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Plant community responses to historical wildfire in a shrubland–grassland ecotone reveal hybrid disturbance response

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Abstract. Most ecotones include structural and taxonomic elements from both adjacent communities, but it remains unclear how these elements function and interact within ecotones. We investigated long-term plant community responses to wildfire in a 7000-km^2 ecotone between mixed-grass prairie and sagebrush steppe ecosystems, which have dramatically different historical fire regimes. We asked whether plant community responses to wildfire in the ecotone were more similar to mixed-grass prairie, sagebrush steppe, or a hybrid of these two. We sampled plant community composition at 70 pairs of transects located inside and outside of wildfires that burned from 1937 to 2012. We determined whether (1) wildfires predicted plant community composition, (2) plant community response to fire varied based on abiotic factors, and (3) effects of wildfire varied based on time since fire. Plant community responses to wildfire did not vary substantially across the study region, despite continuous plant community variation in response to abiotic factors. Overstory responses were characteristic of sagebrush steppe. Burned transects had <10% as much big sagebrush cover as unburned transects, and cover did not increase with time since fire. In contrast, understory plant community responses to fire were similar to mixed-grass prairie. Burned sites had high forb cover in the short term and perennial grass cover in the long term. Within an ecotone, different components of the plant community can maintain functional fidelity to their home ecosystems, despite being spatially juxtaposed. The idea of hybrid disturbance response may provide new opportunities for targeted management within ecotones.

Key words: boundary; *Bouteloua gracilis;* ecological site; *Pascopyrum smithii;* state-and-transition; Thunder Basin National Grassland.

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INTRODUCTION

Ecotones, defined here as broadscale boundaries between biological communities that often co-occur with climatic gradients, generally include structural elements, taxa, and traits from both adjacent communities (Risser 1995, Lamb et al. 2003, Peters and Yao 2012). Research has explored factors that create or maintain ecotones (Allen and Breshears 1998, Daniels et al. 2003, Sankaran et al. 2005, Bestelmeyer et al. 2006, Shiponeni et al. 2014), as well as ecotonal influences on biodiversity and fluxes of matter, energy, and organisms (Ries et al. 2004, Kark and Van Rensburg 2006). Understanding how ecotones respond to disturbance is critical because these transition zones are particularly sensitive to global change agents, including land use change and climate change (Risser 1995, Allen and Breshears 1998, DeSantis et al. 2011, Peters and Yao 2012).

Despite extensive research on the broadscale causes and consequences of ecotones, it remains unclear how disparate, spatially juxtaposed elements interact within ecotones. Ecotones can behave as relatively sharp, non-interactive boundaries (Fig. 1a; Allen and Breshears 1998), broad zones in which adjacent communities smoothly intergrade (Fig. 1b; Taft 1997), mosaics in which two different communities are spatially interspersed without functionally merging (Fig. 1c; de Dantas et al. 2013), areas in which structural or functional components of different communities overlap to create a hybrid community (Fig. 1d; Peters and Yao 2012), or potentially a scale-dependent combination of these. Because different types of ecotones likely respond differently to management, disturbance and global change, a better understanding of the structure and function of ecotones may improve predictive power and enable more effective and strategic management. The lack of such understanding may result in spatially generalized management strategies that fail to achieve objectives.

Wildfire is a prominent driver of ecosystem structure and function, and fire regimes vary dramatically across ecosystems (Pyne et al. 1996, Bond and Keeley 2005, Baker 2006, Littell et al. 2009). In ecotones, fire regimes from adjacent ecosystems often intersect and interactively shape plant communities (Brown and Sieg 1999, Beckage et al. 2009, Littell et al. 2009). At broad spatial scales, fire or lack thereof can influence the location or width of an ecotone, often by altering woody plant abundance (Sankaran et al. 2005, Heyerdahl et al. 2006, Ratajczak et al. 2014). Different plant communities associated with adjacent ecosystems can also influence fire behavior and spread via differences in microclimate, fuel loads, and fuel connectivity (Beckage et al. 2009, Ratajczak et al. 2014, Just et al. 2016). In some ecotones, fire can be associated with or help to maintain spatial patchiness in which two different ecosystems are spatially interspersed but internally coherent, coexisting as alternative stable states (Kitzberger and Veblen 1999). For example, in the Brazilian Cerrado, grassy savannas experiencing frequent fire are interspersed with closed-canopy woodlands that experience infrequent fire due to low fuel connectivity (de Dantas et al. 2013).

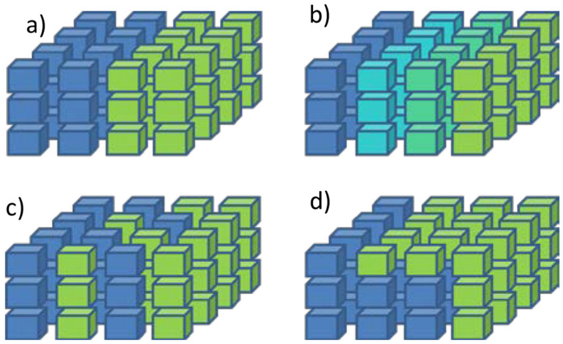

Fig. 1. Ecotones may include (a) hard boundaries between different biological communities, (b) intergrading communities, (c) communities interspersed in a mosaic pattern, and (d) overlapping or hybrid communities which contain components from both of the adjacent community types.

We investigated multidecadal plant community responses to wildfire in a 7000-km^2 ecotone between mixed-grass prairie and sagebrush steppe, two of North America's dominant ecosystems which together cover at least one million km^2 (Coupland 1992, Miller et al. 2011). Plant communities in these ecosystems have dramatically different historical fire regimes. Sagebrush steppe ecosystems found in North America's Intermountain West are typically intolerant of fire, and frequent fires in these systems can lead to invasion by annual grasses and degradation (Baker 2006, Davies et al. 2011, Balch et al. 2013). In contrast, prairie ecosystems in the Great Plains are resistant to fire and the combination of fire and grazing can increase the provisioning of multiple ecosystem goods and services (Fuhlendorf et al. 2009, Vermeire et al. 2011, Augustine and Derner 2015, Scasta et al. 2016).

The effects of wildfire are poorly understood in the ecotone between sagebrush steppe and prairie grassland ecosystems. Across much of North America, mountain ranges create natural boundaries separating these ecosystems. However, the two ecosystem types and their respective historical fire regimes abut in northeast Wyoming without natural topographic barriers (Littell et al. 2009). A dendrochronological study from the study region indicates a history of relatively frequent but patchy fire at a 70-km^2 scale (fire-free interval ~seven years, but most individual trees burned only once or twice during the >400-yr record, Perryman and Laycock 2000). Wyoming big sagebrush, or *Artemisia tridentata* subsp. *wyomingensis* Beetle & Young, was common in this region at the time of European settlement (Welch 2005, survey notes from Public Land Survey System). However, work from ~250 km north of our study region suggests that this shrub can take >100 yr to recover post-fire (Cooper et al. 2011). Using a chronosequence design, we investigated whether plant community responses to historical wildfire within the ecotone were more similar to mixed-grass prairie, sagebrush steppe, or a unique mixture of these two ecosystems. In locations spanning the broad ecotone, we asked as follows:

1. Does plant community composition vary predictably between burned and unburned sites?
2. Does the relationship between fire presence/absence and plant community composition vary based on soils or landscape characteristics?
3. Does plant community composition in burned sites vary based on time since fire?

METHODS

Study region

The study occurred across a 7000-km^2 region centered on the United States Forest Service (USFS) Thunder Basin National Grassland (TBNG) in northeast Wyoming, USA (43°12′–43°57′ N; 104°27′–105°23′ W). Mean annual precipitation ranges from 250 to 350 mm per yr, and most precipitation falls during the spring and summer. Mean monthly temperature ranges from −5°C in December to 22°C in July. Vegetation includes a shrub layer dominated by *Artemisia tridentata* subsp. *wyomingensis*. Common graminoids include the C_4 (warm-season) perennial grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, the C_3 (cool-season) perennial graminoids *Carex filifolia* Nutt., *Hesperostipa comata* (Trin. & Rupr.) Barkworth, and *Pascopyrum smithii* (Rydb.) Á. Löve, and the annual grasses *Bromus tectorum* L. and *Vulpia octoflora* (Walter) Rydb. Common forbs include *Alyssum desertorum* Stapf, *Plantago patagonica* Jacq., *Lepidium densiflorum* Schrad., and *Sphaeralcea coccinea* (Nutt.) Rydb. The cactus *Opuntia polyacantha* Haw. is also common.

Study design

The study had a hierarchical, stratified sampling design. From the USFS, we obtained a database of wildfire perimeters that included most wildfires >1 ha that burned within TBNG since 1988. For additional (mostly smaller) fires, the USFS had ignition point locations and fire sizes, but not perimeters. We combined perimeters with conservatively buffered ignition point data to identify 28 regions that had burned once but, to the best of our knowledge, had not reburned since 1988. Using local knowledge and historical aerial photography, we also identified the perimeters of two older fires (one from 1937 and one from 1974), which, to the best of our knowledge, had never reburned. Fires ranged from 4 to 3525 ha in size and occurred 2–77 yr prior to sampling. Most burns (21 out of 30 fires) occurred during July and August, though burn dates ranged from June 12 (six fires in June) to October 21 (three fires in October). Fire size and fire weather can influence plant community responses, but here we focus on vegetation responses that are relevant across a wide range of fire sizes and intensities.

Within each of the 30 fires, we stratified our sampling by ecological sites, which represent unique soil–climate–plant community types (Soil Survey Staff 2015), to ensure data were representative of edaphic variability. We sampled within the seven most common ecological sites, based on the dominant ecological site represented within each soil map unit (Soil Survey Staff 2015). After excluding lowlands and unmapped areas (the latter mostly badlands and mines), 98.6% of the study region was mapped as one of these seven ecological sites. Sampling intensity was roughly proportional to the amount of land area dominated by each ecological site: Loamy (R058BY122WY, covers ~38% of study region, comprises 35% of sample), Shallow Loamy (R058BY162WY, 15%, 21%), Sandy (R058BY150WY, 10%, 11%), Clayey (R058BY104WY, 6%, 9%), Shallow Clayey (R058BY158WY, 6%, 9%), Shallow Sandy (R058BY166WY, 6%, 9%), and Saline Upland (R058BY144WY, 3.5%, 7%; Soil Survey Staff 2015).

For each ecological site within each fire, we randomly placed a 30-m-long transect. Each of these burned transects was paired with an unburned transect. To create transect pairs, we first identified an ecological site occurring within the fire. For that ecological site, we delineated two large polygons (6.2 ± 0.4 ha in size) matched as well as possible for slope, aspect, and topographic wetness index (TWI) values derived from a 10-m digital elevation model (DEM; Gesch 2007, Soil Survey Staff 2015). One polygon was located inside and one outside the fire perimeter (the latter within 1000 m of the perimeter and inside the same allotment and ecological site). Because our questions focused on upland areas that dominate the region of interest, polygons were drawn to avoid steep slopes (95% of polygons had maximum slopes <15%) and drainage bottoms (95% of polygons had maximum TWI values <13). Within each polygon, we randomly placed a 30-m-long transect oriented in a random direction and >25 m from the fire perimeter. Transects colonized by prairie dogs or with a clear history of anthropogenic soil disturbance (e.g., farm equipment debris on transect) were excluded from analysis.

This strategy yielded a sample size of 140 transects across 30 fires (Appendix S1: Fig. S1). We sampled transects from 29 May 2014 to 20 August 2014. Paired transects were almost always sampled within a 5-d period (67 out of 70 pairs) and were 505 ± 295 m apart (mean ± 1 SD). Transects were 168 ± 129 m from the mapped wildfire perimeter (mean ± 1 SD), and all but three transects were <500 m from the perimeter.

Data collection

*Vegetation.—*At every third meter along each transect, we visually estimated vascular plant cover by species in 20 × 50 cm quadrats using 12 cover classes (0–1%, 1–10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80%, 80–90%, 90–99%, and 99–100%). We estimated canopy cover (i.e., plant material that would intercept a raindrop), not canopy closure (i.e., polygons drawn around plant canopies). For portions of the quadrat with no foliar or basal vascular plant cover, we estimated cover of other entities (e.g., lichen, moss, litter, and bare ground) using the same cover classes. For shrubs, we also estimated canopy cover using the gap intercept method (Herrick et al. 2005). Results were similar to quadrat-based results, and we therefore focus on the latter for methodological consistency across plant functional types.

*Soils.—*We collected soil cores at 5, 10, 15, and 20 m along each transect. We used a standard soil auger (7 cm diameter) and separated soil into 0–10 and 10–30 cm layers. Within each layer, samples from the four cores were pooled, and a subsample of the homogenized material was extracted for texture analysis. Subsamples were air-dried and passed through a 2-mm sieve. Soil particle size at each depth was determined using the hydrometer method (Bouyoucos 1962).

Data analysis

*Abiotic predictors.—*We used a 10-m DEM to obtain transect-scale average values for elevation, slope, aspect, and the topographic wetness index (TWI; Gesch 2007). All pixels at least partially inside a 15-m buffer around the transect midpoint were included in the averaging process. We used the parameterized regression on independent slopes model (PRISM) to obtain 30-yr average climate data for each transect. For the 800-m PRISM pixel intersecting each transect's midpoint, we downloaded annual and monthly values for maximum, mean and minimum temperature, maximum vapor pressure deficit (VPD), and cumulative precipitation. We aggregated monthly data into seasonal values for spring (April–June), summer (July–September), fall (October–December), and winter (January–March). Soil texture data (described above) were also included in the abiotic predictor set.

We checked for collinearity among abiotic predictors and determined that soil predictors were highly correlated with one another (most $|r| > 0.70$). Climate predictors were also highly correlated and were also correlated with elevation (most $|r| > 0.60$). Correlations among variables were linear, so we used a principal components analysis (PCA) to combine multiple, correlated predictor variables into fewer axes of relevant variation (Appendix S1: Table S1). PCA results on soil texture data yielded two soil predictors—one separating sandy from clayey or silty soils, and the second separating silty from clayey soils. The PCA on climate data revealed four independent climatic predictors (Appendix S1: Table S1). Climate axis 1 described variation in maximum temperature and vapor pressure deficit across the region. Climate axis 2 focused on variability associated with growing season minimum temperatures and spring precipitation. Climate axis 3 described variability in winter minimum temperatures and summer rainfall, and Climate axis 4 was associated with summer and fall precipitation variability. Several climate predictors were loosely associated with geography; for example, northwestern sites tended to be cooler (lower scores on Climate axis 1) than southeastern sites (Appendix S1: Fig. S1). For all subsequent analyses, the abiotic predictor set included slope, aspect, TWI, the two soil PCA axes (hereafter called "clayey" and "silty"), and the four climate PCA axes (hereafter called "heat," "warm spring/summer, wet spring," "warm winter, wet summer," and "wet summer/fall").

Community-level ordination.—We used ordination to determine whether fire or abiotic factors affected plant community composition. To identify differences in overall plant community composition, we used a non-metric multidimensional scaling (NMDS) ordination (Lepš and Šmilauer 2003). We performed NMDS using the vegan library (Oksanen et al. 2013) in R (version 3.0.1). To prepare data for NMDS analysis, we averaged data across the 10 quadrats (subplots) along each transect to generate transect-scale cover values (hereafter called absolute cover, N = 140). We then calculated the relative cover of each plant species as its percent of total plant cover within each transect (this excludes bare ground, litter, lichen, and moss to generate a metric of plant community composition rather than ground cover). We excluded plant species that occurred in <5% of the 140 samples (Harrison et al. 2010, Alday et al. 2013). Subsetting reduced the dataset from 129 species to 48 species (Appendix S1: Table S2).

For both relative and absolute cover (the latter including entities such as bare and litter), we identified how many dimensions were necessary to create an NMDS ordination (function metaMDS) with stress ≤0.15 using Bray-Curtis distances and Wisconsin square root transformations (McCune and Grace 2002). To determine whether fire or interactions between fire and abiotic factors were associated with overall plant community composition, we ran a PerMANOVA (function adonis) on the results of each ordination with abiotic predictor variables, fire presence/absence, and all two-way interactions between fire and abiotic predictors.

We used vegan's envfit function, which evaluates multidimensional correlations between NMDS site scores and independent environmental predictors, to further evaluate and visualize the effects of fire and abiotic predictor variables on plant community composition. We ran envfit on all four NMDS axes together and on each separate pair of NMDS axes. We also evaluated pairwise correlations between each species and multiple NMDS axes. This approach allowed us to examine not only which environmental factors were associated with overall variation in community composition, but also how species, samples, and environmental factors were oriented relative to one another along multiple axes in ordination space.

Functional group analyses.—We used linear mixed models (LMMs) and AIC_c-based model selection to examine fire and abiotic factor effects on the absolute cover of each of 12 functional groups: C3 perennial graminoids, C4 perennial grasses, all perennial graminoids, native annual grasses (*V. octoflora*), non-native annual grasses (*B. tectorum* + *Bromus arvensis* L.), forbs, big sagebrush (*A. tridentata* only), other woody plants, cactus, litter, lichen and moss, all vascular plants, and bare ground (Appendix S1: Table S2). All 129 species were included in calculations of functional group cover in order to capture rare species' contributions to cover. After running a full, global model with fire, abiotic predictors, and all two-way interactions, we removed any non-significant ($P > 0.10$) two-way interactions and then performed model selection on the resultant, reduced model. To account for our hierarchical stratified sampling design, we included fire and transect pair nested within fire as random factors. During the model selection process, model structure remained identical except for fixed factors. Models with a ΔAICc <4 were averaged to create a final, average model for each response variable. Responses were transformed when necessary to meet model assumptions.

Fire age.—Finally, to determine whether effects of fire varied with fire age, we repeated the entire process after excluding unburned transects and replacing the fire (yes/no) predictor with fire age (years since fire). Methods were identical to those described above except for the functional group models for *A. tridentata* cover. Because only nine out of 70 burned transects had *A. tridentata* cover >0, we were unable to analyze data using a Gaussian distributional assumption. Instead, we ran generalized LMMs (GLMMs) with a binomial distribution to determine whether fire age or abiotic predictors were associated with the presence (cover >0) of *A. tridentata* in burned areas. All LMMs were conducted in R 3.3.1 using the nlme package (Pinheiro et al. 2013), and GLMMs were conducted using the lme4 package (Bates et al. 2015). We compared and averaged multiple models using the MuMIn package (Bartoń 2015). Results are reported as conditional model averages or means ± 1 SE.

RESULTS

Community-level ordination

Four-dimensional NMDS ordinations were required for both relative and absolute cover (stress = 0.15, non-metric fit $R^2 = 0.98$ for both relative and absolute cover ordinations). PerMANOVA results were similar across the two ordinations and emphasized the importance of multiple abiotic drivers of plant community composition (Table 1). In both PerMANOVAs, effects of wildfire varied significantly across topographic positions (significant fire X slope and fire X TWI interactions), but did not vary significantly based on aspect, soil texture, or climatic predictors (Table 1). Sites were not obviously clustered in multivariate space, but rather exhibited continuous variation along multiple axes (Fig. 2).

Envfit results for relative cover indicated that NMDS Axes 1 and 3 were strongly linked to climate, soil texture, and fire (Table 2, Fig. 3). Focusing on NMDS Axis 3 revealed that hotter sites, burned sites, and sites with less silt had high relative cover of C_4 grasses (*Bouteloua gracilis, Sporobolus cryptandrus* (Torr.) A. Gray) and *Artemisia pedatifida* Nutt, and low relative cover of *Artemisia tridentata*, *Artemisia frigida* Willd. and the C_3 perennial graminoids *Koeleria macrantha* (Ledeb.) Schult, *Carex duriuscula* C.A. Mey,

Table 1. PerMANOVA results (based on type III sums of squares) for NMDS ordinations on relative and absolute cover.

Model	df	Relative cover			Absolute cover		
		R^2	F	P	R^2	F	P
Total	19	0.38	–	–	0.35	–	–
Warm spring/summer, wet spring	1	0.08	15.82	<0.001	0.06	11.24	<0.001
Clay	1	0.05	9.76	<0.001	0.05	8.38	<0.001
Fire	1	0.04	7.96	<0.001	0.04	7.41	<0.001
Heat	1	0.03	5.49	<0.001	0.02	4.58	<0.001
Aspect	1	0.02	4.74	<0.001	0.02	4.28	<0.001
Silt	1	0.02	4.13	<0.001	0.02	4.17	<0.001
Wet summer, warm winter	1	0.02	3.49	<0.001	0.02	2.91	0.002
TWI	1	0.02	3.02	0.002	0.01	2.41	0.01
Wet summer/fall	1	0.02	3.12	0.005	0.02	2.90	0.006
Slope	1	0.009	1.69	0.07	0.01	1.37	0.18
Fire × slope	1	0.01	2.08	0.03	0.02	2.78	0.005
Fire × TWI	1	0.01	2.07	0.03	0.02	3.28	0.002
Fire × heat	1	0.009	1.77	0.07	0.006	1.03	0.4
Fire × wet summer/fall	1	0.006	1.18	0.3	0.006	1.14	0.3
Fire × silt	1	0.005	0.97	0.5	0.005	0.86	0.6
Fire × aspect	1	0.004	0.77	0.6	0.003	0.48	0.9
Fire × warm spring/summer, wet spring	1	0.003	0.64	0.8	0.003	0.48	0.9
Fire × clay	1	0.003	0.52	0.9	0.003	0.63	0.8
Fire × wet summer, warm winter	1	0.002	0.32	0.99	0.003	0.52	0.9
Residuals	120	0.62	–	–	0.65	–	–

Note: Abiotic predictors included topographic wetness index (TWI), slope, aspect, and PCA axis scores for two soil axes and four climate axes (see Appendix S1: Table S1 for more details).

Hesperostipa comata, *Elymus trachycaulus* (Link) Gould ex Shinners, and *Pascopyrum smithii* (Fig. 3a; Appendix S1: Table S2). A wide variety of annual and perennial forb species had higher relative cover in burned, hotter sites (Fig. 3a; Appendix S1: Table S2). Focusing on Axis 1 revealed that sites with high clay content, dry and cool springtime climates, or northwest-facing aspects had different community composition than sites with more sand or silt, warmer, wetter springtime climates, or southeast-facing aspects (Fig. 3a). Coarse-textured, southeast-facing sites, and sites with warm, wet springs were associated with higher relative cover of the perennial graminoids *H. comata*, *Carex filifolia*, and *Sporobolus cryptandrus*, the annual grasses *Bromus tectorum* and *Vulpia octoflora*, and several forbs (Fig. 3a; Appendix S1: Table S2). In contrast, sites with more clay, dry and cool springs, or northwest-facing aspects had higher relative cover of the perennial grasses *B. gracilis*, *E. trachycaulus*, *K. macrantha*, and *Poa secunda* J. Presl, the annual grass *B. arvensis*, several woody species, including *A. tridentata*, *Gutierrezia sarothrae* (Pursh) Britton & Rusby, and *A. pedatifida*, and a diverse array of perennial and annual forbs (Fig. 3a; Appendix S1: Table S2).

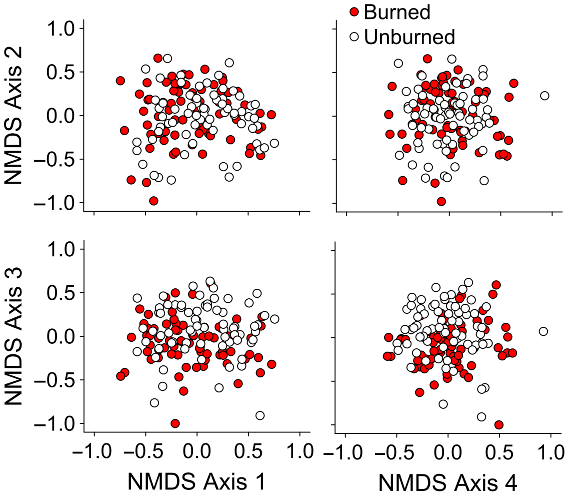

Fig. 2. Site scores (N = 140) plotted on the four NMDS axes. Position relative to Axes 1 and 3 was significantly associated with the presence of historical wildfire.

Non-metric multidimensional scaling Axis 2 was associated with local topography (TWI and slope) and with regional variation in growing season climate (Table 2, Fig. 3b). Swales, flat sites, and sites with cool growing seasons and dry springs were associated with higher relative cover of several perennial graminoids (*B. gracilis, P. smithii, P. secunda*, and *C. duriuscula*), annual grasses (*B. tectorum* and *V. octoflora*), and annual forbs (Fig. 3b; Appendix S1: Table S2). On ridgetops, slopes, and sites with warmer growing seasons and wetter springs, relative cover was high for *H. comata*, *C. filifolia*, and a suite of perennial forbs (Fig. 3b; Appendix S1: Table S2).

Non-metric multidimensional scaling Axis 4 was not well predicted by fire or any abiotic factors, though it was weakly associated with growing season climate and aspect (Table 2, Fig. 3b).

Table 2. Envfit results for NMDS ordination of relative cover.

	NMDS axis pair						All axes
Predictors	12	13	14	23	24	34	1234
Fire	0.02	**0.05****	0.02	**0.04****	0.004	**0.04****	**0.03****
Aspect	**0.06***	**0.05***	**0.07****	0.04	**0.06***	**0.05***	**0.11****
TWI	**0.13*****	0.004	0.007	**0.12*****	**0.13*****	0.004	**0.13****
Slope	**0.07****	0.006	0.01	**0.08****	**0.09****	0.02	**0.09****
Heat	**0.09****	**0.31*****	**0.08***	**0.26*****	0.03	**0.25*****	**0.34*****
Warm spring/summer, wet spring	**0.34*****	**0.15*****	**0.2*****	**0.2*****	**0.25*****	**0.06***	**0.41*****
Warm winter, wet summer	0.02	0.02	0.03	0.02	0.03	0.03	0.05
Wet summer/fall	0.02	0.02	0.03	0.006	0.02	0.02	0.04
Clay	**0.34*****	**0.34*****	**0.38*****	0.001	0.04	0.04	**0.38*****
Silt	**0.16*****	**0.21*****	**0.15*****	**0.07****	0.02	**0.07***	**0.23*****

Notes: Numbers represent r^2 values relating fire and abiotic predictors to NMDS scores for each axis combination. Asterisks and bolding indicate significance ($^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$). Abiotic predictors included topographic wetness index (TWI), slope, aspect, and PCA axis scores for two soil axes and four climate axes (see Appendix S1: Table S1 for more details).

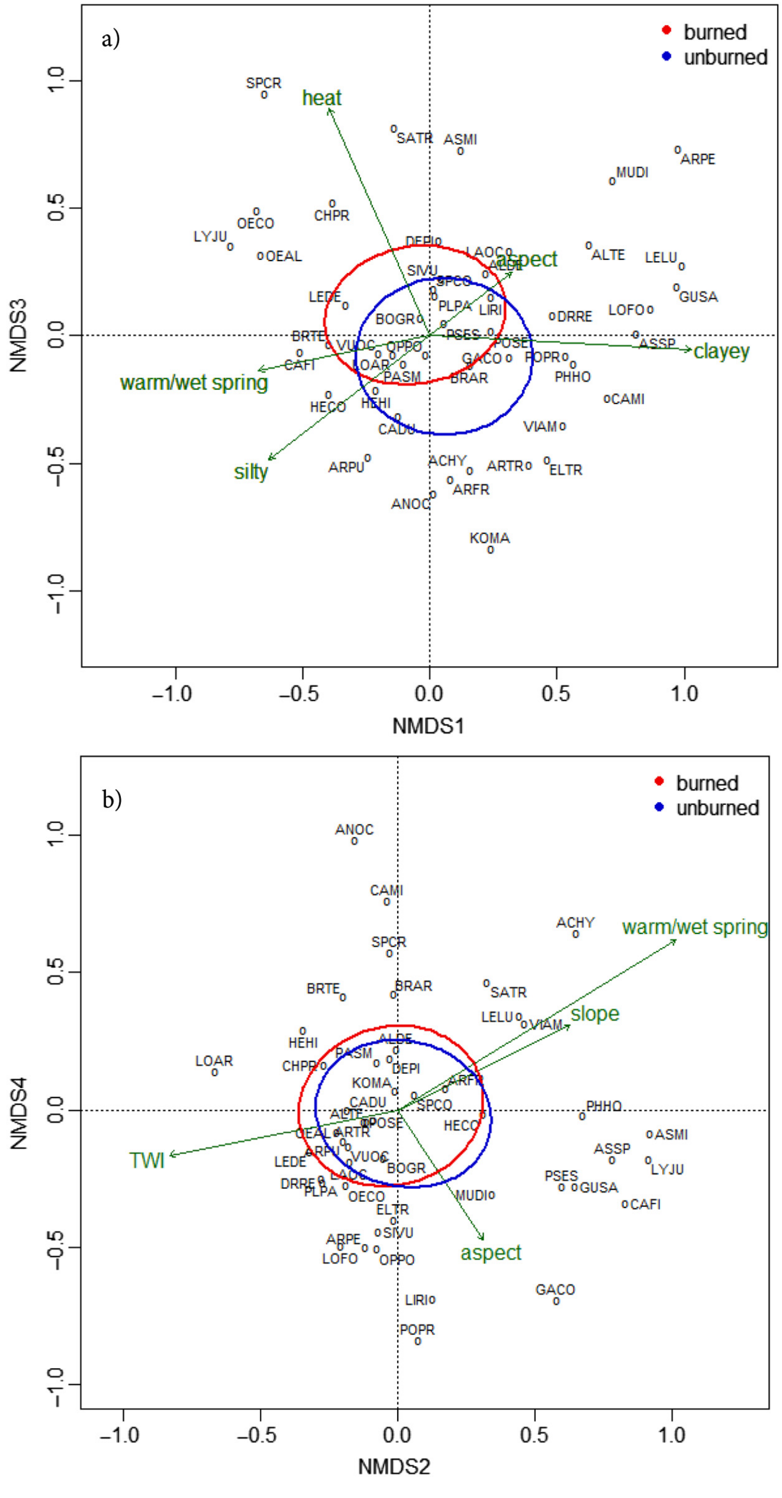

Fig. 3. Species scores plotted on NMDS axes along with environmental predictors significantly correlated with these axes (Table 2). Species codes display the first two letters of the genus followed by the first two letters of the species; see Appendix S1: Table S2 for the full list.

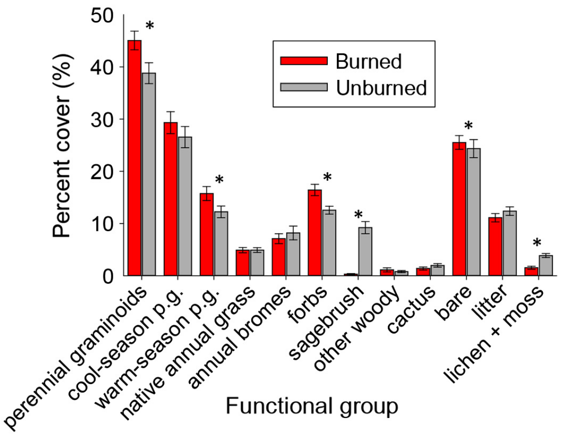

Fig. 4. Effects of fire on the absolute cover of multiple functional groups. Asterisks indicate functional groups for which model selection indicated a significant main effect of fire or significant interactions between fire and other abiotic factors (Table 3). Abbreviation p.g. is perennial graminoids, and bare is bare ground.

This axis separated communities with a high relative cover of *B. gracilis, O. polyacantha, V. octoflora,* and *P. patagonica* from communities with a high relative cover of *P. smithii*, *Bromus* spp., and *Camelina microcarpa* Andrz. ex DC. (Fig. 3b; Appendix S1: Table S2).

Results for the NMDS ordination of absolute cover roughly paralleled those for relative cover, though absolute cover data provided additional insights about non-plant ecosystem components (Appendix S1: Tables S2, S3). Axes 1 and 3 revealed that unburned sites and cooler sites had more litter, moss and standing dead sagebrush, while burned sites and hotter sites had more bare ground and mammal dung (Appendix S1: Table S2). Clayey sites had higher cover of bare ground, rock, and lichen, while sandy sites had higher cover of litter (Appendix S1: Table S2). Axes 2 and 4 revealed a distinction between communities with more litter and communities with more lichen, moss, and bare ground (Appendix S1: Table S2).

Functional groups

Compared to unburned transects, burned transects had 3% as much absolute cover of *A. tridentata*, 39% as much lichen and moss cover, 16% more perennial graminoid cover, and 31% more forb cover (Fig. 4, Table 3). Differences in perennial graminoid cover were driven by C_4 perennials, which had almost 30% higher cover in burned transects than in unburned transects (Fig. 4, Table 3). For *A. tridentata* and perennial graminoids, cover values were associated with interactions between fire and environmental predictors (Table 3). In unburned areas, sites with higher TWI (lower topographic positions) had more *A. tridentata* cover and less perennial grass cover. In burned areas, *A. tridentata* cover was low and perennial grass cover was high regardless of topographic position (Fig. 5a, c). Similarly, in unburned areas, *A tridentata* cover declined as maximum temperature increased across the region. However, burned sites had low *A. tridentata* cover regardless of temperature (Fig. 5b). Bare ground also reflected interactive effects of fire and abiotic factors (Table 3). In unburned areas, bare ground tended to increase with TWI, slope, and clay content, but these relationships were weaker or even opposite in burned areas. Cover of other functional groups did not differ significantly between burned and unburned transects, though most of these groups were sensitive to other environmental predictors (Appendix S1: Table S4).

Fire age

Four-dimensional NMDS ordinations were necessary to describe plant community composition inside burned areas (stress = 0.15, nonmetric fit R^2 = 0.98 for both relative and absolute cover ordinations). At the whole community scale, fire age and interactions between fire age and climate had significant effects on community composition (Relative Cover PerMANOVA Fire Age $P = 0.02$, Fire Age × Wet summer/fall $P = 0.003$; Absolute Cover PerMANOVA Fire Age $P = 0.03$, Fire Age × Wet summer/fall $P = 0.001$, Fire Age × Warm winter, wet summer $P = 0.04$). Envfit analyses for both relative and absolute cover suggested that fire age was most closely associated with NMDS axis 4 (Appendix S1: Tables S5, S6, Fig. S2). Older burns had higher relative cover of *P. smithii*, *C. duriuscula*, moss, litter, and a few annual forbs, whereas younger burns had higher relative cover of *E. trachycaulus,* rock, and a wide array of annual and perennial forbs (Appendix S1: Table S7).

Functional group analyses provided additional information about how plant communities

Table 3. Model selection results for absolute cover of functional groups.

Average model	Coeff.	SE	*P*
All perennial graminoids			
(Intercept)	49.85	8.75	<0.0001
Warm spring/summer, wet spring	2.91	0.95	<0.0001
Warm winter, wet summer	−1.52	1.2	0.21
Wet summer/fall	−0.37	0.99	0.71
Unburned	14.4	8.25	0.09
Slope	−0.58	0.89	0.52
Silt	3.2	1.27	0.01
TWI	−0.76	1.43	0.6
Unburned × Silt	−3.14	1.9	0.1
Unburned × TWI	−4.3	1.69	0.01
Clay	−0.2	0.41	0.63
Heat	0.04	0.25	0.89
C4 perennial graminoids			
(Intercept)	3.57	0.21	<0.0001
Heat	0.12	0.04	0.006
Unburned	−0.45	0.19	0.02
Warm spring/summer, wet spring	−0.17	0.08	0.03
Silt	−0.11	0.11	0.32
Forbs			
(Intercept)	3.84	0.17	<0.0001
Unburned	−0.47	0.14	0.0008
Clay	0.13	0.04	0.0007
Wet summer/fall	0.14	0.09	0.11
Silt	−0.13	0.07	0.08
Artemisia tridentata			
(Intercept)	0.2	0.17	0.24
Unburned	0.83	1.77	0.64
Heat	0	0.02	0.94
TWI	−0.01	0.05	0.85
Unburned × Heat	−0.27	0.07	<0.0001
Unburned × TWI	0.72	0.21	0.001
Silt	−0.13	0.05	0.02
Bare ground			
(Intercept)	44.5	12.6	0.0006
Wet summer/fall	1.27	0.931	0.18
Unburned	−43.1	17.2	0.01
Slope	−2.04	1.44	0.16
Clay	0.851	0.66	0.2
Silt	−2.49	0.988	0.01
TWI	−2.74	1.9	0.16
Unburned × Slope	3.87	1.83	0.04
Unburned × Clay	1.74	0.878	0.05
Unburned × TWI	6.43	2.69	0.02
Warm spring/summer, wet spring	−0.596	0.606	0.3
Warm winter, wet summer	0.0263	0.767	0.97
Heat	0.169	0.368	0.7
Lichen and moss			
(Intercept)	−0.767	0.208	0.0003
Unburned	1.4	0.228	<0.0001
Silt	−0.266	0.125	0.04
Clay	0.146	0.0644	0.03
Warm winter, wet summer	0.117	0.106	0.3

Notes: Model averaging was performed on all models for which ΔAICc was <4. Average coefficients are displayed for each parameter included in the model averaging process. Abiotic predictors included topographic wetness index (TWI), slope, aspect, and PCA axis scores for two soil axes and four climate axes (see Appendix S1: Table S1 for more details).

change with time since fire. Fire age was important in the averaged models for lichens and mosses as well as forbs (see Appendix S1: Table S8 for model selection results). Lichen and moss cover increased significantly with time since fire (Fig. 5d, Fire Age coefficient = 0.06 ± 0.016, *P* = 0.0003). Forb cover declined significantly with time since fire (Fig. 5e, Fire Age coefficient = −0.04 ± 0.012, *P* = 0.0008). Nine out of 70 burned transects had *A. tridentata* cover >0, and the presence of *A. tridentata* did not vary based on fire age (Fig. 5f; Appendix S1: Tables S8, S9). In the nine burned transects with *A. tridentata*, average cover was 2.3 ± 0.7% and all cover values were ≤ 6% (Fig. 5f).

DISCUSSION

Plant communities in the ecotone between sagebrush steppe and mixed-grass prairie ecosystems revealed strong abiotic gradients and also a surprisingly consistent response to wildfire. The latter suggested that this ecotone displays a hybrid disturbance response in which shrubs function like sagebrush steppe, while the herbaceous understory functions like mixed-grass prairie.

Overstory

In unburned areas, *A. tridentata* shrub cover varied continuously along axes defined by soil texture, climate, and topography. Cover varied from under 5% to over 20%, and was highest at sites with low maximum temperatures (most of which were in the northwestern part of the study region, Appendix S1: Fig. S1), cool and dry springtime climates, low landscape positions (swales), and high clay content (Figs. 3, 5).

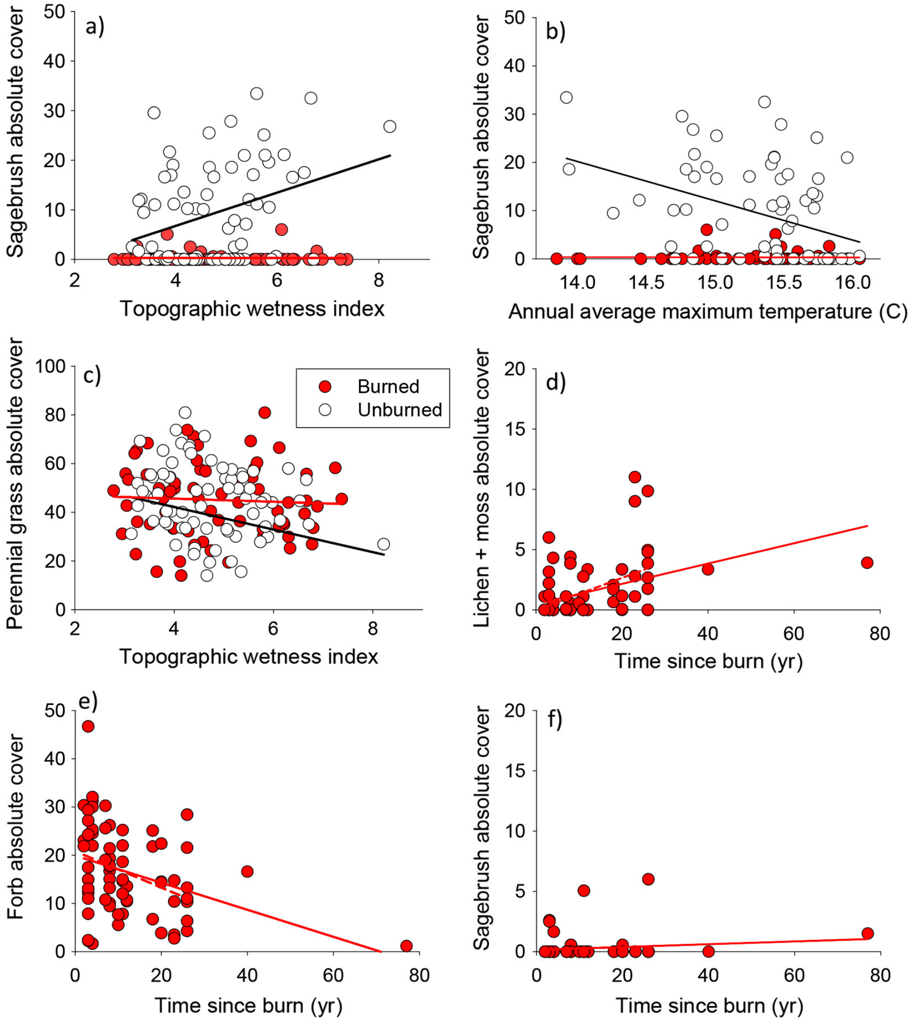

Fig. 5. Complex effects of fire on the absolute percent cover of different functional groups. Big sagebrush cover was significantly influenced by interactions between fire and (a) topography and (b) climate. Perennial grass cover (c) responded significantly to interactions between fire and topography. Fire age significantly affected the cover of (d) lichens and mosses and (e) forbs, but did not affect the cover of (f) big sagebrush. See Table 3 for model selection results. Dotted red lines display best-fit lines excluding the two oldest fires.

Despite strong gradients associated with abiotic factors, wildfires across the entire study region consistently reduced *A. tridentata* cover to nearly zero for multiple decades (Figs. 4, 5; Appendix S1: Table S9). These results are broadly consistent with findings from the Intermountain West (Baker 2006) as well as more local results from southeastern Montana (Cooper et al. 2011). In our study region, the loss of fire-sensitive *A. tridentata* creates a mosaic of persistently shrub-free patches at broad scales (tens of kilometers). In contrast to a similar study in a different shrubland–grassland ecotone, mosaic patterns in our study region were not strongly associated with soil heterogeneity (Buxbaum and Vanderbilt 2007). Instead, burned areas had consistently low *A. tridentata* cover regardless of soil type.

Our chronosequence study documented relatively slow recovery times for *A. tridentata* canopy cover in burned areas (more than 80 yr). These rates match well with rates documented in southeastern Montana (estimated at 138 yr, Cooper et al. 2011) and areas further west (50 to >120 yr, Baker 2006). Slow recovery of *A. tridentata* may be driven in part by fast recovery of fire-resistant understory plants, which create biotic resistance (Porensky et al. 2014, Shiponeni et al. 2014). Slow recovery rates also raise questions about the prevalence of *A. tridentata* in this fire-prone ecotone. Both fire and *A. tridentata* were prevalent in this landscape prior to European settlement (Perryman and Laycock 2000, Welch 2005). We hypothesize that despite frequent ignitions, complex topography (e.g., unvegetated breaks and persistently wet swales) and black-tailed prairie dog (*Cynomys ludovicianus*) colonies caused extensive fuel discontinuities in this landscape. Along with patchy post-ignition precipitation, these fuel discontinuities likely resulted in most wildfires being constrained to small, patchy areas, as observed in the one dendrochronological study from this region (Perryman and Laycock 2000).

Understory

Like shrub cover, understory plant community composition was strongly affected by abiotic factors, including soil texture, topography and climate. Clayey and silty sites were associated with a diverse array of perennial graminoids and annual and perennial forbs (Fig. 3a), while sandy sites were associated with a smaller group of species and more non-natives (Stohlgren et al. 1999). Species associated with high TWI (i.e., lower landscape positions), low slopes, and northwest aspects were also found more commonly at sites that had cooler, drier springtime climates. This may reflect the importance of late-season vs. early-season water availability as a driver of community composition across this water-limited region. For example, *H. comata* and *C. filifolia* were associated with sandy sites, ridges, slopes, and warmer, wetter springtime climates. These cool-season graminoids are able to take advantage of early-season moisture and are unaffected by dry conditions later in the summer and fall (Derner et al. 2008, Irisarri et al. 2016). In contrast, the dominant C_4 grass, *B. gracilis*, was associated with clayey sites, swales, and northwest aspects, all of which should be associated with more moisture late in the growing season.

In terms of fire response, the understory plant community in our study region did not experience post-fire invasion by non-native annual grasses (see also Porensky and Blumenthal 2016), and burned sites were characterized by high perennial graminoid and forb cover (Fig. 4). Wildfire led to a 10- to 20-yr pulse in forb abundance (Fig. 5e), and this response has also been observed in more mesic prairie ecosystems (Lett and Knapp 2005). While a similar study in Montana found that C_3 perennial graminoids increased after prescribed summer fires (Vermeire et al. 2011), summer wildfires in our region were associated with increases in C_4 grass cover and no significant change in C_3 graminoid cover (Table 3, Fig. 4). The resilient understory community response to fire observed in our study region is typical of western Great Plains prairies (Vermeire et al. 2011, Augustine et al. 2014). Compared to the Intermountain West, the Great Plains historically experienced more frequent wildfires (Whisenant 1990, Brown and Sieg 1999, Ratajczak et al. 2014), and most plants native to the region are tolerant of above-ground disturbances, including fire and grazing (Fuhlendorf and Engle 2004, Brudvig et al. 2007). Interestingly, species associated with burned sites were also associated with hotter sites across the region (Fig. 3a). By removing shrub cover and reducing ground surface albedo, wildfires in this region probably increase the amount of solar radiation experienced by understory plants, leading to hotter microclimates. Hotter sites were associated with increased cover of C_4 grasses, and this regional pattern parallels broader climate-driven gradients in C_4 grass cover across the Great Plains (Epstein et al. 1997).

Finally, we saw evidence for an unexplained axis of community variation which separated *B. gracilis* and *V. octoflora* from *P. smithii* and *B. tectorum*. Long-term grazing experiments from mixed-grass prairie and shortgrass steppe suggest that this axis is likely associated with grazing intensity (Fuhlendorf et al. 2001, Porensky et al. 2016, 2017, Sanderson et al. 2016, Augustine et al. 2017). In these studies, lower grazing intensities were associated with less *B. gracilis*, more *P. smithii*, and also more *B. tectorum*.

Implications for management

Managers in this region are working to develop conceptual models of plant community dynamics which will be formalized in ecological site descriptions, or ESDs, and associated state-and-transition models, or STMs (https://esis.sc.egov.usda.gov/Default.aspx). ESDs and STMs form the backbone of one of the world's largest formal land management frameworks (Twidwell et al. 2013) and have been recognized globally as a useful framework for management and ecological synthesis (Wong et al. 2010, Oliva et al. 2016). Ecological sites are partially described as areas that respond similarly to natural disturbances, and responses to fire should therefore be relevant to the development of regional ecological site concepts. We found that plant community composition in this ecotone shifted continuously along several abiotic axes, and communities did not cluster strongly in multivariate space (Figs. 2, 3). Moreover, we found little evidence for differential responses to fire across different soil types or climate zones. Fire generally had the effect of reducing variability associated with abiotic factors and creating more homogenous plant communities post-fire. For example, although swales tended to have higher *A. tridentata* cover and lower perennial grass cover than ridges in unburned areas, burned areas had low shrub cover and high perennial grass cover regardless of topographic position (Fig. 5a, c). Together, our findings suggest that the development of ecological site groups and generalized state-and-transition models (STMs; Bestelmeyer et al. 2016, Duniway et al. 2016) or disturbance response groups (Stringham et al. 2016) might be appropriate for this region. Such tools would streamline the communication of key ecosystem dynamics to land managers. We developed a generalized STM (Fig. 6a), which captures some of the most important abiotic variability in unburned areas and also presents generalized responses of the plant community to wildfire. It is important to note that we have not yet investigated ecosystem responses to other drivers such as grazing; responses to other drivers may vary more substantially across abiotic gradients.

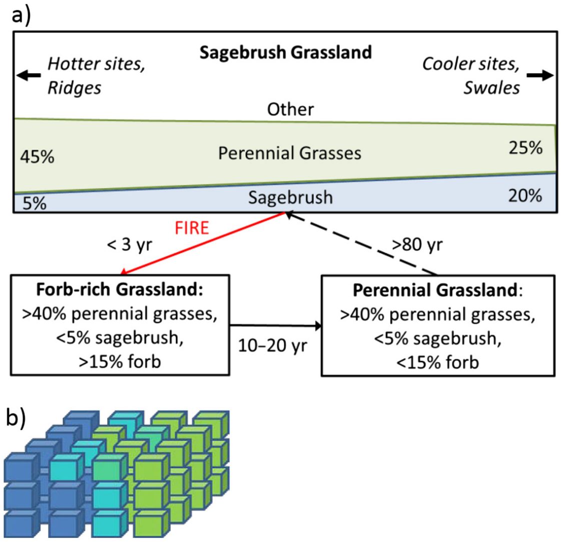

Fig. 6. Conceptual models of plant communities in the Thunder Basin ecotone. (a) In unburned areas, shrub cover shifts along gradients determined by climate, topography, and soil texture. Burning removes shrub cover regardless of abiotic factors, creating patches of persistent grassland that lack sagebrush overstory. Burned patches initially have high forb cover, but forb cover declines with time since fire. (b) The ecotonal plant community exhibits hybrid disturbance response, which leads to a spatial mosaic of grassland patches embedded in a shrubland matrix. In unburned areas, components of the two communities intergrade based on abiotic drivers.

From a practical perspective, our results emphasize that summer burns are not a good management tool for conservation of *A. tridentata* or sagebrush-associated species in this region (see also Beck et al. 2009, 2012). Instead, *A. tridentata* conservation and restoration should focus on clayey sites, swales, and cooler sites where *A. tridentata* already tends to occur with high canopy cover. Although burned areas lack *A. tridentata*, they provide forage resources (perennial grasses and forbs) that are less abundant elsewhere on the landscape. These could be important for both livestock and sage-grouse (*Centrocercus urophasianus*) chicks (Pennington et al. 2016, Scasta et al. 2016). Shrub-free patches also provide grassland bird habitat for lark buntings (*Calamospiza melanocorys*), western meadowlarks (*Sturnella neglecta*), and grasshopper sparrows (*Ammodramus savannarum*) found in mixed-grass prairie with taller vegetation (Augustine and Derner 2015). As reported previously (Porensky and Blumenthal 2016), the understory community in this region appears to resist invasion after single wildfires, potentially increasing managers' ability to use fire strategically to achieve desired goals (e.g., increasing forb cover in areas without sagebrush).

Implications for ecotones

We found evidence that the plant community in TBNG responds to wildfire as a hybrid system in which shrubs respond in a manner typical of sagebrush steppe, while understory species operate more like mixed-grass prairie (Fig. 6b). Each functional group responds in ways that are consistent with its home ecosystem, but spatially these components overlap and also intergrade. Hybrid disturbance responses may be reinforced by ecotonal shrub–grass interactions. For example, fire-sensitive shrubs are likely slower to regenerate in a system where perennial grasses can readily take advantage of post-fire moisture to grow and occupy available space and resources. In the presence of wildfire, hybrid community function leads to a spatial mosaic pattern because burned areas persist as shrub-free, mixed-grass prairie patches embedded within the hybrid community matrix (Fig. 6b). For both the overstory and the understory community, we also found evidence of broadscale shifts in species abundance in response to climate gradients (e.g., heat and seasonality of precipitation). These generally reflected a shift from sagebrush steppe to mixed-grass prairie species, and particularly involved a replacement of *A. tridentata* and C_3 graminoids by C_4 grasses (Figs. 4, 6b).

Together, these findings suggest that a given ecotone may fit into more than one of the categories presented in Fig. 1. Hybrid communities may also intergrade depending on the scale of observation (Hochstrasser et al. 2002, Peters and Yao 2012). Moreover, hybrid disturbance responses in ecotones can lead to patchy ecotone structure even in the absence of abiotic patchiness. Hybrid disturbance response has rarely been recognized in previous research, despite clear implications for how ecotone plant communities are understood and managed. More work is needed to understand whether hybrid disturbance responses are common in ecotones globally. It will also be important to learn whether hybrid disturbance responses operate consistently across multiple management, disturbance, and global change drivers. For example, can our ecotone's hybrid response to wildfire help to predict its response to livestock grazing or drought? With a better understanding of ecotone function, land managers may be able to develop spatially strategic, goal-based plans rather than following spatially generalized management protocols that may lead to suboptimal outcomes in complex ecotones.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2363/full