

Disturbance shapes avian communities on a grassland–sagebrush ecotone

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Abstract. Ecotones, or transitional zones between ecosystems, are often hotspots for biodiversity and targets for conservation. Where the Great Plains meet the sagebrush (*Artemisia* spp.) steppe, an opportunity exists to conserve habitat for the two most imperiled avian guilds in North America, grassland and shrub-steppe birds. This ecotone creates a unique challenge with respect to the management of disturbance processes, such as fire and grazing, because grassland and sagebrush-shrubland birds respond quite differently to disturbance. To address this management challenge and maximize conservation opportunities, we examined the responses of grassland and sagebrush bird communities to disturbance at a grassland–sagebrush ecotone in northeast Wyoming, USA. Specifically, we surveyed bird communities on active black-tailed prairie dog (*Cynomys ludovicianus*) colonies and burned areas, as well as on paired undisturbed points in 2016 and 2017. Bird community structure varied in response to both the presence and type of disturbance. Although alpha diversity of avian species was highest on undisturbed sites and burned areas, only prairie dog colonies provided breeding habitat for the imperiled shortgrass-obligate mountain plover (*Charadrius montanus*), and species turnover (beta diversity) was greatest between on-colony and off-colony points. Furthermore, bird communities were shaped by both disturbance-dependent (e.g., disturbance age) and disturbance-independent (e.g., topography and soils) landscape features. Managers must balance the benefits of high species diversity in undisturbed sagebrush with habitat requirements of other imperiled species like the mountain plover. This may entail prioritizing the amount and distribution of disturbances in relation to population goals for species of conservation concern while simultaneously maintaining a mosaic of all three patch types in this landscape.

Key words: biodiversity; Brewer's sparrow; ecosystem engineer; fire; grasshopper sparrow; mountain plover; prairie dog; topo-edaphic.

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INTRODUCTION

Disturbance processes interact with underlying topo-edaphic heterogeneity to create unique vegetative patterns on the landscape, which in turn influence future patterns of disturbance (Risser et al. 1984, Turner et al. 2001). This pattern–process link is at the center of landscape ecology (Turner 1989), but a pattern–process

perspective has only recently been applied to the study and management of wildlife communities, especially in rangeland systems (Fuhlen-dorf et al. 2017). To conserve the diverse wildlife communities native to rangeland systems, it is critical to understand how disturbance regimes interactively shape and are shaped by wildlife habitat resources (Fuhlen-dorf et al. 2012).

In North American rangelands, grassland and shrubland bird guilds evolved under different historic disturbance regimes. Disturbances were common in the Great Plains, which evolved with drought, fire, ungulate grazing, and burrowing mammals (Samson and Knopf 1994, Anderson 2006). In some parts of this region, disturbances were frequent, intense, and interactive, creating shifting vegetation mosaics that supported diverse habitats and led to increased biodiversity at broad scales (Fuhlendorf and Engle 2001, Skagen et al. 2018). North American grassland birds evolved in the context of these frequent disturbances (Brawn et al. 2001), and some species benefit specifically from fire as well as biotic ecosystem engineering via grazing by large ungulates or burrowing and clipping action by prairie dogs (Johnson 1997, Grant et al. 2010, Augustine and Derner 2012, Ahlering and Merckord 2016). Further, vegetation heterogeneity engendered by patchy disturbance has been linked to higher bird diversity in tallgrass, mixed-grass, and shortgrass prairies (Coppedge et al. 2008, Augustine and Baker 2013, Augustine and Derner 2015).

In contrast, shrubland birds, especially those dependent on sagebrush (*Artemisia* spp.), are less tolerant of disturbance (Knick et al. 2005, Hess and Beck 2012, Carlisle et al. 2018). Sagebrush systems evolved with less frequent and intense disturbance, generally lacking the vegetation clipping of black-tailed prairie dogs (*Cynomys ludovicianus*; Hoogland 2013), and with reduced frequency of fire (Baker 2006). Most sagebrush species cannot resprout following fire (Shultz 2009), so recovery post-burn is on the scale of decades to centuries, instead of years to decades as in grasslands (Baker 2006, 2011, Porensky et al. 2018). Thus, whereas small disturbances may benefit some sagebrush-obligates birds, these species tend to decline with high rates of disturbance (Knick et al. 2005, Beck et al. 2012, Carlisle et al. 2018).

In both ecosystems, habitat loss and shifting disturbance regimes have led to major declines in bird abundance. Following European settlement of the Great Plains mainly during the 1800s, many natural disturbances, including native ungulate herbivory, wildfires, and burrowing mammals, were suppressed to enhance agricultural outputs (Samson and Knopf 1994,

Fuhlendorf and Engle 2001, Davidson et al. 2012, Hoogland 2013, Sayre 2017). These changes may have served to homogenize rangeland landscapes in terms of vegetation structure and species composition (Fuhlendorf and Engle 2001), with negative consequences for many wildlife species, in particular aridland birds (Brennan and Kuvlesky 2005, Fuhlendorf et al. 2006, Sauer et al. 2017). In contrast, in the sagebrush steppe, frequencies of disturbances such as wildfire have increased dramatically (Condon et al. 2011, Balch et al. 2013), destroying the sagebrush on which many bird species rely (Knick et al. 2005, Chambers et al. 2017).

Thus, despite their differing habitat and disturbance requirements, grassland and shrubland bird species are both in critical need of conservation. There exists an opportunity to manage and conserve both of these imperiled bird guilds within the Thunder Basin National Grassland, located in northeastern Wyoming at the ecotone between the Great Plains and sagebrush steppe. While ecotones may be complex from an ecological standpoint, they are crucial foci for managers, as they are often hotspots for biodiversity (Risser 1995). The Thunder Basin landscape currently supports at least 20 bird species listed by the state of Wyoming as Species of Greatest Conservation Need (SGCN; Wyoming Game and Fish Department 2016), in addition to black-tailed prairie dogs, which have experienced approximately a 98% range-reduction following European settlement (Mulhern and Knowles 1997) and are also a SGCN in the state. Some species of concern, including the mountain plover (*Charadrius montanus*), often rely on disturbed habitat for nesting (Augustine and Derner 2012, Goguen 2012) and benefit from prairie dogs or fire. Conversely, imperiled sagebrush-obligates including the sage thrasher (*Oreoscoptes montanus*), Brewer's sparrow (*Spizella breweri*), and the greater sage-grouse (*Centrocercus urophasianus*), which was recently removed from the list of species warranted for federal listing under the Endangered Species Act in 2015 (USFWS 2015), may respond poorly to disturbances that destroy sagebrush plants.

Within the Thunder Basin ecotone, juxtaposed disturbance regimes and substantial heterogeneity in topography and soils (Gosz 1993, Risser 1995) create highly heterogeneous vegetation structure, ranging from mature shrublands to barren prairie

dog colonies, at a relatively fine scale (<10 km). However, it is unclear how grassland and shrubland bird communities that co-occur and interact in this landscape may respond to disturbances and habitat variability at this scale. Identifying how different types of disturbance impact multiple bird species of conservation concern is critical for effective management and conservation in this avian biodiversity hotspot.

To evaluate the consequences of multiple forms of disturbance for a diverse, co-occurring suite of birds in Thunder Basin, we examined avian community response to historic wildfires and active prairie dog colonies within the grassland–sagebrush ecotone. We specifically asked: (1) How do bird communities and alpha diversity (site level) differ between two types of disturbance (burned areas, prairie dog colonies) and undisturbed habitat? (2) What disturbance-dependent and disturbance-independent factors shape the bird community? (3) How do the size and timing of disturbance (time since disturbance; disturbance duration) influence bird communities? and (4) How does beta diversity (species turnover) vary in relation to fire and prairie dog colony disturbances?

We hypothesized that presence vs. absence of disturbances (fire or prairie dogs) would be the strongest driver of divergence in bird community composition and that disturbance type (fire vs. prairie dogs) would additionally predict significant but less dramatic differences in community composition. Furthermore, we anticipated that both disturbance types would reduce species richness relative to communities in undisturbed habitats (due to reduced vertical structure; MacArthur and MacArthur 1961), but that disturbed habitats would support unique species, leading to increased beta diversity across the landscape. Alternatively, we examined whether disturbance-independent factors, particularly underlying topo-edaphic heterogeneity, could mitigate or mask the effects of disturbances, or whether variation among patches with the same disturbance type could be similar to or greater than variation among patches with different disturbance history. Finally, we tested two hypotheses regarding the size and duration of disturbances. First, we hypothesized that larger disturbances would have more distinctive bird communities because they provided a greater

area of habitat distinct from the matrix. Second, we hypothesized that disturbance duration would affect community structure on prairie dog colonies but not burned areas, because vegetation communities remain relatively stable, dominated by native perennial grasses, for decades after fire (Porensky and Blumenthal 2016, Porensky et al. 2018).

METHODS

Study area

Our study was conducted within the U.S. Forest Service (USFS)–Thunder Basin National Grassland in Converse, Weston, and Campbell counties, Wyoming (Fig. 1). Mean annual precipitation ranged from 25 to 35 cm, and it generally fell during spring and summer (Porensky et al. 2018). Dominant shrub species included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), greasewood (*Sarcobatus vermiculatus*), broom snakeweed (*Gutierrezia sarothrae*), and other sagebrush species. Common graminoids included blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comata*), and threadleaf sedge (*Carex filifolia*). Prairie dog colonies had a high proportion of bare ground and were dominated by western wheatgrass, plains prickly pear (*Opuntia polyacantha*), and short-lived forb species.

Study design

In 2016 and 2017, we conducted point counts for birds on prairie dog colonies and paired off-colony sites, as well as on burned areas and paired off-burn sites. We sampled 33 colonies (40 point-pairs total) and 14 burned areas (37 point-pairs total). Spatial perimeters for fires were obtained from the USFS, and prairie dog colony perimeters were mapped by the USFS and researchers in 2015 and 2016. Historic wildfires ranged in size from approximately 5 to 3500 ha, and colonies ranged from 6 to 4000 ha. Fires occurred between 5 and 43 ($\bar{x}$ = 14.6) years prior to the project, and colonies, which were all active during the study, were established between 0 and 15 ($\bar{x}$ = 5) years before our research. For prairie dog colonies, we utilized data from 33 larger transects randomly placed perpendicular to colony edges, composed of 5–8 points (depending on colony size) spaced apart by 250 m.

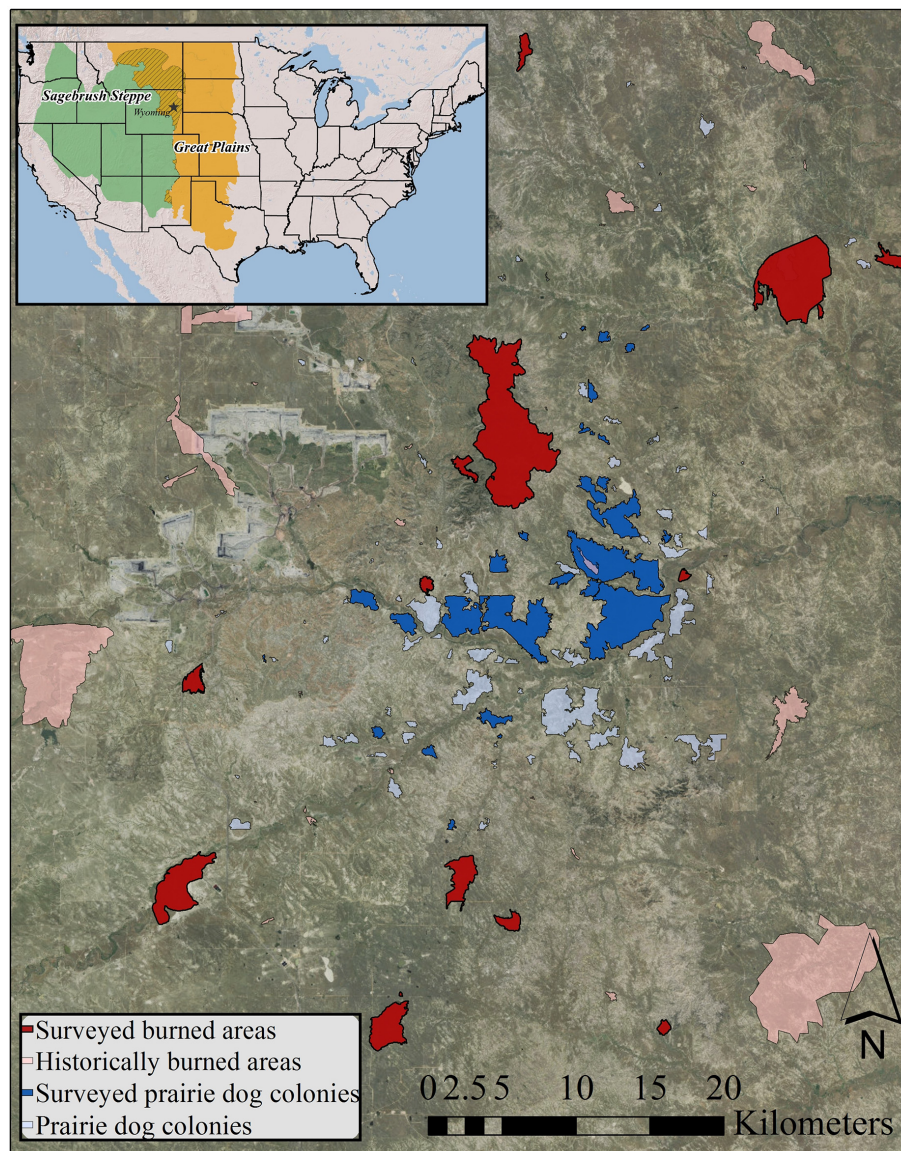


Fig. 1. Location of historically burned areas and active prairie dog colonies in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Surveyed patches shown in bold colors. Inset: location of the Thunder Basin National Grassland at the ecotone between the Great Plains and the sagebrush steppe.

On- and off-colony paired points for our study were randomly selected from each of these transects, such that only two points of each transect were included, and inter-point distances ranged between 0.25 and 1.25 km. Survey locations on burned areas also represented a subset of locations surveyed for a separate study (Porensky et al. 2018), which describes methodologies for sampling point selection. For both colony and

burned area points, the minimum distance between paired points was 150 m to minimize spatial overlap in surveys. We surveyed the avian community at each point once in each year between late May and late June. During each 6-min count, we recorded all species detected from the survey point. We recorded the distance and direction of each detection to facilitate distance sampling. Surveys occurred between 30 min

before sunrise and 10:00 hours on days without high wind or rain (Pavlacky et al. 2017). By traveling to many points via off-road vehicle, we ensured more effective detection of mountain plovers, which display more cryptic behavior in response to observers on-foot (Dinsmore 2003). Although our methods allowed us to detect plovers and passerines, they were not well designed to detect greater sage-grouse, which are better assessed through counts at leks, brood counts, winter flight surveys, or other techniques (Connelly et al. 2003).

We modeled detection probability for focal species using the program DISTANCE (version 6.2, Thomas et al. 2010). We used the complete point-count dataset described in the methods for analysis of focal species abundance, meeting the minimum requirement of 40 detections per species (Buckland et al. 2001). We examined covariates with the potential to affect detectability of each species including weather (temperature, wind, cloud cover), observer, and vegetation structure in a multiple covariate distance sampling framework. We used Akaike's information criterion adjusted for small sample sizes (AIC_c) and goodness-of-fit (chi-squared) to compare models (Burnham and Anderson 2002). Distance-adjusted densities were generated for each species using the top-ranked models. We then used densities to calculate Shannon's diversity (H'), which is a diversity metric that incorporates both species richness and evenness (Shannon 1948, Spellerberg and Fedor 2003).

Vegetation and landscape composition

In June and July each year, we measured visual obstruction (Robel et al. 1970) in two directions every 5 m along a 30-m transect centered on the point-count location ($n = 14$ readings per point per year). We recorded whether the obstructing vegetation was a shrub or herbaceous plant, allowing calculation of both total visual obstruction and herbaceous-only obstruction. We also collected shrub canopy cover data on transects in 2014–2015 using the line-intercept method (Canfield 1941, Herrick et al. 2009). Because shrub canopy cover likely varies minimally across years, we used these data to calculate percent sagebrush cover at each point for the entirety of our two-year study.

Avian habitat quality can be influenced by soils and topography both directly and indirectly

via vegetation responses to underlying topographic patterns (Renfrew and Ribic 2002, Lipse and Naugle 2017). Further, disturbance may be mitigated or enhanced by these same features (Reading and Matchett 1997, Augustine and Derner 2014, Harris and Taylor 2017). As such, we examined both soils and topography within 100 m of each point. We chose this 100-m scale as it was large enough to capture variation in these variables within a territory scale for most focal bird species, but also small enough to minimize overlap between adjacent point-count locations. We used a digital elevation model to generate average values of elevation, slope, and aspect, and we generated a topographic roughness index and topographic wetness index (Gesch 2007, Porensky et al. 2018). We used the SSURGO database (NRCS 2017) to characterize average soil texture (percent clay, silt, or sand) from 0 to 30 cm at each point, and we estimated average 30-yr maximum and minimum temperature at each point (PRISM 2014).

Data analyses

To assess the magnitude of bird community differences among burned areas, prairie dog colonies, and undisturbed habitat, we calculated permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) using the *adonis* function of the *vegan* package in R (Oksanen et al. 2017). As a non-parametric analogue to MANOVA, PERMANOVA partitions variance to generate a test statistic and uses permutational methods to generate *P*-values. We examined the effects of stratum type (prairie dog colony, burned area, undisturbed) and year on community structure.

We used non-metric multidimensional scaling (NMDS; Kruskal 1964) to examine patterns of community structure among disturbance types, disturbance traits, and site-level characteristics to test hypotheses related to questions 1 and 2 above. Non-metric multidimensional scaling is an unconstrained ordination technique that plots points based on the rank-order dissimilarity of multivariate data (here, avian community), such that points with similar communities occur in close proximity in ordination space. Goodness-of-fit of the ordination is determined by ordination stress (Kruskal 1964). We used Bray–Curtis distance as the measure of ecological dissimilarity

(Field et al. 1982). We then used the envfit function to examine correlations between variables associated with vegetation structure, topography, and soils with NMDS ordination axes. Vectors represent the direction of most rapid change in a given variable, with length corresponding to the level of correlation between the variable and ordination. Thus, vectors of the greatest length explain more variation in community structure. We present vectors with correlation coefficients (Oksanen et al. 2017) of $r^2 > 0.05$.

To understand whether abiotic factors and disturbance age or size modulated the community-level avian response to disturbance, we measured the distance in ordination space between points for communities located on prairie dog colonies and the centroid of the prairie dog cluster and similarly measured the distance between points on burned areas and the centroid of the burned area cluster in each year. We reasoned that points closer to centroids represented communities more typical of a given disturbance type, whereas those farther from centroids showed more variation, and thus more divergence from those semi-discrete communities. We then used a mixed-model framework to examine distance to centroid as a function of age of disturbance, size of disturbance, and a suite of abiotic variables including soils and topography, along with a random effect of patch identification (ID; unique identifier for each wildfire or prairie dog colony), to determine whether any of these variables affected community divergence. We modeled burned areas and prairie dog colonies separately, as age of colony has a very different meaning in terms of disturbance intensity compared with age of fire (i.e., colony age is more a metric of disturbance duration, whereas fire age indicates time since disturbance). Single-variable models of distance to centroid were compared using AIC_c (Burnham and Anderson 2002). Where multiple variables were $>2 AIC_c$ better than the null, we also explored interactions.

Finally, we calculated community dissimilarity (beta diversity; Anderson et al. 2011) between paired points on vs. off disturbance types using the betapart package in R (Baselga et al. 2017). The level of community dissimilarity between points on and off disturbed patches may be a function of disturbance type, underlying abiotic differences between points, or some combination

of these drivers. Therefore, we first explored single-variable models predicting community dissimilarity between inside–outside point-pairs, examining the effects of disturbance type and size, as well as the between-point difference in abiotic qualities (e.g., difference between maximum temperature) and biotic structure (e.g., difference in visual obstruction reading (VOR)). This variable set included all abiotic and biotic factors considered above (also see Table 1), as well as a univariate model of inter-point distance between pairs, because proximity may correlate with community similarity irrespective of other habitat traits (Legendre and Legendre 1998). We then examined all combinations of variables that occurred in the best univariate models.

Because we were interested in how disturbance may directly interact with topo-edaphic features within a patch, we also compared two-way interactions between disturbance type and abiotic variables at inside-patch points, to see if these interactions explained beta diversity better than disturbance type alone. All community dissimilarity models included a random effect of Patch ID. We did not explore models including more terms or interactions because of limitations in sample size.

Table 1. Descriptive statistics and correlations between vegetation or topo-edaphic variables and bird community structure (coordinates in NMDS ordination space) in 2016–2017, Thunder Basin National Grassland, Wyoming, USA.

Variable	Mean	Range	r^2	Pr ($>r$)
Visual obstruction (cm)	5.5	0.1–45.4	0.207	<0.001
Sagebrush (%)	4.7	0.0–62.6	0.188	<0.001
Mean roughness	1.1	0.1–5.2	0.142	<0.001
Herbaceous VOR (cm)	4.8	0.5–35.5	0.091	<0.001
Clay (%)	32.9	8.5–45.0	0.068	<0.001
Min temperature (°C)	0.2	–0.09–1.3	0.064	<0.001
Max temperature (°C)	15.5	13.9–16.1	0.059	<0.001
Sand (%)	38.3	17.0–66.6	0.043	0.002
Annual precipitation (mm)	322.1	288.6–335.4	0.035	0.006
Topographic wetness index	5.4	3.1–16.2	0.034	0.006
Aspect	168.7	2.2–359.5	0.021	0.041
Silt (%)	28.9	1.7–57.65	0.002	0.779

Note: NMDS, non-metric multidimensional scaling. Bolded variables were included as vectors in ordination space in Fig. 4.

RESULTS

We observed 50 species during the two years of study, which in addition to our focal species also included raptors, migrants, non-rangeland species (e.g., riparian birds), and eight species that were only detected once (Appendix S1: Table S1). We modeled distance-adjusted densities for the 11 most abundant grassland or shrubland species (Paige and Ritter 1999, Vickery et al. 1999), all of which were either ground or shrub nesters within the study area (Fig. 2). This community included ten birds recognized as species in steep decline by Partners in Flight (PIF 2017; Appendix S1: Table S2), five of which were also species of conservation concern within Wyoming (mountain plover, loggerhead shrike [*Lanius ludovicianus*], Brewer's sparrow, grasshopper sparrow [*Ammodramus savannarum*], and sage thrasher; see Fig. 2). Horned larks (*Eremophila*

alpestris) and western meadowlarks (*Sturnella neglecta*) made up the majority (>50%) of counts in all strata. We documented distinct differences among bird communities related to the presence and type of disturbance (Fig. 2). Mountain plovers were exclusively observed on prairie dog colonies, and horned larks reached their greatest abundance on prairie dog colonies (Fig. 2). Conversely, western meadowlarks and grasshopper sparrows reached their highest abundances on burned sites, and the latter was entirely absent on prairie dog colonies. Sagebrush-obligates, including the Brewer's sparrow and sage thrasher, were rare on both prairie dog colonies and burned areas and were most abundant on undisturbed sites.

We used distance-adjusted densities of these 11 avian species for multivariate community analyses. PERMANOVA indicated stark ($P < 0.001$, $F_{2, 304} = 24.04$) differences among communities

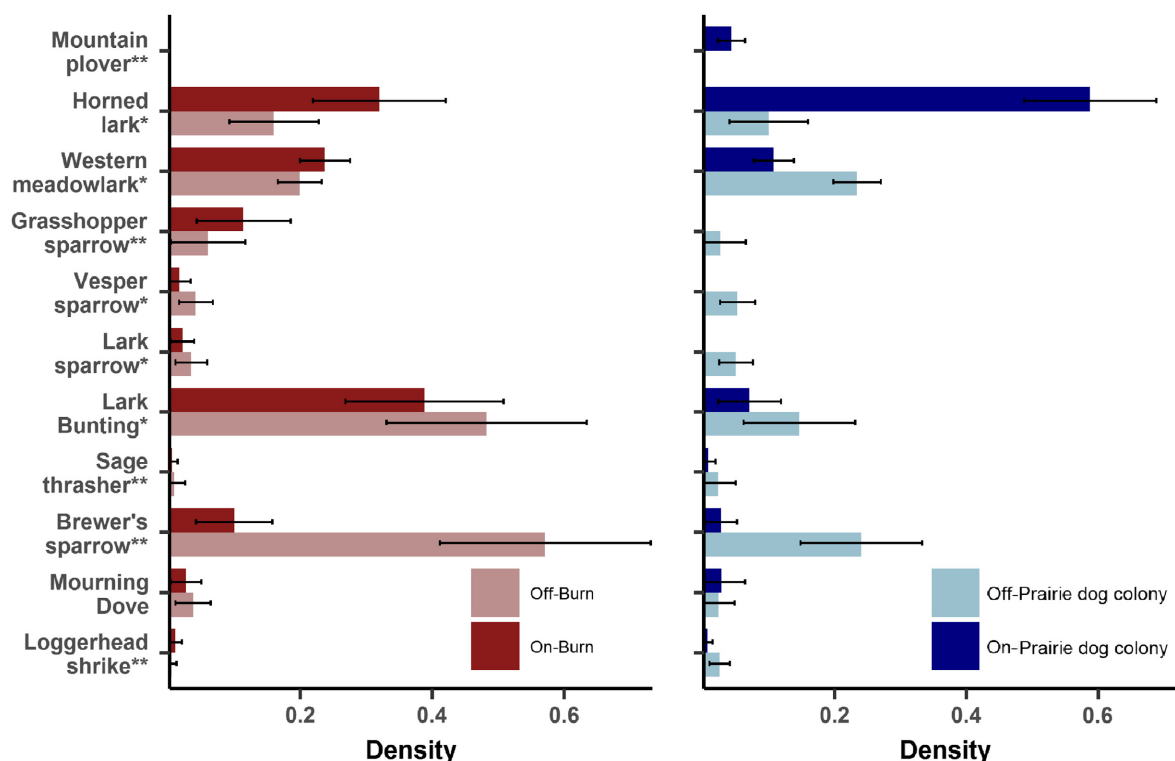


Fig. 2. Distance-adjusted densities (per ha) of 11 abundant avian species on and off fires (red) and off prairie dog colonies (blue) averaged across years, Thunder Basin, Wyoming, USA, 2016–2017. *Partners in Flight (PIF) species in decline (rank 4 or 5), and **species that are both PIF in decline and Species of Greatest Conservation Need in Wyoming.

on burned areas, prairie dog colonies, and undisturbed points, while differences between years were only significant at an alpha of 0.05 ($P = 0.02$, $F_{1, 304} = 2.69$). We found no evidence of an interaction between stratum type and year.

The NMDS ordination converged on a two-dimensional solution with stress of 0.15 and non-metric fit $R^2 = 0.977$. Disturbed sites scored lower on the second (vertical) axis, and bird communities on prairie dog colonies were the most distinct of the four types, in terms of both standard deviation hull overlap (Fig. 3) and species locations in ordination space (Fig. 4). Species locations in ordination space indicate groupings including shortgrass species (mountain plover and horned lark), mixed-grass species (western meadowlark and grasshopper sparrow), and species requiring some component of shrub cover (Brewer's sparrow, sage thrasher; Fig. 4). Nine of fourteen abiotic and vegetation predictors had an $r^2 > 0.05$ (Table 1) and were therefore mapped onto the ordination (Fig. 4). Disturbance-dependent and disturbance-independent site features varied among burned areas, prairie dog colonies, and undisturbed sites (Fig. 5). Prairie dog colonies showed the most distinctive vegetation structure in terms of extremely low visual obstruction and sagebrush cover, followed by burned areas (Fig. 5), but there were also some differences among undisturbed sites, mainly due to their location within the grassland (Figs. 4, 5).

Sage thrashers and Brewer's sparrows, most common on unburned sites, were associated with greater sagebrush cover and visual obstruction, and both lark buntings (*Calamospiza melanocorys*) and vesper sparrows (*Poocetes gramineus*) also trended in this direction (Fig. 4).

Loggerhead shrikes and mourning doves (*Zenaida macroura*) were associated with greater topographic roughness, slope, and greater minimum temperatures. Grasshopper sparrows, and to some extent western meadowlarks, were associated with burned sites. Finally, prairie dog colonies, which were associated with more clayey soils, higher maximum temperatures, lower vegetation structure and sagebrush cover, and gentle topography, supported peak abundances of mountain plovers and horned larks.

On average, bird communities varied slightly more among sites with prairie dogs than among burned sites ($\bar{x} = 1.29$ and $\bar{x} = 1.0$, respectively), as measured by our community convergence metric (i.e., distance from community points to centroids in ordination space). However, an examination of the different drivers of community convergence is more interesting; disturbance size and age predicted community convergence on prairie dog colonies, such that older and larger colonies tended to have more typical bird communities, while areas with greater average annual precipitation showed more community variation (Table 2). No models including the interactions of colony

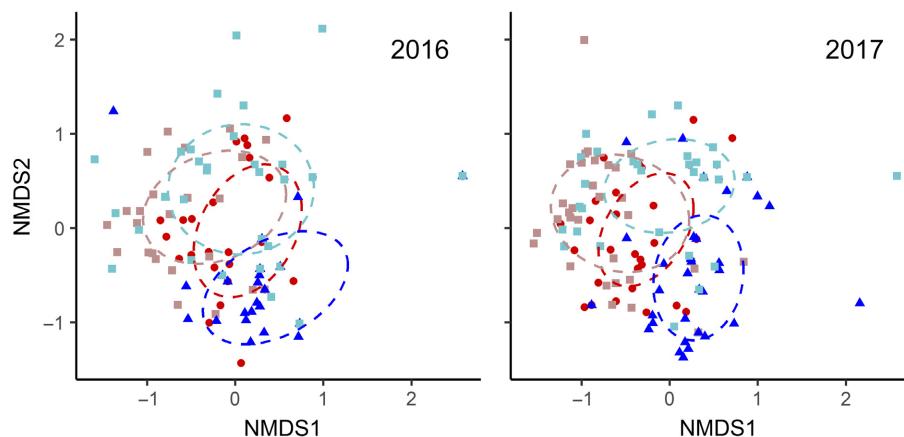


Fig. 3. Non-metric multidimensional scaling ordination representing bird communities in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Points represent bird communities on prairie dog colonies (dark blue triangles), off prairie dog colonies (light blue squares), on burned areas (dark red circles), and off burned areas (light red squares). Ellipses represent standard deviations of each stratum in each year.

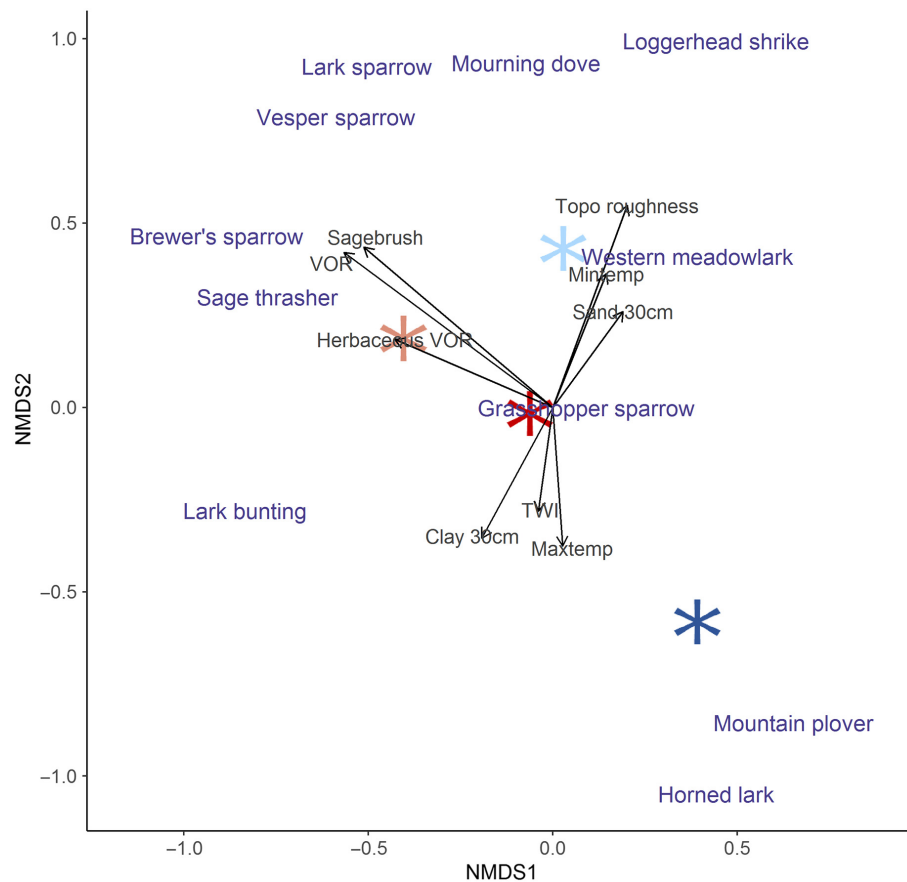


Fig. 4. Bird species locations in ordination space, as well as vector overlay of important site-level variables, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Centroids for inside–outside pairs of communities are presented for prairie dog colonies (on = dark blue; off = light blue) and historically burned areas (on = red; off = pink).

age or area with abiotic features improved upon an additive model including the main effects of age ($\beta = -0.035$, standard error [SE] 0.021) and area ($\beta = 0.318$, SE = 0.133). Conversely, neither disturbance age nor area affected bird community response to historic wildfires (Table 2). Instead, yearly variation was the best predictor and distance to centroid was highest in 2017, whereas minimum temperature performed only marginally (<2 AIC_c) better than the null model.

Alpha diversity (site diversity) was lowest on prairie dog colonies and highest on burned areas and undisturbed sites (Fig. 6). However, beta diversity (community dissimilarity between disturbed sites and paired undisturbed points) was higher for prairie dog disturbance than wildfire

disturbance (Fig. 6). This difference was likely a product both of lower diversity on prairie dog colonies and of the presence of unique species on those colonies. To better understand why community dissimilarity differed between disturbance types, we compared a model including disturbance type (fire or prairie dog) with univariate models of a suite of disturbance-dependent (e.g., VOR) and disturbance-independent (e.g., topography) variables (Table 3A). Disturbance type was the best predictor with $>98\%$ of the model weight, but inter-point distance (km), difference in clay content, and difference in maximum temperature ($^{\circ}\text{C}$) were also >2 AIC_c better than the base model (Table 3A). Examination of additive effects of these four variables indicated a top model including

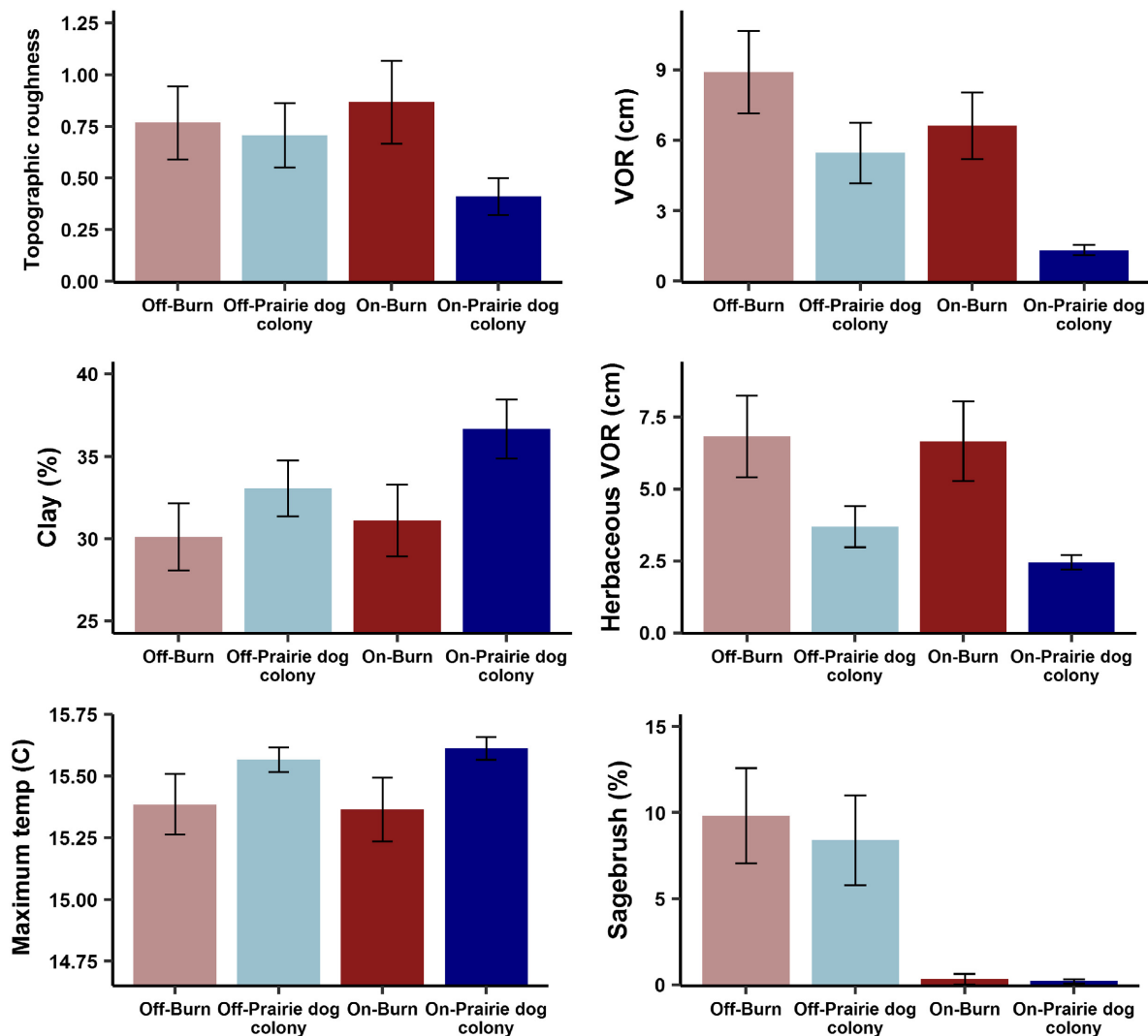


Fig. 5. Variation in disturbance-independent (left figure panels) and disturbance-dependent (right figure panels) variables shaping bird communities, Thunder Basin National Grassland, Wyoming, USA, 2016–2017.

disturbance type ($\beta_{\text{prairie dog}} = 0.21$, $SE = 0.055$) and inter-point distance ($\beta = 0.14$, $SE = 0.067$; Table 3B), but there was substantial model uncertainty (i.e., no one model carried most of the model weight). Only one model examining the interaction between abiotic traits within patch and disturbance type improved on disturbance type alone (Appendix S1: Table S3). The interaction of percent clay within a patch with disturbance type was marginally (0.8 AIC_c) better than disturbance type alone, indicating increasing dissimilarity on prairie dog colonies with increasing clay content (Fig. 7).

DISCUSSION

Disturbance is a key driver maintaining heterogeneity in rangeland vegetation structure (Pickett and White 1985, Ceballos et al. 1999, Fuhlendorf et al. 2017), yielding a mosaic of patches at the landscape scale that provides habitat for diverse wildlife species (Warui et al. 2005, Fuhlendorf et al. 2006, Davidson et al. 2012, Ricketts and Sandercock 2016). Our results show that in a sagebrush–grassland ecotone, disturbances such as wildfire and small burrowing mammals create habitat mosaics that strongly influence avian

distribution and diversity. Contrary to our expectation, disturbance type played a larger role than simple presence/absence of disturbance relative to undisturbed habitat. Indeed, prairie dog colonies harbored the most distinct communities in NMDS ordinations relative to burned areas or undisturbed sites (Fig. 4). Although prairie dog colonies had relatively low alpha diversity, they contributed most to beta diversity relative to undisturbed habitat, largely because they were

the only sites to contain mountain plovers. Neither historically burned areas, prairie dog colonies, nor undisturbed habitat was alone capable of supporting the full suite of avian species—instead, all three patch types were necessary to maintain avian biodiversity in this landscape.

Several important species of conservation concern (sage thrasher, Brewer's sparrow, and loggerhead shrike) were most abundant in the sagebrush-dominated habitats that form a large portion of the undisturbed matrix across this landscape. Although our surveys were not well suited to detecting them, greater sage-grouse also occur in the study region and depend on relatively large, dense stands of sagebrush (Connelly et al. 2011, Knick and Hanser 2011). Sagebrush-associated birds rely on sagebrush for both nesting and foraging substrate (Rotenberry and Wiens 1998, Connelly et al. 2011), and in the case of sage-grouse, for food (Peterson 1970, Walstead et al. 1975). These species have been shown to decline in response to a wide range of factors that reduce the extent and connectivity of sagebrush shrublands, especially anthropogenic disturbances associated with energy extraction (Gilbert and Chalfoun 2011, Hess and Beck 2012, LeBeau et al. 2014) and cultivation (Smith et al. 2016), as well as wildfire (Knick et al. 2005, Hess and Beck 2012, Holmes and Robinson 2013).

Fire and prairie dog grazing reduce sagebrush cover in the northern Great Plains (Johnson-Nistler et al. 2004, Baker 2006, Connell et al. 2018, Porensky et al. 2018). As we hypothesized, these

Table 2. Top models for factors modulating bird community convergence on prairie dog colonies and burned areas in Thunder Basin National Grassland, Wyoming, USA, 2016–2017.

Models	<i>k</i>	AIC _c	ΔAIC _c	Weight
Prairie dog				
Age of disturbance + Area of disturbance	4	121.3	0	0.43
Area of disturbance	3	122	0.6	0.31
Age of disturbance	3	124.6	3.2	0.085
Precipitation	3	126.5	5.2	0.032
Year of study	3	127	5.7	0.025
Aspect	3	127.2	5.8	0.023
Null	2	127.6	6.3	0.019
Historic fire				
Year of study	3	82.2	0	0.964
Minimum temperature	3	91.1	8.9	0.011
Maximum temperature	3	91.9	9.7	0.01
Null	1	89.7	9.8	0.01

Notes: AIC_c, Akaike's information criterion adjusted for small sample sizes. All models include a random effect of Patch ID. Bold indicates the only additive or interactive model better than the best single-variable model.

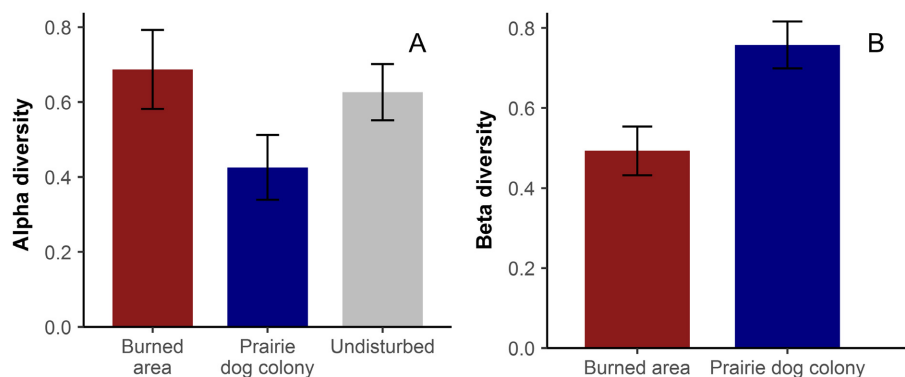


Fig. 6. Alpha diversity (A), calculated as the Shannon index, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Community dissimilarity or beta diversity (B), calculated as Bray–Curtis dissimilarity. Beta diversity was calculated as the difference between paired disturbed and undisturbed points for fires and prairie dog colonies.

Table 3. Univariate models (A) predicting avian community dissimilarity, Thunder Basin National Grassland, Wyoming, USA, 2016–2017, and (B) additive models compared to disturbance type alone.

Model	AIC _c	ΔAIC _c	k	Weight
(A) Univariate				
Disturbance type	34.5	0	4	0.986
Inter-point distance	43.2	8.7	4	0.013
Clay (%)†	49.2	14.7	4	<0.001
Maximum temperature†	53.5	19	4	<0.001
Minimum temperature†	55.1	20.6	4	<0.001
Study year	55.4	20.9	4	<0.001
Sand (%)†	55.6	21.1	4	<0.001
Silt (%)†	56.7	22.1	4	<0.001
Annual precipitation†	57	22.5	4	<0.001
Base model	57.1	22.6	3	<0.001
(B) Additive				
Disturbance type + Inter-point distance	32.4	0	5	0.289
Disturbance type + Inter-point distance + % Clay†	33.3	0.9	6	0.188
Disturbance type + Inter-point distance + Maximum temperature	34.4	2	6	0.106
Disturbance type	34.5	2.1	4	0.1

Notes: AIC_c, Akaike's information criterion adjusted for small sample sizes. Base model consisted of random effect of Patch ID. All additive combinations of variables >2 AIC_c better than the null (bold) were explored.

† The absolute value of the difference between values of inside–outside point-pairs.

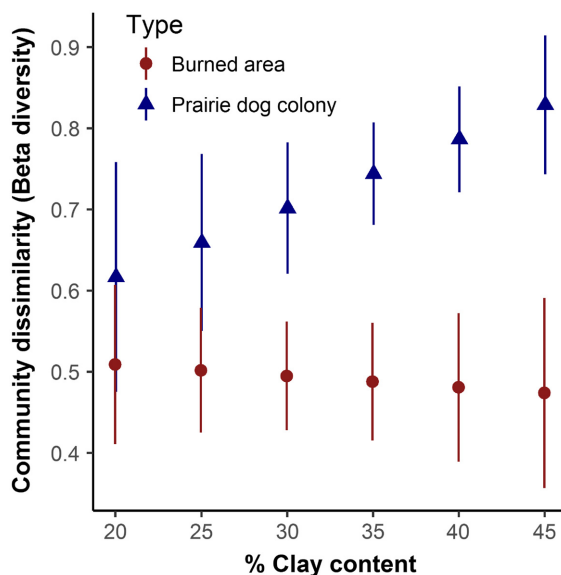


Fig. 7. Interactive effects of clay content (%) within disturbed patch and disturbance type on community dissimilarity in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017.

disturbances reduce available habitat for sagebrush birds (Fig. 2), but simultaneously provide opportunities for distinct grassland bird communities which vary by disturbance type. Continuous

herbivory and clipping by prairie dogs provided the short, sparse plant structure preferred by the mountain plover and horned lark, as well as burrowing owls (*Athene cunicularia*). Although only two observations of burrowing owls occurred in our dataset, this Wyoming SGCN was also confined to prairie dog colonies (Appendix S1: Table S1). Consistent with our hypothesis, larger and older prairie dog colonies tended to have more distinct communities, with higher abundances of these shortgrass species. Our results highlight the critical importance of prairie dogs for mountain plover conservation in this region. Although mountain plovers often benefit from disturbance by prairie dogs within rangelands across the western Great Plains, it appears that in Thunder Basin, as in much of the northern Great Plains, they are almost completely reliant on habitat created by prairie dogs (Dinsmore et al. 2005, Augustine and Baker 2013).

In contrast, mixed-grass species like the grasshopper sparrow were entirely absent on prairie dog colonies but were abundant on burned areas. Grasshopper sparrows are associated with disturbance in the eastern and mid-western portion of their range (Rahmig et al. 2009, Duchardt et al. 2016), but in semi-arid portions of the Great Plains, this and other mixed-grass associates (e.g., western meadowlark) are

often intolerant of grazing regimes or fire that suppress vegetation height and cover (Bock and Webb 1984, Saab et al. 1995, Augustine and Derner 2015). Both grasshopper sparrows and western meadowlarks rely on grass clumps and a moderate litter layer for construction and concealment of ground nests (Vickery 1996), and these habitat features are available within burned areas in the northern Great Plains (Vermeire et al. 2011, Porensky et al. 2018), but entirely absent on prairie dog colonies in the Thunder Basin ecotone. We did not expect fire age to affect bird communities but were surprised that communities did not differ substantially by any aspect of fire disturbance, including size. Given the substantial variation of grasshopper sparrow abundance among burned areas (Fig. 2), it may be that other unmeasured site-level variables or social cues (Andrews et al. 2015) play a greater role in habitat selection than patch size.

Importance of topo-edaphic drivers

Although disturbance was the most important factor structuring bird communities, other disturbance-independent landscape features mediated avian species composition. For example, loggerhead shrike abundance was greater in areas of rough topography. It is likely that shrikes do not show a preference for rugged topography itself, but instead utilize the isolated clusters of trees present along drainages. These sparse areas of tree cover, relatively rare in the landscape, provide shrikes with nesting and perching substrates (Becker et al. 2009).

Soils and topography also have the potential to interact with disturbance processes, leading to increased variation in vegetation structure. For example, our results are consistent with previous studies showing that prairie dogs tend to utilize relatively flat areas (Reading and Matchett 1997). Flat topography combined with constant prairie dog-driven soil disturbance leads to more bare ground exposure and birds associated with bare ground, such as mountain plovers. We also observed a marginal interactive effect of prairie dog disturbance with soil clay content, such that sites on prairie dog colonies where clay content was highest were most dissimilar to paired undisturbed points, while clay content had little effect on dissimilarity of bird communities on burned sites. Clayey soils have been identified as

playing a role in prairie dog burrow construction (Reading and Matchett 1997, Augustine et al. 2012), and may be preferred by prairie dogs; although clay content was higher on prairie dog colonies relative to burned areas or undisturbed habitat (Fig. 5), we still observed variation in clay content on these sites (23.3–45.0%). Compared to coarser-textured soils, clayey soils support shorter, less dense herbaceous vegetation in this ecosystem (Porensky et al. 2018) and have relatively slow infiltration rates, which can lead to more overland flow and/or evaporative loss of soil moisture following heavy spring and summer rains (Martínez-Mena et al. 1998). Thus, soil texture may act synergistically with prairie dog activity to increase bare ground exposure on colony sites, increasing their suitability for shortgrass bird species.

Implications for management

Rangeland landscapes that have not been extensively fragmented by anthropogenic land conversions (e.g., to croplands, exurban development, and/or energy extraction) are becoming increasingly rare worldwide. The remaining minimally fragmented landscapes are increasingly expected to sustain viable local populations of a diverse suite of species of conservation concern, often with conflicting habitat needs. Our findings clearly support the idea that maintaining all components of historic disturbance regimes is necessary to sustain the full suite of native birds, and potentially other guilds of vertebrates, as has also been shown for other iconic and extensive rangelands of North America (Fuhlendorf et al. 2006, Hovick et al. 2014), Africa (Du Toit et al. 2003, Gregory et al. 2010), and Australia (Doherty et al. 2017).

Our findings also highlight that sustaining the full suite of native species will require improved knowledge of how to manage a shifting mosaic of multiple disturbances in amounts and configurations that match conservation priorities and species needs. Unlike some grasslands where transitions among habitats for different species can occur within several years (Hovick et al. 2014), the multi-decadal transition time from disturbed patches back to a shrubland state in ecosystems like Thunder Basin, combined with our finding that burns and prairie dog colonies support unique and distinct bird communities, creates substantial complexity for the management of

disturbance regimes. Large, contiguous areas of sagebrush-dominated rangeland are needed to support greater sage-grouse conservation (Holloran and Anderson 2005, Connelly et al. 2011, Knick and Hanser 2011, Smith et al. 2016), and sagebrush stands additionally support the greatest number of species of conservation concern (Fig. 2). A major challenge in such landscapes will be to maintain adequate amounts of multiple disturbances to support their associated conservation targets, while still minimizing their negative impact on the amount and fragmentation of matrix, undisturbed habitats.

In the case of Thunder Basin, a key consideration in determining the balance between burned vs. colony patches is likely to be the colony-associated mountain plover, which has a far lower global population than the other bird species we detected (Appendix S1: Table S2) and occurs at a much lower population density than other bird species. As a result, a key future research need is to understand the amount and configuration of prairie dog colonies that will sustain mountain plover populations, while still minimizing impacts of prairie dogs on sagebrush extent and connectivity. This conflict may point toward management to promote a greater proportion of colony areas relative to burns, because small burned patches can support much higher densities of conservation targets such as grasshopper sparrows, as compared to plovers on colonies.

Additional complexity arises from the fact that uncontrolled wildfires periodically occur despite the best efforts of land managers. Similarly, prairie dog colonies experience dramatic spatial and temporal variability in their location and extent in response to die-offs induced by plague (*Yersinia pestis*; Augustine et al. 2008, Cully et al. 2010, Hoogland 2013). Thus, managers of extensive rangeland landscapes will need to increasingly consider existing patterns of disturbance of the landscape, desired amounts to meet conservation objectives, and trade-offs associated with potential, uncontrollable future patterns of disturbance, as they attempt to adaptively manage disturbance regimes. These realities emphasize the need to manage disturbance processes in rangelands in relation to their inherent variability rather than for a theorized optimal landscape.

Just as wildfires and prairie dog colonies are not static in time or space, climatic variability also

shapes both avian communities and disturbance processes. We found that year, a proxy of weather variability, interacted with avian community responses to disturbance drivers. Thunder Basin experienced both drought and extremely high temperatures during the survey period in 2016 (NOAA 2016), and abundance of species relying on taller grasses (e.g., grasshopper sparrow) was reduced throughout the study area. Heat and summer droughts are predicted to increase with climate change (USGCRP 2014), and these shifts have the potential to negatively influence bird species that rely on dense vegetation. Over the longer term, increased climate variability may also impact shortgrass-obligate birds, albeit indirectly, via changes in prairie dog population dynamics (Eads and Hoogland 2017). Across broad spatial and temporal scales, climate change has the potential to shift range limits of wildlife species (Walther et al. 2002, Root et al. 2003). The Thunder Basin ecotone currently represents the western or eastern range limit of many grassland and sagebrush bird species, respectively. In this and other ecotones, climate change may shift species composition more rapidly, and potentially in unexpected ways (Allen and Breshears 1998).

CONCLUSIONS

In an ecotone between the sagebrush steppe and the Great Plains, bird communities responded strongly to fire and burrowing mammals, lending further support for the critical role of disturbance regimes in driving biodiversity in North American rangelands (Kotliar et al. 1999, Fuhlendorf et al. 2006, Engle et al. 2008, Augustine and Derner 2015). For example, without black-tailed prairie dogs, the imperiled mountain plover would be rare in or entirely absent from our study area (see also Dinsmore et al. 2005). Prairie dog disturbance also interacted with soil texture such that bird communities on colonies with clayey soils were more distinct relative to those with less clay content. Although disturbance is crucial, the amount and configuration of undisturbed habitat is also important to consider in this ecotonal landscape. Undisturbed habitat is necessary to support sagebrush-obligate birds (e.g., greater sage-grouse, sage thrasher), because sagebrush recovers slowly following disturbance (Baker 2011, Beck et al. 2012). However, we acknowledge the unpredictability of

both disturbance regimes and climate (both current and future) in this system. To guide management in this heterogeneous and dynamic environment, we suggest that future research focus on identifying threshold responses of avian species to the amount and spatiotemporal configuration of multiple disturbances in the landscape.

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