

Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires

G. M. DAVIES,^{1,5} J. D. BAKKER,¹ E. DETTWEILER-ROBINSON,¹ P. W. DUNWIDDIE,¹ S. A. HALL,² J. DOWNS,³
AND J. EVANS⁴

¹School of Environmental and Forest Sciences, University of Washington, Box 354115, Seattle, Washington 98195-4115 USA

²The Nature Conservancy, 6 Yakima St., Ste. 1A, Wenatchee, Washington 98801 USA

³Pacific Northwest National Laboratory, P.O. Box 999, Richland, Washington 99352 USA

⁴The Nature Conservancy, 1917 1st Ave., Seattle, Washington 98101 USA

Abstract. Repeated perturbations, both biotic and abiotic, can lead to fundamental changes in the nature of ecosystems, including changes in state. Sagebrush steppe communities provide important habitat for wildlife and grazing for livestock. Fire is an integral part of these systems, but there is concern that increased ignition frequencies and invasive species are fundamentally altering them. Despite these issues, the majority of studies of fire effects in systems dominated by *Artemisia tridentata wyomingensis* have focused on the effects of single burns. The Arid Lands Ecology Reserve (ALE), in south-central Washington (USA), was one of the largest contiguous areas of sagebrush steppe habitat in the state until large wildfires burned the majority of it in 2000 and 2007. We analyzed data from permanent vegetation transects established in 1996 and resampled in 2002 and 2009. Our objective was to describe how the fires, and subsequent postfire restoration efforts, affected communities' successional pathways. Plant communities differed in response to repeated fire and restoration; these differences could largely be ascribed to the functional traits of the dominant species. Low-elevation communities, previously dominated by obligate seeders, moved furthest from their initial composition and were dominated by weedy, early-successional species in 2009. Higher-elevation sites with resprouting shrubs, native bunchgrasses, and few invasive species were generally more resilient to the effects of repeated disturbances. Shrub cover has been almost entirely removed from ALE, although there was some recovery where communities were dominated by resprouters. *Bromus tectorum* dominance was reduced by herbicide application in areas where it was previously abundant, but it increased significantly in untreated areas. Several resprouting species, notably *Phlox longifolia* and *Poa secunda*, expanded remarkably following competitive release from shrub canopies and/or abundant *B. tectorum*. Our results suggest that community dynamics can be understood through a state and transition model with two axes (shrub/grass and native/invasive abundance), although such models also need to account for differences in plant functional traits and disturbance regimes. We use our results to develop a conceptual model that will be validated with further research.

Key words: Arid Lands Ecology Reserve; *Artemisia tridentata*; *Bromus tectorum*; fire effects; Hanford Reach National Monument; herbicide; native seeding; nonmetric multidimensional scaling; PERMANOVA; repeated disturbance; restoration; state and transition model.

INTRODUCTION

Repeated perturbations, both biotic and abiotic, can lead to fundamental changes in the nature of ecosystems (Paine et al. 1998), including changes in state. In their review of state and transition modeling, Stringham et al. (2003) defined a vegetation state as a complex composed of the soil base and the vegetation structure, that is resistant (able to remain at equilibrium) and resilient

(able to recover) to disturbance, and expressed via a suite of possible vegetation communities. Transitions in state are driven by repeated or ongoing disturbances that cause communities to cross thresholds to new states from which they will not recover without significant intervention. For example, Knick and Rotenberry (1997) demonstrated the gradual loss of shrub-dominated habitats and changes in landscape-scale vegetation structure with repeated wildfires; Kercher and Zedler (2004) documented how sedimentation, nutrient addition, and flooding interacted synergistically to accelerate the invasion of *Phalaris arundinacea* L. (reed canary grass); and Gosper et al. (2010) demonstrated that chaining plus burning led to a significant decrease in the recruitment of serotinous obligate seeders compared to burning alone. Recognition of the fact that variation in,

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⁵ Present address: School of Interdisciplinary Studies, University of Glasgow, Rutherford/McCowan Building, Crichton University Campus, Dumfries, Scotland DG1 4ZL United Kingdom. E-mail: gwilym.davies@glasgow.ac.uk

or changes to, disturbance regimes can fundamentally alter the composition of vegetation communities has led to increasing recognition of the utility of state and transition models (e.g., Laycock 1991, Allen-Diaz and Bartolome 1998, Firn et al. 2010) over traditional linear succession (Sampson 1917) or rangeland condition models (Dyksterhuis 1949) for describing the response of semiarid land vegetation to disturbance.

Sagebrush steppe communities are strongly associated with the Great Basin region of the western United States of America, but extend northward through the Columbia Plateau Ecoregion to Washington State and southern British Columbia (West and Young 2000). These communities provide important habitat for wildlife, including rare and declining species such as Greater Sage Grouse (*Centrocercus urophasianus* Bonaparte) and Columbia Basin pygmy rabbit (*Brachylagus idahoensis* Merriam), and also provide an important rangeland resource with large areas used for livestock grazing. Fire has always been an integral part of these systems, but there is increasing concern that anthropogenic impacts from increased ignition frequencies and invasive species are fundamentally altering them and reducing their diversity and productivity (D'Antonio and Vitousek 1992). Additional threats from land-use intensification, overexploitation, and climatic change (Wisdom et al. 2005) mean that rangeland areas dominated by woody shrubs (most notably *Artemisia* spp.), perennial bunchgrasses, and a diversity of native herbs are in serious decline (Knick and Rotenberry 1997). In addition to fire, these communities are influenced by abiotic factors such as variation in precipitation (e.g., Anderson and Inouye 2001, Bates et al. 2006) and biotic factors including grazing by domestic livestock (e.g., Laycock 1967, Bates et al. 2009).

The invasion of sagebrush steppe habitats by *Bromus tectorum* L. (cheatgrass) promotes more frequent and extensive burns that reduce or eliminate sagebrush and other woody perennials (Whisenant 1990, Knapp 1996, Knick and Rotenberry 1997). The length of historic fire return intervals in sagebrush steppe is a matter of some debate. Estimates range from 50 to 240 years (Baker 2006, Mensing et al. 2006) for systems dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), according to prevailing climatic conditions and livestock grazing levels. Knowledge of the autecology of Wyoming big sagebrush also suggests that fires in the past were normally small in extent (although infrequent large fires could have accounted for a significant proportion of the area burned). Despite the fact that Wyoming big sagebrush systems burn intensely (Sapsis and Kauffman 1991), the species is maladapted to frequent fire. It is an obligate seeder and, although it produces conspicuous amounts of seed each year (Young et al. 1989), seed dispersal drops off steeply away from individual plants (Young and Evans 1989). Wyoming big sagebrush seeds are also

rather short-lived (Young and Evans 1975, Hassan and West 1986) on the soil surface but may survive longer if buried (Wijayratne and Pyke 2009). In addition, germination is strongly related to early-spring water availability, with poor seedling establishment in drier sites (Young and Evans 1989). Such characteristics suggest that the reestablishment of this species is likely to be highly dependent on short- to medium-term variation in weather conditions and rather slow in particularly arid areas. Both Harniss and Murray (1973) and Lesica et al. (2007) reported that, 30 years after fire, cover of big sagebrush had not returned to anywhere near prefire levels. Lesica et al. (2007) further reported that Wyoming big sagebrush was particularly slow to recover. Although shrub recovery is slow following burning, native bunchgrasses and herbs can increase in cover rapidly if invasive species are absent (Cook et al. 1994, Cooper et al. 2007, Davies et al. 2007, Holmes 2007, Seefeldt et al. 2007). If invasive species are present, they may initially be reduced by wildfire but are then able to expand rapidly (Young and Evans 1978); associated native species richness declines significantly (Cooper et al. 2007). Where the recovery of perennial vegetation is rapid, rates of invasion are generally reduced (Chambers et al. 2007).

Although a large amount of fire-related research has occurred in sagebrush steppe systems, many previous studies have examined changes in the populations of individual species or functional groups (e.g., shrubs or bunchgrasses) rather than seeking to understand changes in vegetation community structure per se. Additionally, in systems dominated by Wyoming big sagebrush, most research has focused on how vegetation responds to single fires (e.g., Cook et al. 1994, Evans and Lih 2005, Davies et al. 2007, Seefeldt et al. 2007, Bates et al. 2009) rather than repeated disturbances. In this study, we utilized data from permanent vegetation plots to describe how two large wildfires and postfire restoration activities have changed vegetation patterns, and to understand how communities have responded to these disturbances. Our specific objectives were to examine the size and direction of changes in vegetation communities using "successional trajectories" to infer differences in community resilience to repeated disturbance; to relate these trajectories to changes in the populations of key species and functional groups; and to begin developing a state and transition model that illustrates the observed changes.

METHODS

Study site

Research was completed on the 31 000 ha Fitzner-Eberhardt Arid Lands Ecology Reserve (ALE) in south-central Washington, USA (Appendix A). ALE is a unit of the Hanford Reach National Monument (46°35' N, 119°31' W) and has been off-limits to most development since 1943. Currently, ALE is one of the few remaining areas of native vegetation in south-central Washington;

TABLE 1. Summary of restoration treatments applied between 2002 and 2008 in the 31 000-ha Fitzner-Eberhardt Arid Lands Ecology Reserve (ALE), south-central Washington, USA.

Plot	Community group		Herbicide and year of application			Seeding year		Planting year
	1996	2009	Roundup	Journey	Plateau	Drill	Broadcast	
BRMaP 7	Mid-East (3)	Higher (3)					2008	2007
BRMaP 8	Mid-East (3)	Higher (3)					2003	
BRMaP 12	High (2) Mid-West (1)	Higher (3)						
BRMaP 13	High (3)	Higher (3)						
BRMaP 20	Low (5)	Lower (5)	2002, 2003	2008			2002, 2008	
BRMaP 23	Low (3)	Lower (3)		2008		2008		
BRMaP 24	Mid-West (5)	Lower (5)	2002		2008		2002, 2008	

Notes: Plot numbers were assigned during original sampling in 1996. Each plot consisted of 3–5 transects. All transects in a given plot received the same treatment. Community groups were identified by cluster analysis based on composition in 1996 and in 2009 (see *Results: Identifying broad community types*, Table 2, and Appendix D); in parentheses after the community group name is the number of transects from that plot assigned to each group. Three herbicides were used: Roundup (glyphosate; a broad-spectrum systemic herbicide), Plateau (imazapic; a selective herbicide for pre- and postemergent control of some annual and perennial grasses and some broadleaf weeds), and Journey (glyphosate and imazapic together). Seeding mixes varied between applications but included *Poa secunda* and *Achillea millefolium* plus a mix of bunchgrasses that depended on elevation (Evans and Lih 2005). Drill seeding was applied on the ground; broadcast seeding was applied on the ground and aerially. Planting refers to bare-root *Artemisia tridentata* ssp. *wyomingensis* stock. Plot locations in relation to the geography of ALE and community groups are shown in Appendices A and D.

surrounding lands have largely been converted to wheat fields, orchards, and vineyards. ALE was designated a Federal Research Natural Area in 1971 and incorporated into the National Monument in 2000. Prior to European settlement, the area comprising ALE had been utilized by humans for millennia, with Rattlesnake Mountain being of particular importance to the Yakama tribe (O'Connor and Rickard 2003). Before 1943, the area was used for homesteading, dryland and irrigated agriculture, sheep and cattle grazing, natural gas exploration, and by the military. Since the 1970s, only scientific education and research activities, and limited development of communications infrastructure, have occurred on the Reserve (Hinds and Rogers 1991).

The environment of ALE is extremely varied. Elevation ranges from 130 m in the bottom of the Cold Creek valley to 1070 m along the ridgeline of Rattlesnake Mountain that marks its southwestern boundary. Soils are generally sandy or sandy loams in the lower areas, loamy at mid-elevations, stony loams in higher areas, and lithosols along the ridge of Rattlesnake Mountain. Precipitation varies with elevation from as little as 16 cm per year at low elevations to more than 30 cm per year at the crest of Rattlesnake Mountain. Precipitation was higher than usual at the start of our study in 1996, but was not unusual prior to subsequent monitoring in 2002 and 2009 (Appendix B).

The steep, rugged terrain and variation in substrates engender strong correlations between environmental factors and vegetation communities on ALE. When our first measurements were made in 1996, Wyoming big sagebrush dominated the lower areas, with three-tip sagebrush (*Artemisia tripartita* Rydb.) and green and gray rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt. and *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom and Baird) more common at mid- and higher

elevations. Shrub understories and interspaces were dominated by *Poa secunda* J. Presl and *Pseudoroegneria spicata* (Pursh) A. Löve. Several invasive alien species (e.g., *Sisymbrium altissimum* L., *Salsola kali* L., *Erodium cicutarium* (L.) L'Hér. ex Aiton, *Draba verna* L., and *Holosteum umbellatum* L.) were well established on ALE. *B. tectorum* was common across most of ALE and was particularly dense at lower elevations. ALE continues to contain a number of local and regional endemic plant species as well as wildlife species federally listed as Species of Concern (Evans and Lih 2005).

In 2000, the 24 Command Fire burned 65 000 ha, including ~90% of ALE. In 2007, the Milepost 17 and Wautoma Fires burned 31 000 ha including ~75% of ALE. All of the plots included in this study (see Appendix A) burned in both years. Although these were the largest recent fires, historical records (Rickard et al. 1988, O'Connor and Rickard 2003) and the MTBS (Monitoring Trends in Burn Severity; data available online)⁶ and GeoMAC (Geospatial Multi-Agency Coordination Group; data available online)⁷ databases show that at least 10 other fires >10 000 ha have burned on ALE since 1952. Our plots were not impacted by most of these fires, although one plot (23) was burned by a small fire in 1998, four were burned in the Hanford fire of 1984, and two were burned in 1981. Postfire restoration action following the 2000 and 2007 fires included aerial herbicide application, aerial and drill seeding of native bunchgrasses, and planting of Wyoming big sagebrush. These treatments affected many of our plots, particularly those at low elevations (Table 1).

⁶ <http://mtbs.gov>

⁷ <http://www.geomac.gov>

Data collection

Our research utilized permanent vegetation plots established in 1996 (U.S. Department of Energy 2001). The plots aimed to provide a baseline on the biological resources of ALE and, as such, were designed to span the range of habitats and communities found on the Reserve at that time. Seven plots were established: three in areas dominated by Wyoming big sagebrush, and two each in areas dominated by *A. tripartita* and by *P. spicata*. Each plot covers 20 ha and contains three or five 100 m long vegetation transects. Transect origins were located along the central axis of the plot, 200 m (5 transect plots) or 400 m (3 transect plots) apart, with the first and last transects 100 m from the plot edge. In total, 25 transects were monitored.

Visual estimates of the percent cover (to the nearest 1%) of all vascular plant species were made in 20 × 50 cm gridded quadrats (subquadrats 10 × 10 cm) every 5 m ($n = 20$ per transect). The start, end, and midpoint of each transect were marked with rebar and 1.5-m fiberglass wands, and the corners of the plot were marked with metal T-posts. Individual quadrat locations were marked with pin flags. Data were collected by the Pacific Northwest National Laboratory in 1996 (U.S. Department of Energy 2001), The Nature Conservancy from 2001 to 2004 (Evans and Lih 2005), and the University of Washington in 2009 and 2010. Plant nomenclature follows the U.S. Department of Agriculture's PLANTS database (USDA, NRCS 2010).

Data analysis

We analyzed data from the baseline surveys in 1996, two years following the 2000 wildfire (2002), and two years following the 2007 wildfires (2009). All data were analyzed at the transect level ($n = 25$ transects).

When considered together, communities often contain large numbers of rare species that, although potentially of conservation interest, do not explain broad differences between community groups and can add substantial noise to data (McCune and Grace 2002). Prior to analyses of changes in community composition, we removed rare species (defined as those occurring in <5% of recorded transects over all years). This resulted in the retention of 58 of the 141 documented species (Appendix C). We applied a Wisconsin double standardization (Bray and Curtis 1957) on the species matrix to focus our analysis on changes in the relative abundance of species rather than absolute changes in their cover. Doing so removed some of the differences in total cover caused by abiotic gradients and also minimized differences in cover estimation among observers.

Spatial autocorrelation.—A partial Mantel test (Legendre and Legendre 1998) was used to examine evidence for spatial autocorrelation in our data set while accounting for the strong effect of elevation. Tests were completed with the “mantel” function of the *vegan* package in R 2.9.0 (R Development Core Team 2009).

We tested each year separately using Pearson correlation coefficients and 10 000 permutations.

Identifying broad community groups.—We used hierarchical agglomerative cluster analysis to identify broad communities present in 1996. These communities formed a “pseudo-starting state”; they are not a definitive reference condition but provided a baseline against which to assess the effects of the two fires. We used the Bray-Curtis distance measure, Ward's linkage method, and the “hclust” function of the *vegan* package of R. The appropriate number of groups was identified by examining scree plots while considering the need for parsimony and ease of interpretation. We tested for significant differences between communities using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), as coded in the “adonis” function of the *vegan* package of R, and used the Bray-Curtis distance measure and 10 000 permutations. We conducted an identical hierarchical cluster analysis to identify broad community types present in 2009 to help interpret the net effect of the fires and restoration actions.

Changes in key functional groups.—We examined patterns of change in the transect-level total abundance of four key functional groups: large shrubs, invasive annual grasses (i.e., *B. tectorum*), native perennial herbs (including subshrubs and woody herbs like *Eriogonum heracleoides* Nutt. and *Phlox longifolia* Nutt.), and large native perennial bunchgrasses (excluding the small, shallow-rooted *P. secunda*) between years and between the 1996 community groups. Abundance data were relativized by the total abundance on each transect for these analyses. We used PERMANOVA to test for differences among years, communities, and year × community interactions. Significant results were followed by post hoc tests to examine pairwise differences between communities and year-to-year changes within communities. Analyses were completed using the PERMANOVA+ extension of PRIMER (Clarke and Gorley 2006) and accounted for the repeated-measures structure of the experimental design.

Community trajectories of change.—Change in vegetation community composition following each fire was examined using nonmetric multidimensional scaling (NMDS; McCune and Grace 2002), a powerful ordination technique that is appropriate for ecological data (McCune and Grace 2002). Analysis was completed on data from all years and transects using the Bray-Curtis distance measure and the “isoMDS” and “metaMDS” functions in the *vegan* package of R. Initial analysis was completed using up to 400 runs, random starting locations, and from one to five dimensions. Examination of plots of stress vs. number of dimensions suggested that three dimensions adequately explained variation in the data set. We therefore ran the three-dimensional analysis a second time, again with up to 400 random starting locations, but considered the effects of autocorrelation by using the spatial location of each transect

TABLE 2. The five most common plant species in each community group as identified from the 1996 compositional data.

Community group	Dominant species, by rank				
	1	2	3	4	5
High	<i>Festuca idahoensis</i>	<i>Poa secunda</i>	<i>Pseudoroegneria spicata</i>	<i>Artemisia tripartita</i>	<i>Lupinus leucophyllus</i>
Mid-East	<i>Pseudoroegneria spicata</i>	<i>Bromus tectorum</i>	<i>Poa secunda</i>	<i>Plantago patagonica</i>	<i>Lupinus sulphureus</i>
Mid-West	<i>Poa secunda</i>	<i>Artemisia tridentata</i>	<i>Machaeranthera canescens</i>	<i>Artemisia tripartita</i>	<i>Pseudoroegneria spicata</i>
Low	<i>Bromus tectorum</i>	<i>Artemisia tridentata</i>	<i>Poa secunda</i>	<i>Grayia spinosa</i>	<i>Vulpia microstachys</i>

Notes: Dominance rank order (declining left to right) was assessed by calculating the mean abundance for all transects in a given group. Species traits are given in Appendix C.

(UTM coordinates and elevation) as the starting coordinates for the initial run. The final solution had a stress of 16.97. We visualized landscape-level changes in vegetation composition over time with the “ordihull” function of *vegan* to outline the ordination space occupied by all transects in each 1996 community group. Changes in ordihull size among communities provided a visual representation of changes in landscape heterogeneity over time, whereas the relative positions of data points corresponding to different years attest to changing species dominance. Species centroids were overlaid on the ordination to aid understanding of changes in transect community structure. We examined changes in community composition by plotting the abundance of key species in the ordination diagrams. Individual transect locations were plotted with symbol sizes that represented the relativized abundance for the given species. To examine community trajectories, we calculated the position of the transects relative to their location in 1996 by translating all 1996 data to the origin while preserving the relative locations of the 2002 and 2009 data for each transect.

RESULTS

Spatial autocorrelation

Partial Mantel tests revealed that, even accounting for the strong elevational/environmental gradients present on ALE, highly significant spatial autocorrelation in vegetation communities existed in 1996 ($r = 0.485, P < 0.001$) and 2009 ($r = 0.438, P < 0.001$). Although still significant, the Mantel r statistic was somewhat lower in 2002 ($r = 0.269, P = 0.002$). This suggests that heterogeneity in the community composition of spatially close transects increased following the first fire. Following the second burn, however, nearby transects were once again more similar to one another, indicating that the strong spatial patterning in community composition had been reestablished.

Identifying broad community types

The cluster analysis identified four community groups in 1996. These groups were named Low, Mid-East, Mid-West, and High to reflect their correspondence to the elevation/soil-type gradient on ALE (Appendix D).

Broadly speaking, the Low community was dominated by *B. tectorum* and *A. tridentata wyomingensis*, the Mid-East by *P. spicata* and *B. tectorum*, the Mid-West by *P. secunda* and *A. tridentata wyomingensis*, and the High by *Festuca idahoensis* Elmer, *P. spicata*, and *A. tripartita* (Table 2). These community groups differed significantly in composition (Table 3); this grouping factor explained 48% of the variation in community composition in 1996 (PERMANOVA pseudo- $F_{3,21} = 6.61, P < 0.001$).

Changes in key functional groups

A number of trends were visible in the functional groups that we examined (Fig. 1, Table 4). The “community” main effect was significant for each functional group, indicating that there were some consistent differences among communities. Invasive annual grasses were more abundant and large native perennial bunchgrasses less abundant in the Low community than in the others. Shrubs were missing from the Mid-East community but were present elsewhere. Native perennial herbs were more abundant in the High community than in the others. The “year” main effect was significant only for shrubs and native

TABLE 3. Results of PERMANOVA pairwise comparisons between the 1996 cluster analysis communities, showing change in the amount of information explained by contrasts between community groups (PERMANOVA pseudo- F values) in 1996 vs. 2009.

Community group comparison	High	Mid-West	Mid-East
Mid-West			
1996	5.37***		
2009	4.69***		
Mid-East			
1996	5.70***	4.27***	
2009	2.33*	3.60**	
Low			
1996	10.03***	5.22***	8.51***
2009	8.03***	3.29**	8.29***

Note: All contrasts between community groups within a year are significant. Results with P values for community contrasts that were substantially different in 2009 compared to 1996 are shown in italics.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

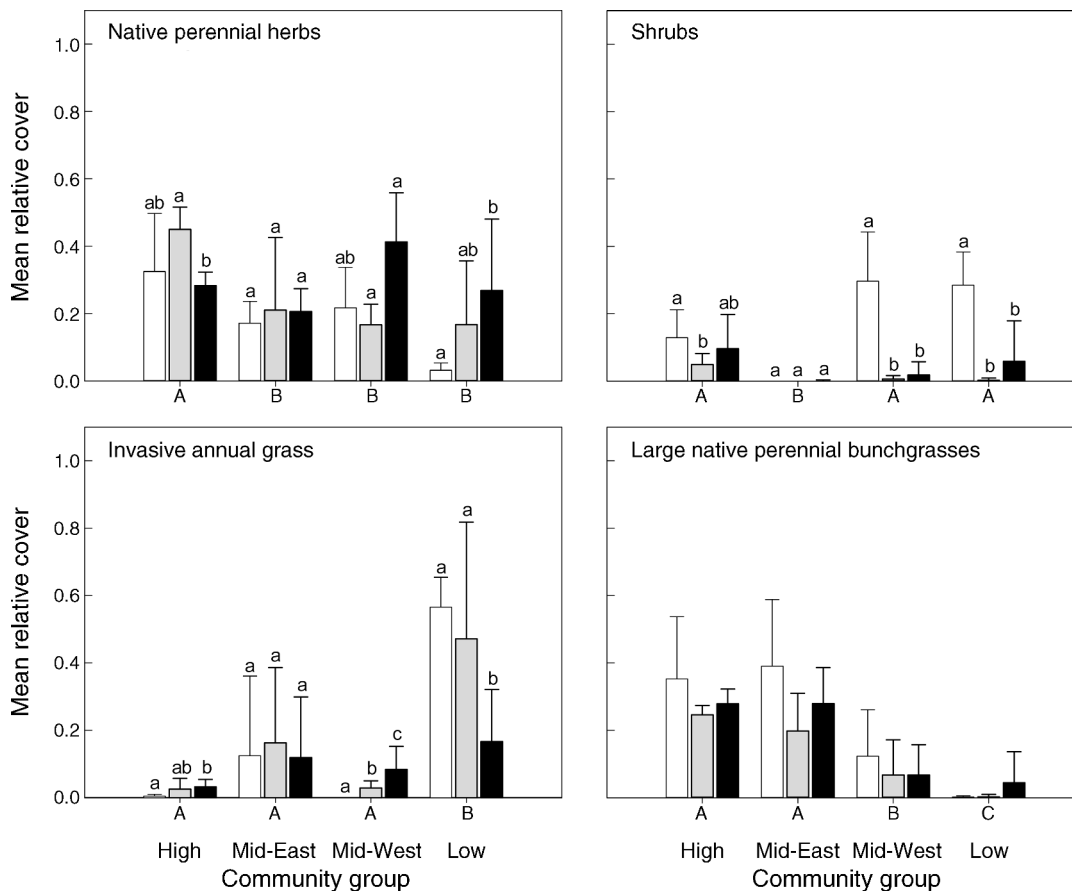


FIG. 1. Relative abundance (mean + SD) of four key plant functional groups in each of four community groups in 1996 (open bars), 2002 (gray bars), and 2009 (black bars) in the Arid Lands Ecology Reserve (ALE), south-central Washington, USA. Differences in cover between communities over all three years are shown in uppercase letters below community names; communities with the same letter are not significantly different ($P > 0.05$). Where the community \times year interaction was significant ($P < 0.05$), differences between years are shown with lowercase letters above each error bar; years within a community with the same letter are not significantly different ($P > 0.05$).

perennial herbs, but the “year \times community” term was significant for each functional group, indicating that temporal trends differed among communities. Invasive annual grasses declined in the Low community while increasing in the High and Mid-West communities. Shrub cover was relatively high in 1996 on all except the Mid-East transects, declined significantly by 2002, and

recovered most strongly in the High community by 2009. Across all communities, cover of large native perennial bunchgrasses only differed significantly between 1996 and 2002. Their cover was significantly greater in High and Mid-East community groups than in Mid-West and Low groups, but in all groups cover generally seemed to be greater in 2009 than in 2002.

TABLE 4. Summary of PERMANOVA analyses examining differences in the relative abundance of four functional groups.

Factor	df	Invasive annual grasses		Shrubs		Native perennial herbs		Large native perennial bunchgrasses	
		F	P	F	P	F	P	F	P
Community	3, 21	13.082	<0.001	5.623	0.006	5.598	0.006	20.394	<0.001
Transect (Community)	21, 42	2.526	0.005	2.481	0.005	1.467	0.137	2.509	0.004
Year	2, 42	2.505	0.091	48.485	<0.001	4.283	0.022	6.360	0.005
Year \times Community	6, 42	2.315	0.050	11.203	<0.001	3.305	0.011	1.811	0.121

Notes: The degrees of freedom (numerator, denominator) were the same for all functional groups. “Community” refers to the community groups identified by the cluster analysis of data from 1996 (Appendix D). Results of pairwise comparisons of community and years within each community are shown in Fig. 1.

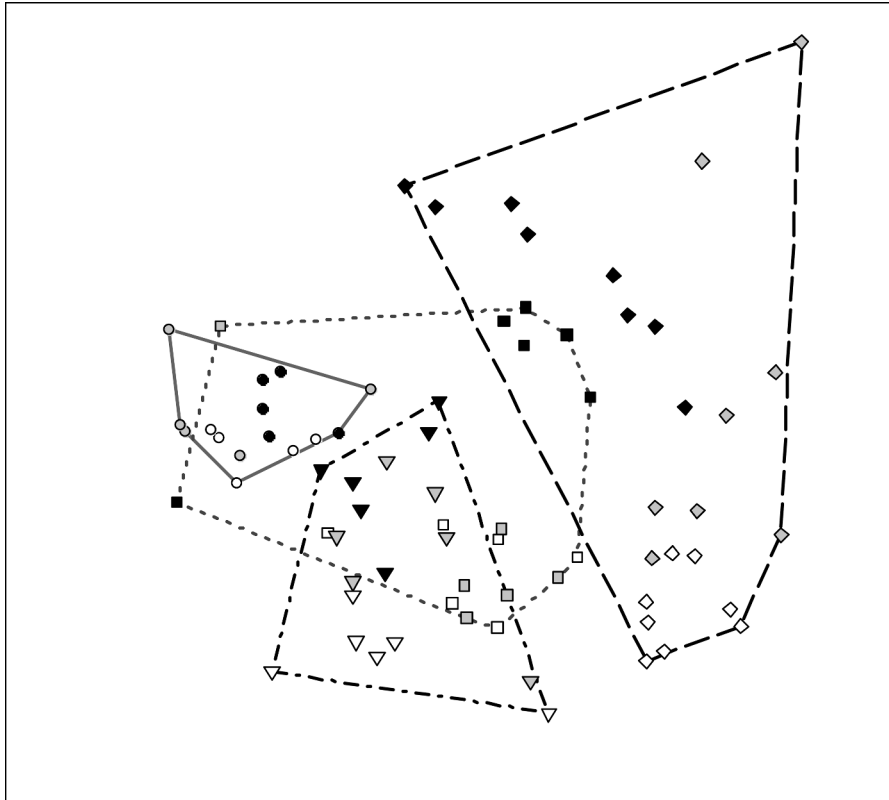


FIG. 2. First two axes of a NMDS (nonmetric multidimensional scaling) ordination of all transects in 1996 (open symbols), 2002 (gray symbols), and 2009 (black symbols). High (circles), Mid-East (triangles), Mid-West (squares), and Low (diamonds) community groups identified in 1996 via cluster analysis (Appendix D) are also shown, each inside a polygon enclosing the area occupied by the given community over all years. The final three-dimensional solution had a stress of 16.97.

Native perennial herbs peaked in 2002 in the High community, but in 2009 in the Low and Mid-West communities.

Community trajectories of change

The four communities remained relatively independent in ordination space (Fig. 2), although the Mid-West community overlapped the others. This overlap reflected changes in composition over time; in 1996 the groups formed relatively tight clusters of points with no overlap.

Trajectories clearly differed among communities (Fig. 3). Low-elevation communities showed substantial change between 1996 and 2002, with little sign of a return to initial conditions by 2009. Mid-East and Mid-West communities showed considerable variation in response to the 2000 fire, diverging from their initial state in multiple directions. Between 2002 and 2009, however, Mid-West transects moved in a more-or-less consistent direction suggesting reduced between-transect heterogeneity, while Mid-East transects continued to show a variable response to the second fire. Only two of the mid-elevation transects showed any evidence of a return toward their starting state. High-elevation transects moved relatively short distances from their

starting state, indicating relatively little response to either fire. Several High transects were closer to their initial composition following the second fire than they were in 2002.

There were considerable changes in the abundance of common species (Fig. 4) and noticeable changes in community composition between years (Fig. 5). In 1996, low-elevation transects, located on the right-hand side of the ordination space (Figs. 2, 4, and 5), were strongly associated with *A. tridentata* and *B. tectorum*, whereas higher-elevations (left-hand side of Figs. 2, 4, and 5) were associated with *A. tripartita* and bunchgrasses such as *P. spicata*, *F. idahoensis*, and *Poa cusickii* Vasey. Species relatively common across all transects, such as *P. secunda* and *P. longifolia*, and those typically found at mid-elevations, such as *Machaeranthera canescens* (Pursh) A. Gray, *Balsamorhiza careyana* A. Gray, and *Lomatium macrocarpum* (Nutt. ex Torr. and A. Gray) J.M. Coult. and Rose, generally occupied the center of the ordination. Two key patterns of change from 1996 to 2009 were clearly visible. First, the change in the relative sizes of the polygons (Fig. 5) suggested a large increase in the variability in composition between transects following the 2000 fire and a decrease in variability from 2002 to 2009. This agrees with the results of the

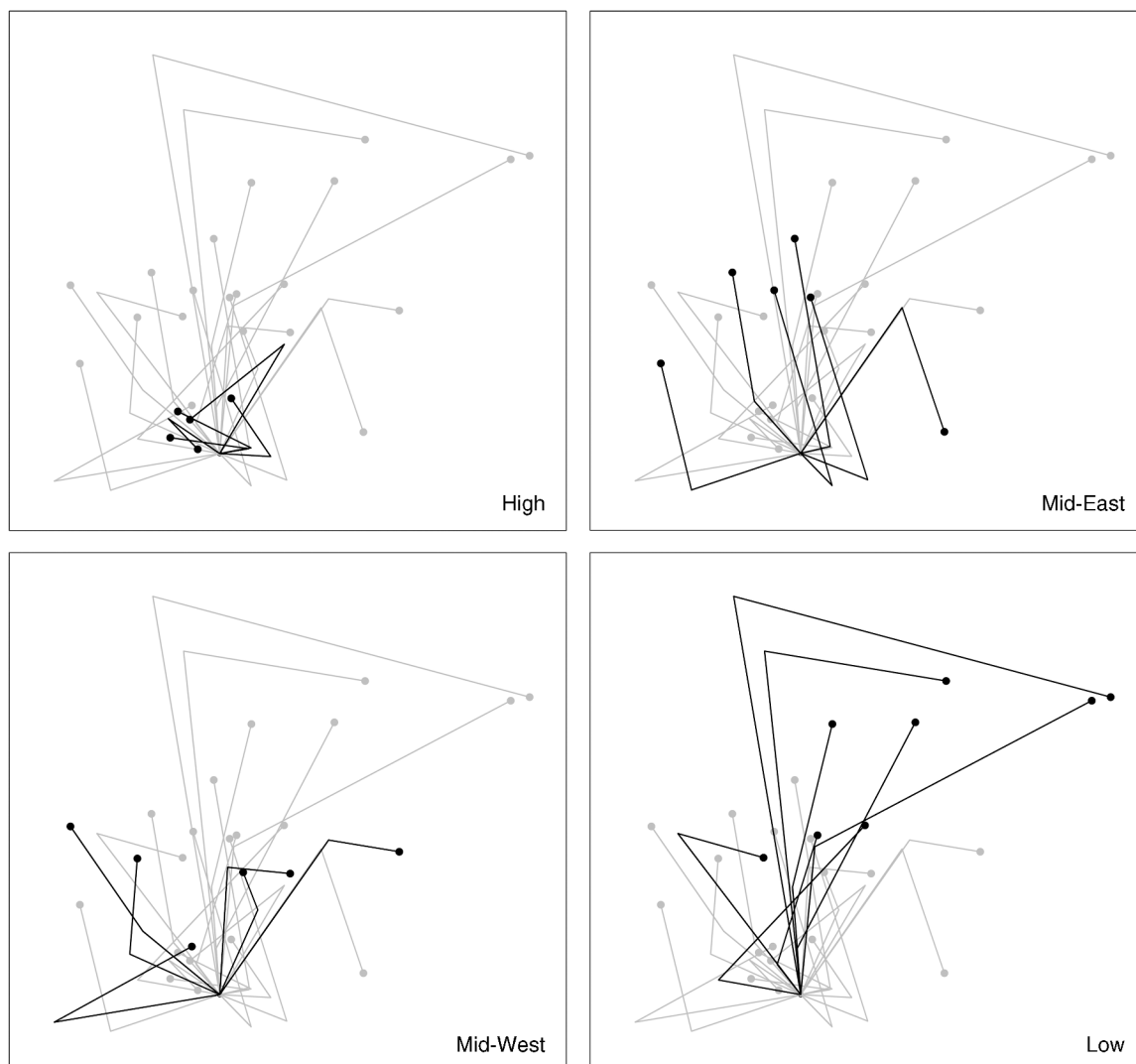


FIG. 3. Trajectories of change in community composition from 1996 to 2002 to 2009 for each community group identified in 1996. Each transect is shown as a vector with its coordinates in the NMS ordination each year translated by those of its 1996 position. As a result, its 1996 position is at the origin, the angle between the two line segments shows its position in 2002, and the circle shows its position in 2009. To facilitate comparisons among communities, each graph contains all trajectories, with those for transects from other communities shown in gray.

Mantel tests. Second, there were noticeable differences in the movement of transects belonging to each community group within the ordination. High-elevation transects moved little, whereas those from lower elevations moved substantially; thus the polygons essentially pivot around the location of higher-elevation transects (Fig. 5). These movements mirror and explain those seen in the community trajectories (Fig. 3). The large movement in the low-elevation transects reflected declines in the abundance of *A. tridentata* and *B. tectorum*, recovery of some native perennial species, and a stronger association with *P. secunda* and early-successional, invasive species such as *S. kali* and *Chenopodium leptophyllum* (Moq.) Nutt. ex S. Watson. The expansion of *P. secunda* at low elevations was

particularly strong (Fig. 4). Mid-West and Mid-East transects appeared to coalesce to occupy positions close to the center of the ordination with the former associated with *Hesperostipa comata* (Trin. and Rupr.) Barkworth, *P. longifolia*, and *S. kali*, and the latter with *P. spicata* and a range of native forbs (Figs. 2 and 5). Higher-elevation sites remained relatively fixed (Fig. 5), occupying similar positions in ordination space in all three years. Species common across high- and/or mid-elevation sites such as *P. secunda*, *P. spicata*, and resprouting shrubs such as *A. tripartita* generally showed only moderate reductions in cover in response to the two fires, whereas others, such as *P. longifolia*, expanded remarkably.

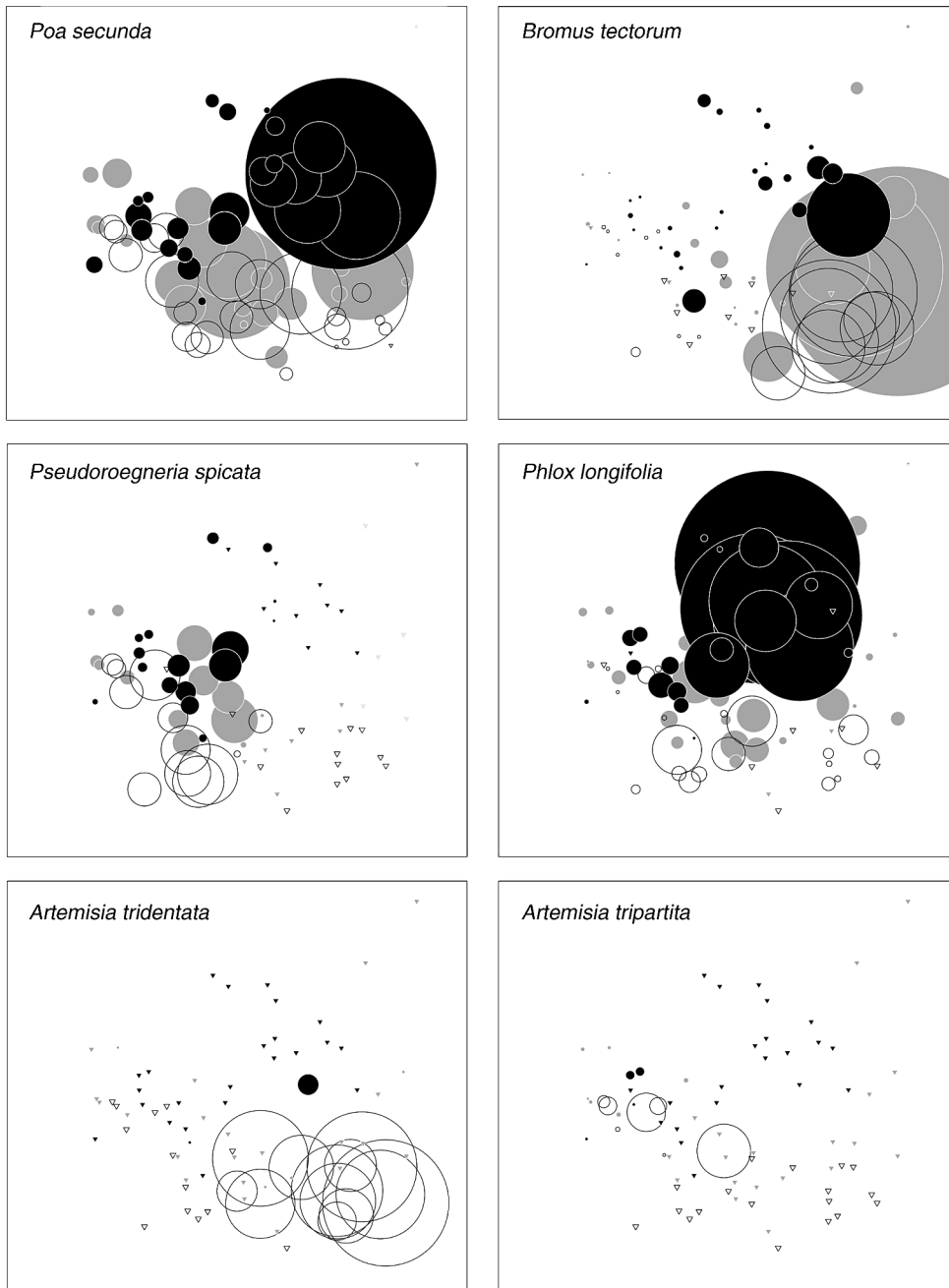


FIG. 4. Changes in the relative cover of the five most abundant species and of *Artemisia tripartita*, which was not widespread but was included for comparison with *A. tridentata*. Data from 1996 (open circles), 2002 (gray circles), and 2009 (black circles) are overlaid onto the same ordination as in Fig. 2. Symbol size is proportional to species relativized abundance (rather than actual cover); the scale is the same for all species. Transects with zero abundance for a given species are shown as small triangles.

The net result of these trajectories was that, by 2009, transects in the Low and Mid-West groups were relatively similar (Fig. 2) and were separated from Mid-East and High groups by differences in large bunchgrass and forb composition. The wide scatter of transects in 2002 (Fig. 2) was suggestive of patchy fire effects and was reflected in the reduced Mantel r statistic for that year. A second fire in quick succession, followed

by restoration treatments, created two community groups dominated by differing bunchgrass and forb species, and led to an increased Mantel r in 2009. Thus, although the 1996 cluster communities remained significantly different from one another overall (PERMANOVA pseudo- $F_{3,21} = 5.16$, $P < 0.001$), the magnitude of the differences decreased considerably (Table 3). A cluster analysis of the 2009 data confirmed these

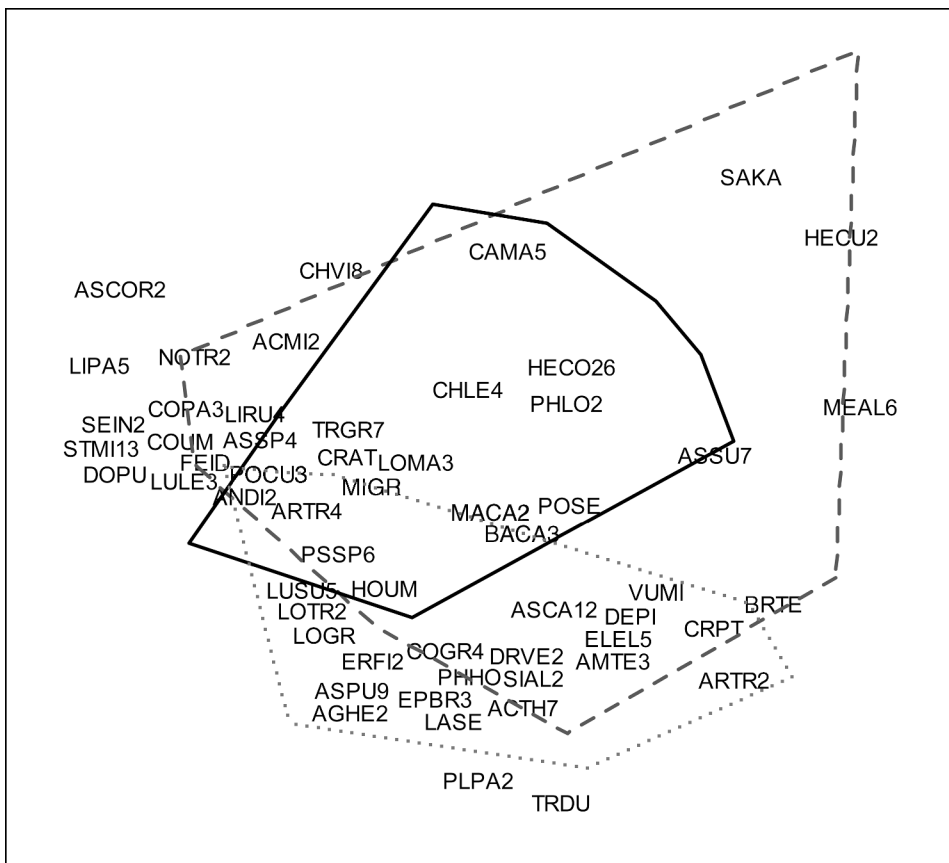


FIG. 5. First two axes of a NMDS ordination of all transects in 1996, 2002, and 2009 (as in Fig. 2), but emphasizing change in landscape-scale vegetation composition. Polygons surround the area occupied by plots in 1996 (dotted line), 2002 (dashed line), and 2009 (solid line). The text shows the centroids of species locations using standard USDA (2010) species codes (Appendix C). One species (*Ambrosia acanthicarpa*) was an extreme outlier in the top right corner; the figure has been cropped to focus on the core area.

patterns and suggested that ALE's vegetation could indeed be reasonably be classified as two community groups (Appendix D), with higher elevations dominated by *P. spicata*, *P. secunda*, *B. tectorum*, and *P. longifolia*, and lower elevations dominated by *B. tectorum*, *S. kali*, and *P. secunda*.

DISCUSSION

Ecologists and land managers have long been concerned that invasion by *Bromus tectorum* and increased fire risk from human activity can interact to generate a wildfire–invasion feedback cycle that results in fundamental changes to sagebrush steppe ecosystem structure and function (Knick and Rotenberry 1997). Although plant communities in semiarid areas can show significant variability in cover and composition over time in response to patterns of precipitation and water availability (Anderson and Inouye 2001, Bates et al. 2006), the magnitude of the changes that we observed indicates that some plant communities within the sagebrush steppe can experience substantial, lasting

changes in vegetation composition following repeated wildfires.

Differences in communities' responses to repeated fires and restoration treatments were largely a function of their initial floristic composition (itself an expression of the strong abiotic gradient and historic disturbance and invasion processes on ALE) and the particular traits of the species present. Prior to the 2000 fire, low-elevation transects were mostly composed of *A. tridentata*, with a heavily invaded understory dominated by *B. tectorum*. In contrast, higher-elevation transects showed generally reduced shrub cover in eastern areas of ALE (resulting from fires prior to 1996) and a stronger association with native perennial bunchgrasses and *A. tripartita*. The dominant species in each of these communities vary significantly in their response to fire. Although *A. tripartita* and perennial bunchgrasses are able to resprout following burning, *A. tridentata* and *B. tectorum* are obligate seeders. Considering the size of the fires and the absence of shrubs afterward, it is unsurprising that we saw little evidence of regeneration. Similarly, although *B. tectorum* is a profuse seed

producer and can disperse relatively readily (Boudell et al. 2002), the successive fires, together with herbicide applications at lower elevations, may have depleted the soil seed bank and thus reduced its dominance. It was, however, notable that by 2002, prior to the application of herbicide, *B. tectorum* had already recovered to, or exceeded, prefire levels (Figs. 1 and 4). Such rapid recolonization by *B. tectorum* following fire is a common observation (e.g., Allen and Knight 1984, Young and Evans 1985). Although relatively wet conditions in 1996 (Appendix B) might explain the relatively high abundance of *B. tectorum* in that year, this cannot explain the significant declines between 2002 and 2009 or the significant increases in abundance witnessed at higher elevations. We therefore suggest that herbicide application was the main cause of the significantly reduced *B. tectorum* abundance at low elevations in 2009. Future work will attempt to quantify the relative roles of repeated fires and restoration in driving community change.

The successive fires have had considerable impacts in lower-elevation communities over and above the loss of shrub cover: these communities moved the farthest from their 1996 state. It should be noted that some of this movement was driven by desirable changes from prefire conditions, such as the expansion of large bunchgrasses (Fig. 1). The effects of reseeding with large native bunchgrasses after the first fire were not detectable in 2002 but, in combination with further reseeding in 2008, may have contributed to a small increase in relative bunchgrass cover by 2009. It should be noted, however, that the comparatively large cover in 2009 (Fig. 1) is due to substantial bunchgrass cover on just a quarter of the transects. That no large bunchgrasses were recorded on the other transects, and the short space of time between seed applications in 2008 and monitoring in 2009, suggest that these changes either are attributable to patchy restoration successes following the first fire or are simply due to declines in the absolute cover of previously dominant shrub and *B. tectorum* populations. There was also a noticeable increase in *P. secunda* (Fig. 4) that may reflect the expansion of existing plants following the removal of shading by the *A. tridentata* canopy, reduced resource competition from *B. tectorum*, and the species' inclusion in restoration seed mixes. Despite these positive changes, low-elevation sites showed little recovery, and in 2009 were dominated by weedy, early-successional species such as *Ambrosia acanthicarpa* Hook., *C. leptophyllum*, and *S. kali*.

At mid-elevations, it was noticeable that, in 1996, the transects separated into two distinct community types: Mid-West and Mid-East. This can largely be ascribed to earlier fires that removed big sagebrush from the eastern transects (Fig. 1). After the 2000 fire, the mid-elevation communities moved in various directions, suggesting that the fire had a rather patchy effect even at relatively small spatial scales. The effects of the second fire were also somewhat variable. Mid-East transects moved in a

variety of directions without showing much evidence of a return to their initial composition. For the Mid-West community, the trend was more unidirectional, with five of six transects continuing to diverge away from their initial composition. In general, however, mid-elevation transects showed less movement from their initial state than those at low elevations. Although there were declines in the relative cover of large bunchgrasses following the first fire, the trend was relatively flat for Mid-West communities and showed an increase in Mid-East communities following the second fire (Fig. 1). Such patterns could be attributable to: (1) higher mortality in 2000 compared to 2007 due to reduced fire severity associated with a lower fuel loading for the 2007 fires; (2) reduced mortality in 2007 due to differences in the time of year when the wildfires occurred (early summer for 2000 and late summer for 2007), meaning that large bunchgrasses and perennial forbs were still active at the time of the 2000 fire; (3) recovery of bunchgrass populations following fire due to the effects of reseeding; (4) declines in cover from 1996 to 2002 due to unusually high productivity in 1996 associated with greater precipitation (Appendix B); or indeed (5) a mixture of all of these factors. Teasing apart these effects will require further investigation. Comparisons of the whole-year polygons (Fig. 5) and species centroids (Fig. 4) suggest a generally reduced association with invasive annual species and an increased association with *P. secunda* and *P. longifolia*. The latter change was particularly noticeable, with remarkable carpets of *P. longifolia* dominating large areas at mid-elevations in 2009 (Fig. 4). Fuel consumption by repeated fires, at least temporarily, will have reduced the abundance of all functional groups, meaning that rapid re-expansion of invasive species should be expected. The invasives currently most commonly found in mid- and higher elevations (*D. verna*, *H. umbellatum*, *S. altissimum*) generally pose less of a threat to ecosystem function than does *B. tectorum*, but their presence may be indicative of initial phases of degradation. Thus, in Mid-West transects, although populations of *B. tectorum* are still relatively small, they have increased significantly over the course of our study despite herbicide applications in 2002 and 2008 on three of the six transects (Fig. 1, Table 1).

High-elevation communities were remarkably resilient to the effects of repeated fire. Their trajectories of change showed minimal movement following the first fire and evidence of a return to close to their initial state following the second. The whole-year polygons (Fig. 5) confirmed such patterns, with the movement from year-to-year essentially pivoting around the location of these transects. As previously discussed, the traits of plants in these higher-elevation communities make them less sensitive to the effects of burning. The lower abundance of invasive species prior to both fires potentially reduced propagule pressure and prevented rapid invasion following the burns. However, these transects did not

receive herbicide applications and it is salient to note that *B. tectorum*, while still not abundant, increased significantly in these locations by 2009 (Fig. 1). The consecutive fires may have reduced the abundance of perennial vegetation and opened up large amounts of niche space, but we are unable to draw robust conclusions on this from our data. Previous research (Chambers et al. 2007) suggests that these sites are now at greater risk from invasion.

Overall, the two fires have led to a significant restructuring and simplification of plant communities across ALE. Heterogeneity increased following the 2000 fire, as seen by the increased polygon area in Fig. 5 and reduced Mantel r in 2002. Variation in fire severity, species sensitivity to fire, abiotic conditions, restoration treatments, and interactions between these four factors may explain the changing patterns in heterogeneity. For example, the reduced shrub cover across all transects and the fact that *B. tectorum* tended to increase where it was previously absent while decreasing where it had been abundant, reduced the difference between sites for some of the most abundant species. In such a situation, variation in the composition of other species can become more important in defining differences between communities. Thus in 2009 two clear community groups can be identified (Appendix D). High-elevation and eastern mid-elevation sites are characterized by bunchgrasses such as *F. idahoensis*, *P. cusickii*, and *P. spicata*. Low-elevation and western mid-elevation sites are characterized by bunchgrasses such as *H. comata*, invasive or opportunistic annuals such as *S. kali*, *A. acanthicarpa*, and *C. leptophyllum*, and forbs such as *P. longifolia*.

On ALE, severely degraded plant communities seem to be associated with harsh environmental conditions (low elevations with sandy soils, widespread postfire soil erosion, higher temperatures, and lower precipitation). Restoration activities following the fires have also had an effect on plant communities: large areas of ALE have received herbicide applications (see Table 1 for types applied) that significantly, if temporarily, reduced the abundance of *B. tectorum*. The effect of seeding with native species was difficult to untangle from the impacts of fire and climatic variability, but successes appeared to be patchy. A key aim of future research is to untangle these interacting factors to understand their relative importance for individual sites' trajectories of change. Further monitoring is required to track how the sites are changing in response to restoration treatments applied after the 2007 fire.

Our approach has a number of drawbacks, including that we only analyzed changes in the relative cover of species. Examining absolute values would better highlight the effects of fire in opening niche space or the loss of community dominants such as *A. tridentata*. Unfortunately, such an approach also risks strengthening the effects of confounding factors such as variation between different observers and interannual variation in phenology caused by variation in the timing of monitoring. In

addition, although ordinating all years together allows us to effectively visualize changes in community composition over time, it also renders us unable to draw strong conclusions about the composition of communities and relative dominance of different species in any one year. Such finer-scale patterns of change are the subject of ongoing research.

Implications for state and transition models

We have demonstrated that repeated disturbances (repeated fire with or without subsequent restoration) can drive significant changes in vegetation. Stringham et al. (2003) cautioned to avoid confusing changes in vegetation community with changes in state, and there indeed has been considerable variation in the literature as this concept has evolved. For example, Allen-Diaz and Bartolome (1998) and Hemstrom et al. (2002) both defined vegetation states that appear to be different communities rather than states, although the latter authors did include a clear threshold between invasive and native-dominated systems. By contrast, McIver et al. (2010) clearly distinguish between native-dominated "reference states" and highly invaded "degraded" states, each containing a number of potential communities. Similarly, Bestelmeyer et al. (2009) defined a model that contains individual states, defined by the relative dominance of species functional groups, each of which contains one or more "phases" of species composition. Our research suggests that it is helpful to distinguish shrub- from grass-dominated states and native- from invasive-dominated states. These two axes outline a model (Fig. 6) that clearly distinguishes between the functional attributes of the system.

Responses to disturbance, however, are dependent on the nature of the disturbance regime and the functional traits of the plant community. Disturbances such as fire can differ strongly in frequency, pattern, and size, and therefore can have different effects on the vegetation. Repeated burns can cause transitions among communities and potentially over state boundaries. Conversely, fires that leave behind some nearby shrubs, perhaps because a small area is burned or the fire is patchy, allow recolonization of obligate seeder species like Wyoming big sagebrush. Thus, although the community at the patch scale may become grass- rather than shrub-dominated, it does not cross a fundamental threshold in state. Functional traits linked to regeneration and dispersal are also important. Communities dominated by resprouting species, such as perennial bunchgrasses and shrubs such as *A. tripartita*, *E. nauseosa*, and *C. viscidiflorus*, will show greater resilience to fire than those dominated by obligate seeders. In contrast, traits favoring rapid dispersal by invasives, such as *S. kali*, *S. altissimum*, and indeed *B. tectorum*, may increase propagule pressure in burned areas and encourage more rapid transitions.

On ALE, low-elevation transects previously dominated by sagebrush and *B. tectorum* have crossed a shrub-

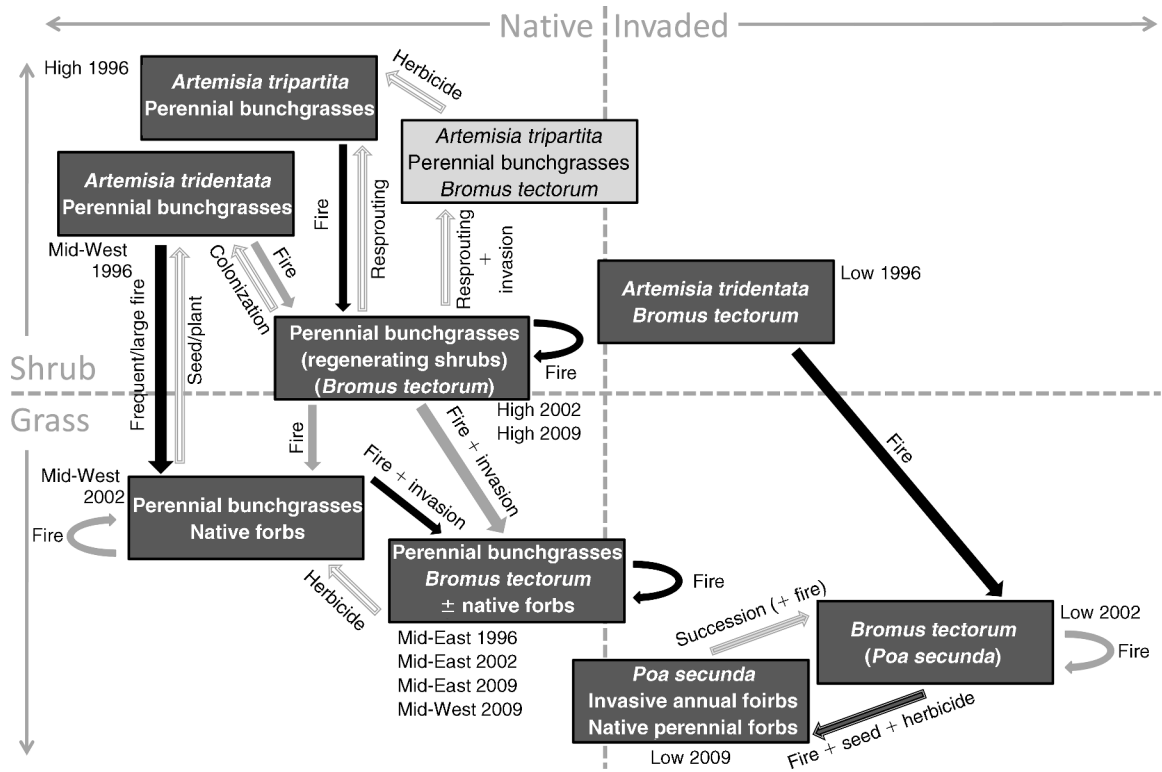


FIG. 6. State and transition model for sagebrush steppe with one dimension related to relative shrub/grass dominance and the other to the degree of invasion by exotic species. Each quarter of the diagram represents a separate state containing a number of community types. Community types observed in our study are shown as dark gray boxes; included near each is a list of the community group \times year combinations that exemplify it. A hypothesized community type is shown as a light gray box. Dominant species or functional groups are listed within each box; important species or groups that are present but not dominant are shown in parentheses. Disturbances cause transitions that may push communities over compositional thresholds into a different quarter of the diagram, and hence into a new state. Some communities overlap state boundaries because they can be considered “in flux,” with their final state to be determined by the nature or frequency of future disturbances. Transition causes are labeled using solid arrows for fire and outlined arrows for restoration activities and regeneration. Key transitions seen in our study are shown as black arrows; other potential transitions are shown in gray.

presence threshold due to the frequent fires, lack of shrub seed source, and competition for resources with *B. tectorum*. The current community is dominated by *P. secunda* and *B. tectorum*, and is dynamic but unlikely to return to any semblance of a sagebrush steppe community without significant intervention. *B. tectorum* was already abundant on these transects in 1996, indicating that it had already crossed an invasion threshold that reduced its resilience to future burns. Mid-elevation sites showed altered community structure when they first lost their shrub cover (either in, or prior to, the 2000 fire). Subsequent fires mean that there are now few individuals from which shrub recolonization can occur, and these areas have entered a grassland state (Fig. 6). The presence of *B. tectorum*, currently at low levels due to herbicide applications, also pushes the communities closer to an invasive-dominated state.

Continued monitoring and data from sites spanning a wider range of fire and restoration histories are needed to generalize our model and to include a more complete range of potential transitions. Nevertheless, our model

allows us to make a number of generalizations about patterns of change in the sagebrush steppe. Although abiotic conditions are important in structuring vegetation, communities will be most resilient to repeated fire if they are dominated by resprouting species and have low densities of invasive species. Such communities may be arrayed anywhere on the shrub/grass axis. Although repeated fires do not seem to precipitate a change in state in grass-dominated communities, they prevent colonization by obligate seeders such as big sagebrush and thus prevent transition to a shrub-dominated state. For communities with big sagebrush, good cover of native bunchgrasses, and few invasives, fires will cause substantial movement away from their initial composition. Where fires are small, or some shrubs survive, this change will not result in a fundamental change in state. Where there is invasion by *B. tectorum* and repeated burns, however, a transition to a grassland-dominated invasive state will occur. Finally, when low-elevation sites become invaded by *B. tectorum*, their fuel structure almost guarantees that fires will be extensive and severe.

Burns in such communities expose them to a significant risk of shrub-to-grass and native-to-invasive state transitions, and the harsh environmental conditions make restoration activities challenging.

Implications for management and restoration

Invasive plants represent a challenge for the restoration of robust native plant communities. Some communities are more robust than others, although repeated fires may create an opportunity for invaders by opening up niche space. On ALE, repeated fires and herbicide application appear to have significantly, but no doubt temporarily, reduced populations of the key invader *B. tectorum* at lower elevations. The fires have also created significant amounts of empty niche space for which native and invasive plants can now compete. Controlling invasive populations and preventing reinvasion must be a priority, either via seeding or out-planting with competitive native plants, or by continued herbicide application. Differences in fire severity, disturbance history, and restoration treatments between different areas of our study site make it difficult to untangle the effects of each of these factors. In particular, we do not know how our Mid-West and Low-elevation communities would have responded to repeated fires without follow-up herbicide applications. As a result, our state and transition model (Fig. 6) presents a number of hypotheses (gray arrows) about the potential effects of invasion and management that need quantitative testing. It is worrying that higher-elevation transects, although generally recovering better than others from the effects of the fires, now have greater relative cover of *B. tectorum* than prior to the first fire. Reducing the spread of invasive species in such areas is important if we are to enable native plant communities to move back toward their high-quality, prefire state. Despite such concerns, the reduced abundance of *B. tectorum* at lower elevations does present an opportunity to reestablish high-quality sagebrush-dominated vegetation across ALE, although this window is likely to be short-lived (Humphrey and Schupp 2001, Eiswerth et al. 2009). Significant efforts have been made to reestablish populations of native plants at lower elevations, but, given the short time interval since these were applied, it remains too early to judge their success.

Although restoration efforts can play a key role in constraining the invasion of alien species (Bakker and Wilson 2004), there is also evidence that native plants can facilitate *B. tectorum* invasion (Belnap and Sherrod 2009, Goergen 2009). Increasing populations of *B. tectorum* may be inevitable without novel management approaches. Identifying areas that can, in essence, be treated as buffers to protect regions where degradation is not so severe might allow restoration elsewhere to meet with greater success. Fuel management and control of invasives should be priorities in such zones. There has been recent discussion about the relative importance of restoring ecosystem function as opposed to exact pre-

disturbance communities (Brown et al. 2008). On highly disturbed sites at low elevations, we suggest that the focus should be on restoring function and rapidly filling niches with species that can effectively compete with *B. tectorum* for resources.

Conclusions

Repeated disturbances challenge many of the assumptions implicit in conceptual models of vegetation succession and rangeland health. In the sagebrush steppe, they can cause precipitous declines in the abundance of some shrubs, but, when combined with postfire herbicide treatments, they may also at least temporarily reduce populations of some invasive annuals. Repeated burns simplify landscapes by removing fire-intolerant species, depleting soil seed banks, simplifying niche diversity (Davies et al. 2008), and reducing overall vegetation cover. The direction of communities' trajectories of change, and their resilience to repeated fire, are strongly governed by species traits. For example, the resilience of higher-elevation communities is related to the ability of dominant species to resprout. At lower elevations, traits such as rapid dispersal and increased competitive ability under higher stress conditions (e.g., drought avoidance and early-spring resource preemption) seem to explain the switch from dominance by *A. tridentata*/*B. tectorum* to dominance by *P. secunda*/*S. kali*. This latter community does not represent a stable state, because *S. kali* is likely to be displaced by recovering *B. tectorum* populations (Allen and Knight 1984). Following repeated disturbance, communities will continue to change due to the large amounts of empty niche space available. Propagule pressure (Lockwood et al. 2005) may play a crucial role in determining the extent to which alien species are able to take advantage of this situation. We propose a state and transition model that has some important differences from those presented previously, specifically the need to separately account for grass/shrub and native/invasive states as well as the impacts of compounded disturbances and species traits. Nevertheless, our conclusions are similar to those of Hemstrom et al. (2002) and McIver et al. (2010), whose models also suggest that aggressive restoration work reestablishing native shrubs, bunchgrasses, and herbs will be required to reestablish "classic" sagebrush steppe vegetation on highly disturbed, lower-elevation sites. To succeed, these efforts will also need to continue to control invasive species and their effects on fuel load and continuity. We suggest that state and transition models that characterize sites according to shrub/grass and native/invasive dominance will allow us to better visualize potential changes in shrub canopy and ground layer vegetation structure. Such models require further development, but should allow managers to develop effective restoration treatments and to predict the likely impacts of a particular disturbance.

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SUPPLEMENTAL MATERIAL

Appendix A

Maps showing the location of the Arid Lands Ecology Reserve and the monitoring plots in relation to the Reserve's strong elevational gradient (*Ecological Archives* A022-082-A1).

Appendix B

Precipitation records from the local meteorological station between 1980 and 2009 (*Ecological Archives* A022-082-A2).

Appendix C

List of species present on >5% of transect/years used in this study, including species names, life-form, status (native/invasive) and USDA Plants Database code (*Ecological Archives* A022-082-A3).

Appendix D

Dendrograms and maps of ALE showing the results of cluster analyses on vegetation in 1996 and 2009 (*Ecological Archives* A022-082-A4).