), and the 2011–2017 Cropland Data Layers (US Department of Agriculture–National Agricultural Statistics Service [NASS]). The orange cover type represents areas classified as non-cropland by NASS, but cropland by NLCD.

space, reflecting the dense network of rural roads. Outside of the Nebraska Sandhills, patches of contiguous rangeland that include areas > 1.6 km from a fragmenting cover type under the "best case" scenario are most widespread in the Flint Hills of Oklahoma and Kansas and in northeastern Oklahoma, with smaller and more isolated patches occurring in the counties of Archer, Clay, Jack, and Shackelford in Texas; Pontotoc and Murray in Oklahoma; Marshall, Roberts, and Grant in South Dakota; and Marshall in Minnesota. Portions of the Sheyenne National Grassland in Ransom County, North Dakota are > 800 m from fragmentation, but no part of this grassland was identified as > 1.6 km from fragmenting land uses, even under the "best case" scenario. In contrast to the remainder of the tallgrass prairie types, the Nebraska Sandhills are one of the least fragmented vegetation types within the entire Great Plains (Figs. 3–5). Portions of the southern and central Sandhills contain extensive, contiguous rangelands including areas > 6.4 km (4 mi) from any fragmenting land cover, and 50% of the entire region consists of rangelands > 800 m from any fragmenting land cover (Table 2; see Figs. 3–5).

In northern mixed prairie types, conversion to cropland has been especially severe in the eastern portion (bluestem/needlegrass/wheatgrass type), with only 23.6% (and potentially an additional 2.6%) in grassland (see Table 2 and Figs. 3–5) and only 1% occurring in patches > 800 m from fragmenting land cover. Encouragingly, at least 57.6% and 68.6% of the two more arid vegetation types remain in grassland (see Table 2), but only 11% of the needlegrass/wheatgrass type and 5% of the grama/needlegrass/wheatgrass types occur > 1.6 km from fragmenting land cover. Within these latter two vegetation types, the largest areas of contiguous rangelands in South Dakota are on and around Badlands National Park, Buffalo Gap National Grassland, and the Pine Ridge Indian Reservation; on the Cheyenne River Indian Reservation and adjacent private lands in Stanley County; and in Harding and Butte Counties north of the Black Hills. In Montana, contiguous mixed-grass rangelands > 1.6 km from fragmentation occur on intermingled private, state, and Bureau of Land Management (BLM)-administered lands across Phillips, Valley, Garfield, Rosebud, Custer, and Carter Counties. In Wyoming, contiguous rangelands > 1.6 km from fragmentation are most prevalent on and near the Thunder Basin National Grassland, plus extensive portions of Johnson, Campbell, and Converse Counties. The least fragmented mixed grass rangelands in North Dakota occur on and near the Little Missouri National Grassland and Theodore Roosevelt National

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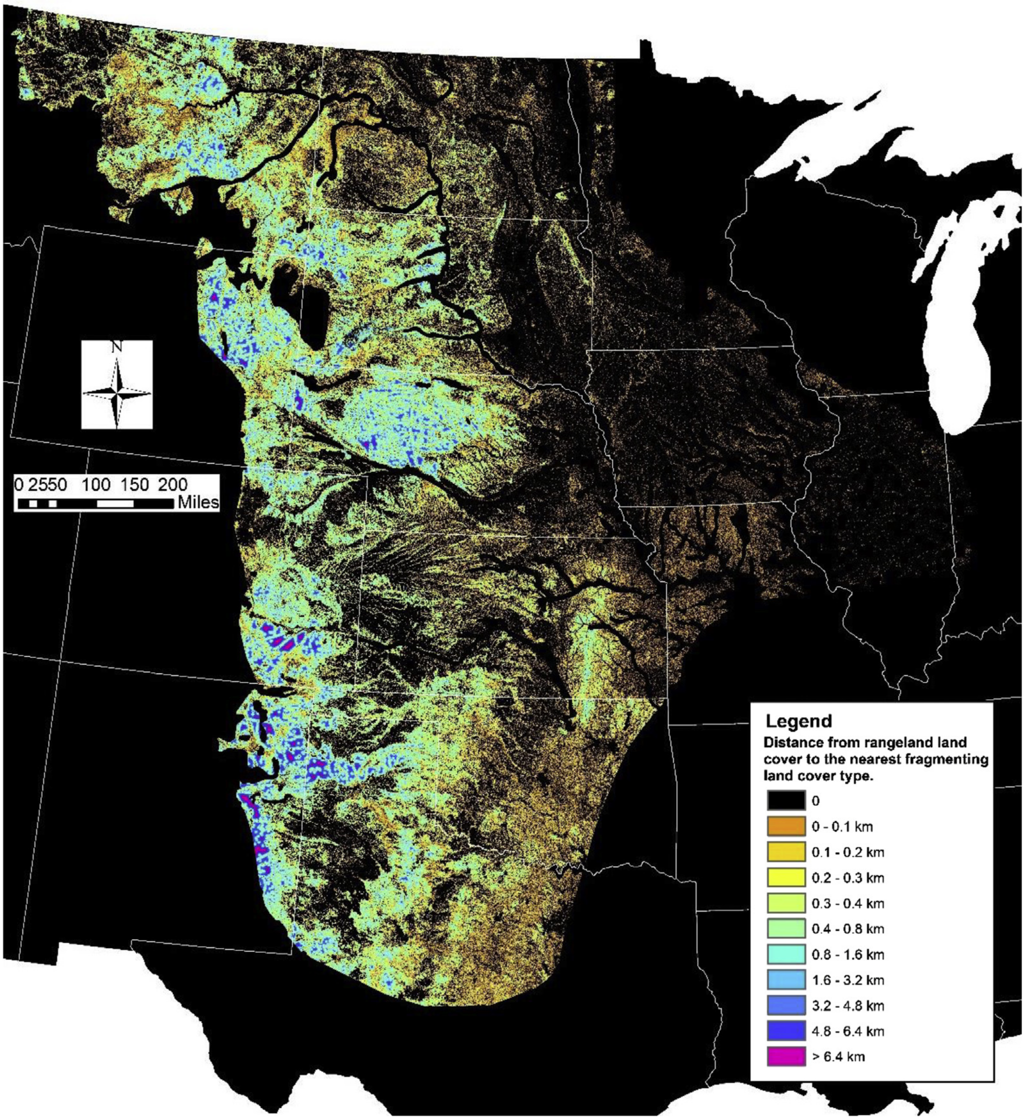

Figure 3. Variation in the degree of fragmentation of Great Plains measured in terms of distance to cropland, forest, or developed lands. This map depicts a "best case" scenario in which 1) croplands are mapped based only on the US Department of Agriculture—National Agricultural Statistics Service Cropland Data Layers (2011—2017), 2) all grass-dominated cover types including hay fields and improved pasture are considered rangelands, and 3) developed open space (as defined by the National Land Cover Database) are assumed to not be a fragmenting land cover type.

Park, but areas > 1.6 km from fragmenting land cover are relatively rare due to the prevalence of cropland near and forest within this landscape.

In the southern mixed prairie, > 40% of the bluestem/grama vegetation type is rangeland, but this region has been extensively fragmented by cropland and woody plant encroachment (see Figs. 3—5). Only 2% of the region occurs > 800 m from fragmenting land cover. Remaining contiguous rangeland within the bluestem/grama type is concentrated in south-central Kansas and on the border between Oklahoma and the Texas Panhandle, especially in Collingsworth County. We note that this region has been strongly affected by juniper encroachment (Scholtz et al. 2018), which our analysis does not fully capture because we included shrublands as rangeland, and only assessed woody encroachment via the development of forest. In contrast to the bluestem/grama region, extensive portions of the shinnery and sandsage/bluestem vegetation types persist as large, contiguous rangeland patches containing areas > 1.6 km from fragmenting land covers (see Figs. 3—4), due to sandy soils minimizing conversion to cropland. The shinnery type still retains 33% of the area as rangelands > 1.6 km from any fragmenting land cover, primarily along the Canadian River corridor in the Texas Panhandle. Large, contiguous areas of sandsage/bluestem occur on and around the Comanche National Grassland in southeast Colorado and across intermingled private and state lands in northeastern Colorado. In the mesquite savanna vegetation types, large patches of rangeland > 1.6 km from fragmentation (which comprise ~5% of the total landscape) occur primarily on privately owned lands in the western half of the region (see Figs. 2—4).

In the shortgrass steppe (grama/buffalograss type), at least 56% remains as rangeland, with 13% in areas > 1.6 km from fragmenting land cover. Large, unfragmented rangelands occur in southeastern Colorado, northeastern New Mexico, the western fringe of the shortgrass steppe in east-central New Mexico, and in Andrews County, Texas (see Figs. 2—4). Portions of these landscapes are associated with the Comanche, Kiowa, and Rita Blanca National Grasslands and BLM-administered lands in New Mexico, but most is privately owned. A smaller region of shortgrass rangeland

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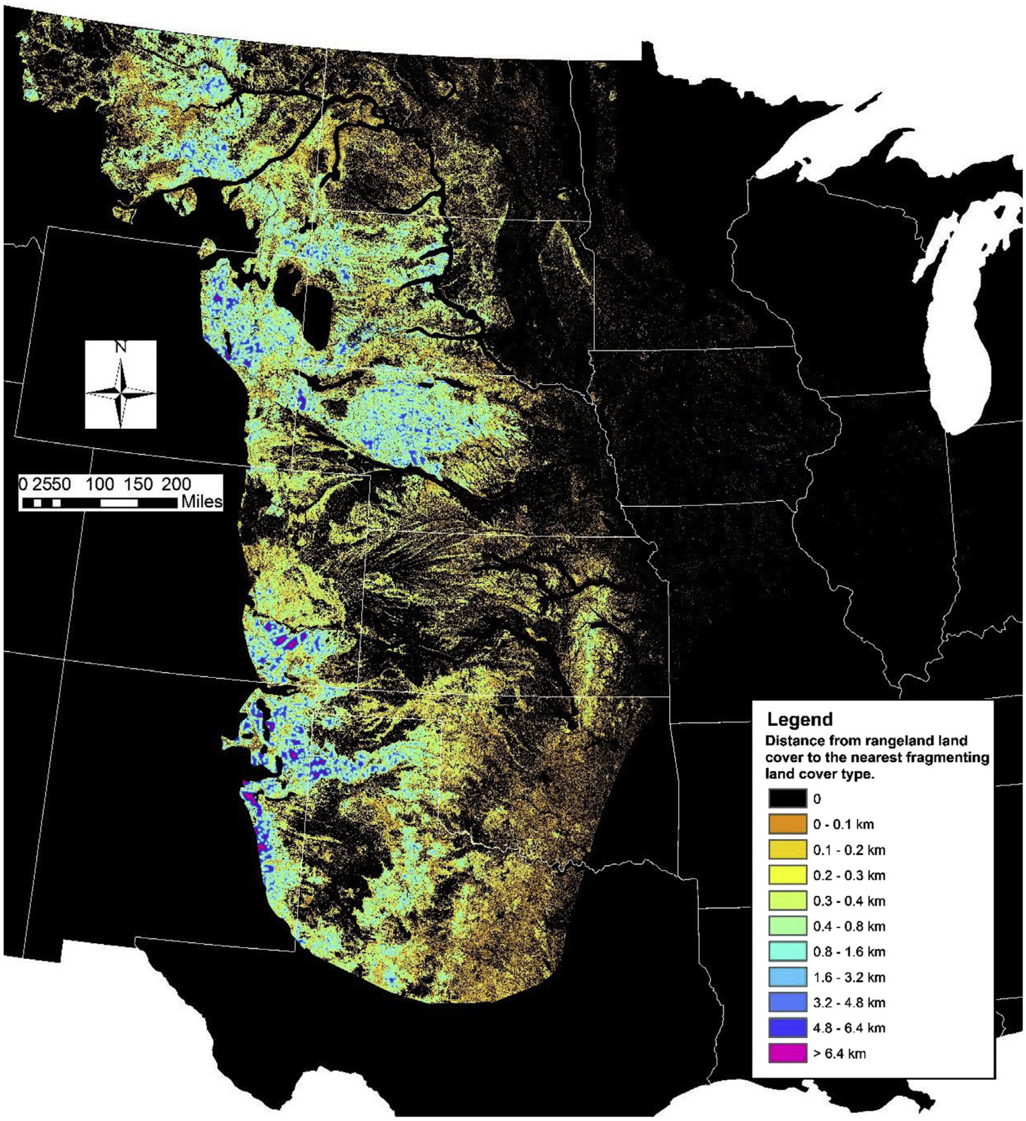

Figure 4. Variation in the degree of fragmentation of Great Plains measured in terms of distances to cropland, forest, or developed lands. This map depicts a 'worst case' scenario in which 1) croplands are mapped based on the US Department of Agriculture–National Agricultural Statistics Service Cropland Data Layers (2011–2017) and the 2011 National Land Cover Database (NLCD), 2) hay fields and improved pasture are not included as rangelands, and 3) developed open space (as defined by NLCD) is included as a fragmenting land cover type.

containing areas > 1.6 km from fragmentation occurs on and around the Pawnee National Grassland in Colorado and adjacent private lands surrounding Cheyenne, Wyoming.

The contrast between our "best case" and "worst case" scenarios was most notable in the tallgrass prairie (other than the Nebraska Sandhills), as well as in the bluestem/needlegrass/wheatgrass type of the northern mixed prairie, the bluestem/grama and sandsage/bluestem types of the southern mixed prairie, and in the shortgrass steppe (grama/buffalograss) (see Table 2). The estimated amount of rangeland in the tallgrass prairie types decreased by 7–17% when improved pasture and hay and UGC categories were excluded from the definition of rangeland, and the amount of rangeland > 800 m from fragmenting land cover declined by > 50%. The latter change was due to the inclusion of rural roads as a fragmenting land cover in the "worst case" scenario. Finally, the amount of shortgrass steppe as rangeland increased by 3.6% under the "best case" scenario, and the amount of rangeland > 800 m from fragmentation declined by a third (see Table 2).

In addition to the direct loss and fragmentation of rangelands by land conversion, the conservation of pattern and process in rangelands (sensu Fuhlendorf et al. 2012) is compromised by the complex land ownership patterns that characterize much of the region. Landownership boundaries within contiguous areas of rangelands can impede movements of both fire and grazers, via fences (Jakes et al. 2018) and via differences in management objectives and practices among landowners. A full quantification of these sources of fragmentation is beyond the scope of this paper, but we illustrate the complexity of land ownership patterns in Weld County, Colorado (Fig. 6), which is one of the largest counties in the western Great Plains and encompasses the Pawnee National Grassland. Although the majority of Weld County consists of large contiguous areas of rangeland (see Fig. 6a), these contiguous areas are characterized by a highly complex land ownership pattern, which affects wildlife populations. For example, black-tailed prairie dogs are controlled on the lands represented in black and on many of the private lands of varying colors in Figure 6b, whereas control

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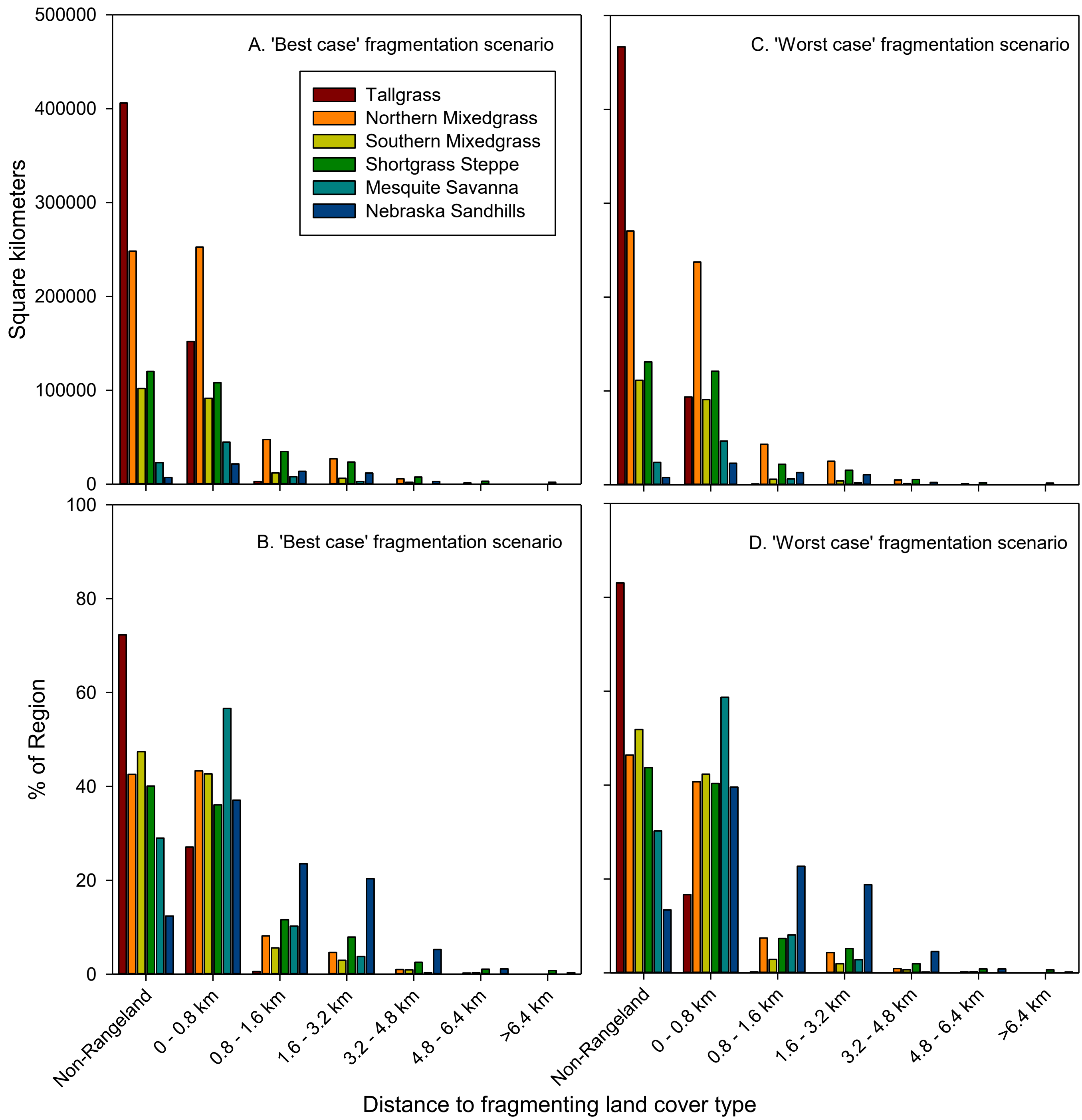

Figure 5. Variation in the degree of fragmentation of US Great Plains rangelands based on two different assumptions concerning which land cover types cause fragmentation. In both cases, we calculated the total area in each ecoregion within varying classes of distance to cropland, forest, or developed lands, but the two different scenarios made different assumptions about how croplands are mapped and which land cover types constitute "rangelands" (see Figs. 3 and 4 and methods for details).

is limited or prohibited on lands depicted in light blue (Pawnee National Grassland).

Discussion

Grassland Loss and Fragmentation

Previous analyses have reported on the extreme degree of grassland conversion in the Great Plains, particularly in the eastern ecoregions (e.g., 13.4% of the tallgrass prairie [excluding Nebraska's sandhills] remaining; Samson et al. 2004; see also Comer et al. 2018). These estimates expressed grassland loss in terms of "percent of historic vegetation remaining," where lands converted to cropland but then restored to grassland and lands managed as pasture or hay fields were considered to be converted grassland. Our analyses show substantially more grassland and shrubland remaining in many of these ecoregions. For example, we estimate that 35.1% of tallgrass prairie (excluding the Nebraska Sandhills) currently occurs as grassland or shrubland, and an additional 2.8% remains in the "uncertain grass or crop" category (see Table 1). At

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Table 2
Percentage of total area in each of 14 major vegetation types in the US portion of the Great Plains (see Fig. 1) estimated to occur as nonrangeland or as rangeland of varying distances to a fragmenting land cover type (see Figs. 3 and 4). Numbers to the left of each slash symbol show results from a "best case" scenario (see Fig. 3), and numbers to the right of each slash symbol are the estimate from a "worst case" scenario (see Fig. 4), which made different assumptions about the definition of rangeland cover types and the definition of fragmenting land cover types (see methods).

Potential natural vegetation type	Percentage of area occurring as rangeland of varying distances to fragmenting land cover types						
	Nonrangeland	0.01-0.8 km	0.81-1.6 km	1.61-3.2 km	3.21-4.8 km	4.81-6.4 km	> 6.4 km
Tallgrass prairie							
Bluestem Prairie	79.3/85.9	19.8/13.7	0.8/0.3	0.2/0.1	0/0	0/0	0/0
Bluestem Savanna Mosaic	78.5/95.8	21.4/4.2	0.1/0	0/0	0/0	0/0	0/0
Blackland and Cross Timbers Prairie	43.2/53.6	55.9/46.1	0.8/0.2	0/0	0/0	0/0	0/0
Juniper/Oak and Oak Savanna	54.8/62.7	44.9/37.2	0.3/0.1	0/0	0/0	0/0	0/0
Nebraska Sandhills	12.4/13.4	37.1/39.5	23.5/22.7	20.3/18.8	5.2/4.5	1.1/0.9	0.3/0.2
Northern mixedgrass							
Grama/Needlegrass/Wheatgrass	28.5/31.4	47.6/46.1	13.0/12.2	8.3/7.9	2/1.8	0.5/0.5	0.1/0.1
Needlegrass/Wheatgrass	39.2/42.3	48.0/46.0	7.9/7.2	4.1/3.7	0.7/0.7	0.1/0.1	0/0
Bluestem/Needlegrass/Wheatgrass	70.1/76.4	28.4/22.9	1.3/0.6	0.2/0.1	0/0	0/0	0/0
Southern mixedgrass							
Bluestem/Grama	54.6/59.5	42.6/39.6	2.4/0.8	0.3/0.1	0/0	0/0	0/0
Sandsage/Bluestem	41.5/46.3	44.7/50.3	10/2.6	3.5/0.6	0.3/0.1	0.1/0	0/0
Shinnery	9.4/10.5	38.8/45.1	19/17.4	20/17.4	8.5/6.4	3.1/2.3	1.1/1
Shortgrass steppe							
Grama/Buffalograss	40.1/43.7	36.1/40.4	11.6/7.3	7.9/5.2	2.5/1.9	1.1/0.8	0.8/0.6
Mesquite savanna							
Mesquite/Buffalograss	31.1/32.5	55/57.1	10/7.8	3.6/2.6	0.3/0.1	0/0	0/0
Mesquite savanna	15.3/15.5	66.9/69.2	11.8/10	4.9/4.3	0.9/0.7	0.2/0.2	0/0

the same time, our fragmentation analysis for tallgrass prairie shows that aside from the Nebraska Sandhills, at most 0.2% of tallgrass prairie occurs in locations > 1 600 m (1 mi) from a fragmenting land cover type, similar to the conclusions based on minimum dynamic areas of remaining prairie (see Fig. 1 in Samson et al. 2004). Thus, our land cover analyses (see Tables 1 and 2) reveal that more of the eastern Great Plains remains in rangeland cover than previously thought, but that remaining rangelands still predominantly occur in small, highly fragmented patches that likely contain substantially altered plant species composition relative to the historic condition. Fragmentation of this magnitude clearly has the potential to alter movements and metapopulation dynamics of a broad range of fauna in the region. Linking these patterns more directly to the ecology of specific species will require more detailed analyses of specific regions and landscape than we can provide here, but our land cover and fragmentation results are available to support such efforts (https://gpsr.ars.usda.gov/greatplainslandcover/). At broader spatial scales, we emphasize that even in the western Great Plains, where > 50% of the mixedgrass, shortgrass, and mesquite savanna regions persist as rangeland, the spatial distribution of rangelands is still highly fragmented. In both northern and southern mixed grass, < 6% of the

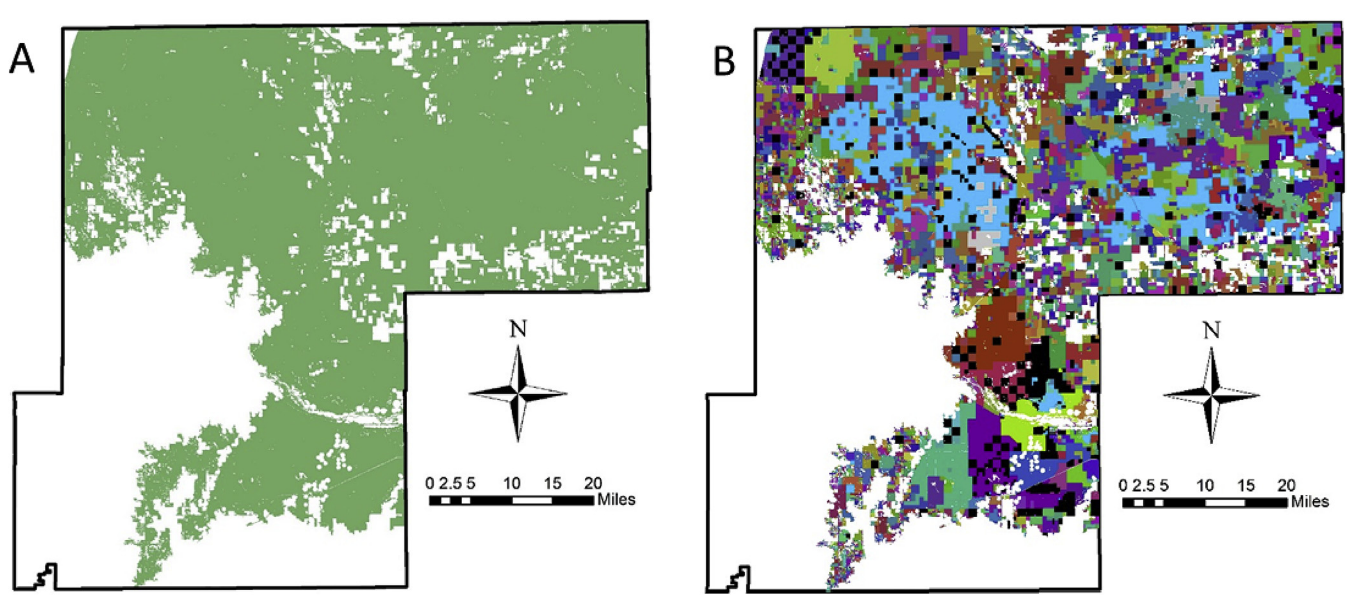

Figure 6. The distribution of large, contiguous areas of rangeland in Weld County, Colorado when viewed as a single land cover type (*green polygons* in map A) or when viewed in terms of individual landowners (*polygons of varying colors* in map B). In map B, each color represents a different landowner, where *light blue* represents federal ownership (Pawnee National Grassland) and *black* represents lands owned by the state of Colorado. Although the northeastern portion of Weld County appears to contain the largest contiguous block of rangeland, this portion of the county contains a complex mosaic of landowners. In contrast, some of the largest contiguous blocks of rangeland under a single ownership are located in the northwestern and southcentral portion of the county. Land ownership patterns are a potential additional source of fragmentation for some native species. For example, black-tailed prairie dogs are controlled on the lands represented in *black* and on many of the private lands of varying colors, whereas lands depicted in *light blue* are managed in the opposite manner.

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Table 3
Amount and percentage of area of each of 9 National Grasslands occurring > 800 m (0.5 mile) from a property boundary.

National grassland	State	Total area (ha)	Area (ha) > 800 m from property boundary	% of Area > 800 m from property boundary
Buffalo Gap	SD	265 102	98 007	37.0
Little Missouri	ND	451 319	142 859	31.7
Sheyenne	ND	33 200	8 554	25.8
Thunder Basin	WY	224 005	56 023	25.0
Rita Blanca	OK/TX	38 119	8 900	23.3
Comanche	CO	179 662	38 160	21.2
Grand River	SD	75 800	15 174	20.0
Pawnee	CO	77 954	9 468	12.1
Black Kettle	OK	13 464	46	0.3

entire landscape consists of rangeland > 1.6 km (1 mi) from a fragmenting land cover type. Only in the shortgrass steppe and Nebraska Sandhills do we begin to identify some larger, contiguous rangeland landscapes, with 12% and 27% of the region > 1.6 km from fragmenting land cover, respectively. These findings indicate that efforts to restore rangelands in a manner that enhances native plant diversity and does so in a spatial context that enhances connectivity among conserved and restored rangelands are central to conserving Great Plains biodiversity.

Differences between the results of our “best case” versus “worst case” scenario analyses also support this conclusion. For example, the estimated total extent of rangeland in the bluestem/needle/wheatgrass, bluestem/grama, and sandsage/bluestem vegetation types declined by 6.3%, 4.8%, and 4.9%, respectively, under our worst relative to best case scenarios. Furthermore, in all three aforementioned vegetation types, the amount of rangeland > 800 m from fragmentation was more than halved under the worst relative to best case scenario. These results indicate that the inclusion of the UGC category, which likely includes CRP and other restored grasslands, in the definition of “rangeland” substantially reduced fragmentation, such that both the amount and spatial location of restoration efforts are important in reconnecting existing rangelands. In addition, we note that improvements in remote sensing and ground-based mapping of rangeland composition and conservation value could reveal new opportunities to enhance landscape connectivity. Hereafter, we highlight several potential opportunities to reverse the pattern of rangeland loss and fragmentation illustrated in Figures 2 and 3.

Opportunities: Stitching Grasslands Back Together

Incentive Programs to Restore Grasslands and Native Wildlife

The CRP, signed into law as part of the Food Security Act of 1985, is the largest voluntary, private-lands conservation program in the United States and represents a key mechanism for grassland restoration in the Great Plains. CRP enrollment in the Great Plains reached a peak of 10.6 million ha (26.3 million acres, or 5.5% of the Great Plains) in 2007 and has since declined annually, with 6.7 million ha (16.5 million ac; 3.2%) of the Great Plains enrolled in 2017. Although we have not conducted a spatial analysis, the 3.2–4.5% of the Great Plains enrolled in CRP over the past decade likely comprises much of the area mapped as “uncertain grassland or cropland” by the fNLCD-CDL product (see Table 1) and likely contributes to the substantial difference in degree of rangeland fragmentation quantified by our best case versus worst case scenarios (see Table 2 and Figs. 3–4).

Over time, the focus of CRP has shifted from primarily a soil erosion and land retirement program to one that targets a combination of water quality improvement, soil erosion prevention, and wildlife habitat improvement on environmentally sensitive agricultural lands, via enrollment in a ten- or fifteen-year contract. The early days of CRP saw 9.4 million ha (23.2 million ac) enrolled in the Great Plains by 1990, most planted to grass monocultures, often using non-native grass species whose seeds could establish quickly and were inexpensive. Furthermore, these grasslands remained ungrazed and unburned in most years, in part due to the program’s focus on prevention of soil erosion, thereby suppressing the historic disturbance regime and limiting the value of CRP grasslands to native wildlife (King and Savidge 1995; McCoy et al. 1999).

Importantly, 46 different practices are now eligible for application to lands enrolled in either a general (competitive enrollment) or continuous (noncompetitive) signup nationwide, with priority being placed on the types that offer the highest diversity of native grasses, forbs, and shrubs. As of July 2018, 5.6 million ha (14.0 million acres) nationwide were enrolled in general CRP and an additional 3.3 million ha (8.1 million acres) were enrolled in continuous and other targeted contracts, with most of these acres being in the Great Plains. Thus, CRP practices have substantial potential to influence patch size and connectivity of rangeland habitats.

Recognizing opportunities for improvement to biodiversity, the CRP program later placed priority on enrollment offers that targeted establishing or improving stand diversity. Midcontract management practices (disturbance, such as high-intensity grazing, prescribed fire, or tillage, often followed by interseeding additional grass and/or forb species) were originally optional but have now become required practices. Such management can shift low-diversity CRP stands toward more diverse grasslands and enhance opportunities for grazing and fire to become functional processes within CRP grasslands. Unfortunately, the types of practices applied and the frequency of midcontract management varies substantially from state to state and often does not include prescribed burning (FSA 2018a). We suggest that a major opportunity for increased conservation of pattern, process, and biodiversity is the broader incorporation of fire and grazing into midcontract CRP management in all Great Plains states.

Another underused opportunity is transitioning of lands enrolled in CRP to working rangelands that will not be recultivated when CRP contracts expire. One recent advance is the CRP Grasslands signup opportunity, authorized by the 2014 Farm Bill, which allows landowners and operators to protect grassland, including rangeland and pastureland, while maintaining the areas as working lands through 14- or 15-yr contracts (FSA 2018b). CRP Grasslands emphasizes support for grazing operations to maintain and/or improve plant and animal biodiversity. Participants retain the right to conduct common grazing and haying practices within the parameters set forth in the conservation plan developed with assistance from NRCS. CRP lands with contracts nearing expiration are targeted for enrollment, and cost share is available for infrastructure such as fencing and water development to maintain the grass cover, which aids in incorporating these lands into a grazing program.

One example of an advance in grassland landscape restoration comes from a grass-roots effort, Preserving CRP Grassland Benefits in Western Nebraska, which could serve as a model for broader application in the Great Plains. This locally led effort sought to convert lands expiring from CRP in the early 2010s into grazed grasslands. At the time, 106 800 of the 154 600 ha of CRP in the Nebraska Panhandle were set to expire between 2009 and 2012, with no option for CRP contract renewal. Recognizing the threat that these lands could revert to cultivated cropland, the three Natural Resource Districts (NRDs) in the Panhandle, the Natural Resources Conservation Service (NRCS), the Nebraska Game and Parks Commission (NGPC), and several other conservation entities developed a partnership to promote the maintenance of expiring CRP as grassland using livestock grazing. Cost-share incentives for grazing infrastructure and education on grazing management were components. A Nebraska Environmental Trust Fund Grant was secured to help with these efforts. Even though CRP enrollment was reauthorized during the project, 8 321 ha (on 102 different projects) benefitted over a 6-yr period as producers chose to convert them to working grasslands rather than entering into another CRP contract.

The Lesser Prairie-Chicken is one species that has benefitted dramatically from CRP grasslands. One key to this success was the spatial targeting of CRP enrollments with appropriate vegetation diversity in counties with both existing Prairie-Chicken habitat and populations and where CRP could enhance connectivity and size of grassland patches (Spencer et al. 2017; Sullins et al. 2018). Recent work shows that annual survival of Prairie-Chickens is greater in landscapes with larger grassland patch size and greater patch richness, as well as in portions of those landscapes farther from fences (Robinson et al. 2018). Given that new enrollment of lands into the CRP program is limited, targeting enrollment in locations that increase grassland patch size is important (Robinson et al. 2018). In addition, as discussed by Spencer et al. (2017) "one approach to retain CRP fields as grassland, but in the face of reduced CRP contract enrollment, is to retain the primary land use of these as working grasslands (NRCS 2016)." The use of the Environmental Quality Incentives Program (EQIP) to share the costs of necessary infrastructure such as boundary fencing and water sources can enhance the conversion of these lands to working grasslands (NRCS 2016), while also recognizing the need to consider the potential effects of fencing density and type on wildlife (Patten et al. 2005; Jakes et al. 2018; Robinson et al. 2018). Similar efforts facilitated by nongovernmental organizations that address other grassland-breeding birds (e.g., Ducks Unlimited) enhance these types of transitions. Habitat modeling for other grassland birds can also help guide the selection of localities where transitions of CRP to working grassland should be emphasized (e.g., Lipsey et al. 2015; Niemuth et al. 2017). For example, spatial targeting of CRP enrollment in landscapes with existing tallgrass prairie can enhance habitat and abundance of Henslow's sparrow, another grassland bird of conservation concern (Herse et al. 2017).

Another innovative application of the EQIP program is the NRCS Black-Footed Ferret Special Effort, which provided technical assistance and direct financial support to ranchers who agree to manage a portion of their land to maintain BTPD populations and allow the reintroduction of black-footed ferrets (BFFs). The program's goal was to promote voluntary, incentive-based conservation of these species on private and tribal lands. This program was particularly valuable in that it changed the management objectives (and associated practices) on a property, without necessarily adding fragmenting infrastructure such as fencing. A key limitation is uncertainty in how to maintain contracts over longer time scales than a single contract. To the extent that such programs can be implemented across multiple adjacent landowners, or with landowners adjacent to other lands managed for prairie dog conservation, there is great potential to increase the size of grassland patches managed in a common framework. Continued modifications that allow the CRP and EQIP programs to address landscape-scale habitat needs of Great Plains fauna are needed, particularly through spatial targeting of key locations or landscapes in order to link together existing grasslands, rather than simply addressing field- or pasture-scale soil and water conservation.

Landownership Patterns and Cross-Boundary Management

The complexity of the land ownership pattern displayed for grasslands in Weld County, Colorado (see Fig. 6) is typical of many Great Plains counties. The coordination of management objectives across property boundaries and reductions in the ratio of boundary length to the area of properties managed for biodiversity conservation will clearly enhance the capacity for grazers and fire to move across broader landscapes and interact with the inherent variability in soils, topography, and weather patterns. Most public lands within the Great Plains currently occur in highly fragmented spatial patterns. For example, analysis of boundary patterns in nine National Grasslands managed by the US Department of Agriculture−Forest Service extending from North Dakota to New Mexico shows that only two (Buffalo Gap and Little Missouri National Grasslands) have > 30% of their land base occurring in areas > 800 m (0.5 mi) from a National Forest System property boundary (Table 3). This land ownership pattern creates major challenges for the conservation of controversial species such as BTPDs and mobile species such as elk, for which adjacent private and state lands can have nearly opposite management objectives.

Boundary management for BTPDs can be an especially significant source of conflict, as their colonies can frequently expand across distances of 800 m in 1−2 yr (Augustine et al. 2008), and management options to prevent such movement can be expensive and contentious (Luce et al. 2006; Miller et al. 2007). It is notable that the Buffalo Gap National Grassland currently has the greatest proportion of its land base occurring in contiguous blocks of grassland distant from property boundaries (see Table 3). This resulted from a program to conduct land exchanges (i.e., exchanges of National Forest System and private land of equal value) to reduce boundary complexity over the past 2 decades. This effort, combined with portions of Buffalo Gap National Gap occurring adjacent to the Badlands National Park and the Pine Ridge Indian Reservation, has facilitated the recovery of BTPD in this landscape and supports the most successful BFF reintroduction site in the Great Plains (US Fish and Wildlife Service 2013). Similarly, lands originally granted from the federal government to the states upon their creation were in the form of two sections (2.56 km^2 properties) within each township of the Great Plains, creating a fragmented state land ownership pattern. Ongoing efforts to conduct land exchanges in states such as Colorado have enhanced the development of landscape-scale Stewardship Action Plans for many properties and allowed for creation of Stewardship Trust Lands that are subject to a higher standard of care, planning, and management by both the State Land Board and lessees. Such plans and trust lands address habitat needs of species of conservation concern and enhance livestock and native grazer movement, as well as metapopulation dynamics of sedentary species, at spatial scales far larger than the original 2.56 km^2 properties.

Finally, the vast majority of Great Plains grasslands are privately owned and managed by people who care deeply about conservation of the land but also need to make a living. Managers of private rangelands often acknowledge the importance of wildlife conservation but place this as a far lower priority than livestock production (Kachergis et al. 2014; Sliwinski et al. 2018). Engaging these people to manage disturbance regimes at larger spatial scales will require acknowledging that domestic livestock grazing can function as an essential rather than a degrading component of Great Plains disturbance regimes. Programs and strategies to enhance livestock movement at greater spatial scales and increase spatio-temporal variability in grazing intensity can enhance contributions

Please cite this article as: Augustine, D et al., Thinking Like a Grassland: Challenges and Opportunities for Biodiversity Conservation in the Great Plains of North America, Rangeland Ecology & Management, https://doi.org/10.1016/j.rama.2019.09.001

to wildlife conservation (Fuhlendorf et al. 2006; Derner et al. 2009; Toombs et al. 2010). Purchases of contiguous rangelands by nongovernmental organizations and/or establishment of conservation easements to consolidate private properties and connect existing public lands has also made important contributions to the conservation of native grazers (and in some cases increased utilization of prescribed fire) and has increased notably in use and scale nationwide over the past decade (Owley and Rissman 2016).

The need to coordinate management objectives and practices across property boundaries and jurisdictions to conserve Great Plains fauna has been recognized by many authors, organizations, managers, and agencies (e.g., Samson and Knopf 2004; Fuhlendorf et al. 2012; NRCS 2016). Yet cross-jurisdictional management remains a major challenge within a region that is predominantly private land intermingled with public lands managed by 11 states, 3 provinces, > 1 000 counties and administrative divisions, and at least 4 different federal agencies in the United States alone. Samson and Knopf (2004) proposed that establishment of more meaningful state and federal agency designs is necessary to advance Great Plains grassland conservation. In particular, they suggested that consolidation or realignment of federal agencies and improved state-federal collaboration would reduce conflicting approaches to species conservation and enhance conservation cost-effectiveness. Progress in this regard has been limited over the past 15 yr, but the history of efforts to conserve the Lesser Prairie-Chicken in the southern Great Plains suggests some opportunities to advance cross-boundary management efforts. In some cases, even small nature reserves or other public lands, when managed in a manner that includes effective outreach and interactions with surrounding private landowners, can serve as catalysts for landscape-scale conservation and directly enhance wildlife conservation (Miller et al. 2012). Success in such efforts relies on application of novel advances in the science and practice of engaging landowners. Outright purchase of private ranches and conversion to conservation-oriented operations can in some cases also produce valuable outcomes for wildlife conservation that include increasing the scale and pattern of grazing by both livestock and bison (e.g., Kohl et al. 2013), but such efforts will be enhanced where they are linked with an understanding of current economic, political, and cultural issues within the landscape (Miller et al. 2012; Davenport 2018).

The need for cross-boundary management frameworks in the Great Plains was formally recognized > 20 yr ago, when in 1997 the US Fish and Wildlife Service (USFWS) announced an initiative called the *High Plains Partnership for Species at Risk* (HPP). This initiative encouraged landowners, agricultural organizations, and conservation groups in actions to benefit the Lesser Prairie-Chicken and other declining wildlife species in the southern Great Plains. The initiative was born out of the five state wildlife agencies forming the Lesser Prairie-Chicken Interstate Working Group (LPCIWG), which developed a region-wide conservation strategy for this species and many other species associated with LPC habitat. The group worked with the Great Plains Partnership of the Western Governors' Association and received funding from the National Fish and Wildlife Foundation to coordinate a partnership of diverse stakeholders to advance region-wide, proactive, voluntary solutions to the decline of the Lesser Prairie-Chicken. The Initiative identified measures that would benefit the Lesser Prairie-Chicken and promote voluntary participation in habitat restoration projects, including a series of demonstration projects in Lesser Prairie-Chicken range, technical and financial assistance to landowners for habitat restoration and improvement projects, and research into the relationship between Lesser Prairie-Chicken habitat needs and range management practices.

From 1998 to 2003, momentum for this effort grew. Letters to the USFWS Director at the time highlighted the accomplishments, which included > 36 000 ha of conservation efforts across the five states within the range of the Lesser Prairie-Chicken. While initial efforts demonstrated interest by a broad spectrum of stakeholders, it lacked participation from the energy development and delivery sectors and eventually dissolved due to a lack of dedicated funding. Although conservation opportunities were directed at landowners, proponents did not engage with oil and gas companies, rural electrical cooperatives, and wind-power companies. Another limitation of the initiative was to clearly demonstrate how the funds invested would mitigate the need to list the Lesser Prairie-Chicken under the Endangered Species Act. Proponents did not present a strategic conservation plan that would clearly allow for other economically important industries to continue across the landscape and contribute to the conservation of the species. Finally, promotional materials about the effort displayed the action area as being the entire Great Plains, giving the impression that local actions would have minimal contribution to initiative goals while potentially restricting developmental activities.

Over the next decade, the LPCIWG transitioned from collecting information on Lesser Prairie-Chicken ecology, as it had done during the HPP, to evaluating conservation actions benefitting Lesser Prairie-Chickens. This ultimately led to the Lesser Prairie-Chicken Range-wide Conservation Plan (LPCRWP; Van Pelt et al. 2013) developed by the LPCIWG and collaborators, which incorporated several lessons from the HPP experience. One important modification was to evaluate the location and juxtaposition of potential habitat, with the intent that restoration would be implemented in the same habitat types being impacted by management or development activities and would enhance habitat connectivity. Also, measures were developed to ensure the quality of the habitat being managed or restored was equal to or better than the area being impacted. Finally, the LCPRWP conservation effort was depicted visually using the Western Association of Fish and Wildlife Agencies' Crucial Habitat Assessment Tool (CHAT), allowing land managers to target their activities and visualize the contribution to the broader landscape. Finally, there was recognition for the need for a shifting mosaic of grassland conservation efforts across the landscape to address changing precipitation patterns and prolonged droughts, instead of focusing investments on permanently protected areas, which could become unsuitable with changing climate. We suggest that efforts to restore working rangelands in portions of the Great Plains outside the LPC range be spatially targeted in a similar manner and use visualization tools that enhance communication of broader, landscape-scale conditions, and goals among agencies, landowners, businesses, and the public. The development of rangewide plans with similarly associated institutions as the LPCRWP for species such as BTPD and other prairie grouse (Greater Prairie-Chicken, Sharp-Tailed Grouse, and Greater Sage-Grouse) would be one potential means to enhance collaboration and coordination of grassland restoration in the remainder of the Great Plains. Consistent funding sources and commitments at federal, state, and local levels may help ensure such plans and institutions do not follow the fate of the HPP.

Management Implications

Across the Great Plains, conservation of native fauna is constrained by the loss and fragmentation of rangelands, as well as the limited spatial scales over which fire and fauna can move, interact, and influence Great Plains vegetation. Here, we quantified contemporary patterns of rangeland patch size and fragmentation across all the major historic grassland, shrubland, and savanna vegetation types in the US portion of the Great Plains (https://doi.org/10.1016/j.rama.2019.09.001). Our maps and analyses identify significant opportunities for landscape-scale conservation and restoration in the western half of the Great Plains. Continued restoration of marginal croplands to grassland, in spite of declining opportunities for enrolling lands in CRP, will depend on expanding innovative programs that transition existing CRP to working rangelands, managed with grazing and fire to support enhanced plant and habitat diversity. Most public land in the Great Plains remains highly fragmented and intermingled with private lands that often have conflicting goals for biodiversity conservation. Coordination of management objectives across broader landscapes, as has occurred in South Dakota on portions of Buffalo Gap National Grassland adjacent to the Badlands National Park and the Pine Ridge Reservation, is critically needed in additional portions of the Great Plains to facilitate conservation of the full suite of native grazers, including prairie dogs and their associated species. In addition, our land cover analyses identify many key areas of contiguous rangeland in predominantly private ownership, where conservation may be enhanced through voluntary incentive programs that provide compensation for harboring species or creating habitats that conflict with traditional livestock production objectives. The development of adequately funded institutions to facilitate cross-boundary management and restoration within broad landscapes could rely on lessons learned in the ongoing efforts to conserve landscapes for the Lesser Prairie-Chicken. All of these efforts rely on accelerating the slow but ongoing shift from thinking about and managing grasslands at the scale of individual pastures to focusing restoration and conservation efforts at the scale of dynamic grassland landscapes.

Acknowledgments

We thank Justin Derner for discussions and suggestions on this manuscript, the organizers of the Great Plains Grassland Summit for creating this special edition, and Rowan Gaffney for advice on land cover analyses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2019.09.001.

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Please cite this article as: Augustine, D et al., Thinking Like a Grassland: Challenges and Opportunities for Biodiversity Conservation in the Great Plains of North America, Rangeland Ecology & Management, https://doi.org/10.1016/j.rama.2019.09.001