Multiple fires and landscape factors affect vegetation composition over time and interact to affect biological soil crust cover

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Abstract

Multiple fires and landscape factors affect vegetation composition over time and interact to affect biological soil crust cover.

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Vegetation and biological soil crusts (BSCs) in arid lands are affected by abiotic landscape factors, interactions among organisms, and disturbance. Multiple disturbances may affect communities differently than a single disturbance because thresholds of resistance can be overcome, moving a community toward a new stable state. In the shrub-steppe in the western United States, the historical fire return interval was more than 100 years, but with the spread of an invasive annual grass, *Bromus tectorum,* and increased anthropogenic ignitions, large fires are becoming more frequent. Plots across an elevational gradient in the Columbia Basin were monitored between 1994 - 2010 to investigate trajectories of vegetation response to large fires in 2000 and 2007. Communities differed from their initial composition after each fire. Low elevation communities that had Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), a species that burns with relatively high severity and does not resprout, became characterized by fire-tolerant native and early seral invasive species. Restoration efforts prevented dominance by invasive species. Higher elevation plots were resilient, maintaining much of their pre-fire composition because most characteristic species resprouted. The long term changes demonstrate interactions among topographic position, vegetation, and disturbance. BSCs in northwest cool deserts are dominated by mosses and lichens with varying tolerance for shading from vegetation and varying rates of recovery from disturbance. Transects were surveyed for cover of BSC and vegetation in 2010. Structural Equation Modeling (SEM) was used to assess direct and indirect effects of landscape, vegetation, and disturbance factors on BSC. Elevation positively affected vegetation and BSC cover indirectly through soil texture. Number of years since last fire was significantly negatively related to moss and *B. tectorum* cover. Lichen cover was positively related to moss cover and negatively related to *B. tectorum*. Understanding successional relationships in the landscape context allows prioritization for restoration. Preserving high elevation bunchgrass communities protects extant BSC cover and active management of low elevations, such as removing invasive species and planting native species, may assist BSC recovery and prevent transition into an alternative vegetation state.

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Changes in sagebrush shrub-steppe vegetation in response to multiple fires

Introduction

Response of ecosystems to a single disturbance has been investigated extensively, but recently, attention has focused on multiple disturbances outside the range of historical variability (White and Jentsch 2001). A disturbance is a discrete event that removes biomass or changes available resources (White and Jentsch 2001). Compound disturbances, whether of a physical or biological nature, may yield ecological "surprises" (Paine et al. 1998), such as novel species combinations or functional attributes. A system that is resistant or resilient to a single perturbation may be significantly altered in structure or function by multiple disturbances that push an ecosystem past a threshold (Suding et al. 2004). The system then has stable alternative or novel compositions or processes that persist with a new set of feedback processes.

Species differ in tolerance to disturbance. Community composition may reflect site characteristics such as elevation, soil type, or disturbance history. If there is heterogeneity across the landscape, effects of disturbance will not be uniform (Turner 1989). Plant functional traits can help explain responses to biotic (e.g. competition from invasive species) and abiotic (e.g. fire or wind erosion) factors and give an indication to the effect on the ecosystem functioning (McIntyre et al. 1999). Functional groups may differ in access to deeper water sources, standing biomass, and strategies for recovering from disturbance (e.g. seeding versus resprouting). As the relative proportions of these groups change, the water use, flammability, and total cover of the system will change (Lavorel and Garnier 2002). Abundance and specificity of species may give insight into driving processes of community change (Bakker 2008).

The purpose of this study is to investigate these three scales (community, functional group, and species) in response to multiple fires in sagebrush shrub-steppe. Long-term data can show changes over time. Patterns of change associated with disturbance can be used to assess responses to disturbance (del Moral and Lacher 2005). Changes within a community type can show increasing or decreasing heterogeneity. The magnitude of change between subsequent years can indicate severity of disturbance or relative resilience between different community types. Changes to functional groups can show which are susceptible to or facilitated by changing resources and conditions. Species turnover and species identity can give an indication of successional trajectories.

The extent of the sagebrush shrub-steppe ecosystem of the Intermountain West has declined dramatically due to anthropogenic activity and invasive species (Noss et al. 1995). The historical fire return interval was formerly 60-100 years (Knapp 1996) but with the expansion of an introduced annual grass, *Bromus tectorum*, return intervals are being dramatically reduced. Invasions alter ecosystem processes, creating functional and compositional change (Dantonio and Vitousek 1992). The spread of *B. tectorum* leads to conditions for a grass-fire cycle (Knapp 1996) with frequent, large fires that can prevent sagebrush steppe ecosystems from following historical post-disturbance successional trajectories. Understanding responses to multiple threats are essential to retain diversity at the community, functional group, and species level.

Questions

1. Which environmental factors were associated with vegetation composition prior to burning?
2. How did low elevation and high elevation communities change over time with multiple fires? What factors contributed to the magnitude of change in each group?
3. How did different functional groups respond to multiple fires?
4. Which species characterized the low and high elevation communities and how did they change over time and with multiple fires? Which species experienced least inter-annual variation and what characteristics do they share?
5. Is there evidence that the system is moving toward an alternative stable state?

Methods

Site

Much of the shrub-steppe habitat has been converted to agriculture or degraded by heavy grazing. The Atomic Energy Commission (now Department of Energy (DOE)) requisitioned 625 square miles around the town of Hanford (Benton County, WA) for plutonium production in the Manhattan Project in 1943, displacing several homesteads and pasture land. In 1962, the area was fenced to exclude trespassing livestock and off-road vehicles. The Arid Lands Ecology Reserve (ALE) (46.42' N, 119.58' E) was established in 1967 to protect some of the high-quality sagebrush shrub-steppe habitat within the Hanford site.

Elevation on ALE ranges from 150 to 1100m (Figure 1). Lower elevations (below ~400 m) have loamy sand soils, including Warden Silt Loams, Esquatzel Silt Loams, and Ritzville Silt Loams, while higher elevations have loam soils including Lickskillet Silt Loams and Ritzville Silt Loams (NRCS 2011) (Figure 2). The higher elevation slopes are often stony loam with exposed bedrock fragments of basalt, and gullies are very rocky.

The climate is semiarid, with average July temperature of 25°C and average January temperature of 0°C. There is 175 mm of precipitation annually, most falling during winter months (October-April) (DOE 2010).

ALE contained many vegetation types across the elevational gradient with relatively stable and distinct groups of species prior to 2000, including stands of mature sagebrush (*Artemisia tridentata* ssp. *wyomingensis, Artemisia tripartita*), areas of mixed perennial grasses (*Pseudoroegeneria spicata, Poa secunda, Festuca idahoensis, Achnatherum hymenoides*), and areas of higher disturbance with invasive species (*B. tectorum, Salsola kali*) (Table 1).

There have been several large fires and many smaller fires documented on ALE since the 1950s. Recent fires have been larger with shorter return intervals between them than previously estimated (Knapp 1996). For example, the 24 Command fire in June 2000 removed much of the canopy vegetation of *A. tridentata* ssp. *wyomingensis* and burned a total of 66,000 hectares (31,000 ha on ALE) (Northern States Burned Area Emergency Rehabilitation Team 2000) and was the largest fire recorded in the region. The Wautoma and Milepost 17 fires in 2007 burned 31,000 ha, largely overlapping the footprint of the 2000 fire (Figure 1) (First Strike Environmental/Shaw BAER Team 2007).

Sampling Design

Vegetation plots were established in 1994 by David Wilderman for the "Biodiversity Inventory and Analysis of the Hanford Site" project for The Nature Conservancy (Soll et al. 1999). Fifty-six plots, each 5 m × 20 m in size, were established across ALE. Plots were subjectively situated to collect data where the vegetation had not been previously mapped. Areas that were highly disturbed or invaded were excluded.

Although the plots were not permanently marked, their locations were recorded with GPS and they were photographed.

Forty-two of the plots were relocated by GPS and photos by Jim Evans for The Nature Conservancy in 2001-2004 and were permanently marked (Evans and Lih 2005). The same vegetation cover groups were used as in 1994, but not all plots were visited in every year of monitoring (Figure 1, Appendix A). Plots were selected to represent a range of pre-fire vegetation types and *B. tectorum* invasion.

The plots were remonitored in 2009-2010 by the University of Washington Fires @ ALE project using the same methods. Timing of visitation attempted to match previous years by monitoring low elevation sites beginning in April and ending at higher elevations at the end of May.

For each plot, percent cover of vascular plants were recorded to the midpoints of cover classes bounded as follows: Present- < 1%; 1% - 5%; 6% - 15%; 16% - 25%; 26% - 35%; 36% - 45%; 46% - 55%; 56% - 65%; 66% - 75%; 76% - 85%; 86% - 95%; 96% - 100%. This scale reflects the slightly skewed nature of error of estimation, where extreme values have less error of estimation (Hatton et al. 1986). When observer error trials were run with Evans who had conducted the surveys in 2001 - 2004, the 2009 - 2010 crew was up to several classes lower in estimates of cover. Therefore all species data were relativized by total vegetation cover for analysis.

Soil type was recorded from soil maps (NRCS 2011). Elevation, aspect, and slope were extracted from 10m Digital Elevation Models (USGS 1999) and used to calculate Heat Load Index (HLI) (McCune and Keon 2002), with latitude held constant because it has little effect on resulting HLI due to low variation in latitude among the sites.

Analytical Methods

All data from the 42 plots recorded by Evans were used from 1994, 2001 – 2004, and 2009 – 2010 (Table 3). Species' morphological and duration groups follow USDA PLANTS Database (2011) and codes are in Appendix B. Unknown species and species recorded only to family were removed. These plants accounted for a total of 1.3% of the cover of all plots in all years. *Vulpia microstachys* and *V. octoflora* were lumped as *Vulpia* sp., and *Astragalus reventiformis* and *Astragalus columbianus* were combined as *Astragalus* cf. *reventiformis* due to difficulty in distinguishing these species.

Most analyses were conducted in R version 2.8.1 (The R Foundation 2008) using only species present on >5% of plots and standardizing by species maxima and row totals.

Initial community

A Mantel test was run testing for spatial autocorrelation using the “Vegan” package in R with Pearson’s correlation method compared to 9999 permutations. A Bray-Curtis (or "Sorensen's") distance matrix was used for vegetation data, and a Euclidean distance matrix was used for spatial data.

Cluster analysis was performed on abiotic data to form groups of plots with similar abiotic traits. HLI, elevation, and the middle value for sum of silt and clay for each soil type were relativized by range and converted to a distance matrix using Euclidean distances. The "hclust" function in the "stats" package was used with Ward's method. Groups were selected based on the dendrogram (Appendix C) (McCune and Grace 2002). The two groups that resulted were used as community groups throughout the remaining analysis.

Cluster analysis of vegetation composition in 1994 was performed with Bray-Curtis distance of the species matrix. The flexible-β method was used with the "agnes" function in the "Cluster" package, with $\beta = -0.25$ (McCune and Grace 2002).

Changes in community groups

To assess differences in composition and differences in magnitude of composition change, Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001) was used with Primer 6 version 6.1.13 with PERMANOVA+ version 1.0.3 from PRIMER-E Ltd (2009, IvyBridge, UK) (Clarke 2006). A Bray-Curtis distance matrix was calculated. For magnitude of composition change, the Bray-Curtis distance of each plot between subsequent measurements (1994 - 2001, 2001 - 2002, 2002 - 2003, 2003 - 2004, 2004 - 2009, and 2009 – 2010) were selected and Euclidean distance matrix of these distances was calculated in PRIMER. In both analyses, year, plot, and group × year were all fixed effects to account for repeated measures design. The main effect of group was not tested because grouping was based on abiotic factors. Pairwise comparisons were made at $\alpha = 0.05$. Permutation of residuals was performed under a reduced model and type III partial sums of squares with 9999 permutations.

Nonmetric Multidimensional Scaling (NMDS) was used to visualize community structure in groups and over time. This indirect ordination method is robust to mixed skewness and extreme skewness (Minchin 1987) and in this dataset, most species have extreme right-skewed tails, and a few have bimodal distributions. NMDS performs well with large datasets and is superior at displaying the overall relationship among samples rather than primary environmental gradients (Clapham 2011). Environmental gradients were already accounted for by the group designation making NMDS an acceptable method. A Bray-Curtis distance measure was used in the "metaMDS" function in the “Vegan” package in R. Two, three, four, and five dimensions were run with 20 maximum random restarts. The number of dimensions was selected for low stress and ease of interpretability. For visualization, the configuration was rotated using principal components analysis so that variance was maximized on first dimension. Functional group, nativity, and abiotic factors were fit to display on the ordination using the "envfit" function in the “Vegan” package with 9999 permutations. "Ordihulls" represent the projected two-dimensional ordination space occupied by each community group. To visualize the magnitude of change over each year interval, arrows connected each plot between successive years.

Functional Groups

Average relative cover (the proportion of each species cover to the total cover for that plot in that year) of five life form functional groups was calculated for annuals (including biennial) forbs, annual grasses, perennial forbs, perennial grasses, and shrubs (McIntyre et al. 1999). Analysis of variance in relative cover by plot and year was performed for each functional group in each community group separately.

Species Analysis

Species density was calculated as the average number of species recorded on each plot. Dominant species were determined by taking average relative cover of the species per year within each community group. Indicator Species Analysis (ISA) was used for each year separately to find species with high specificity and fidelity to each group (Bakker 2008). All species were included in case rare species for the total dataset were more important in a given year. Only the five species with the highest indicator value and $p < 0.01$ are presented.

Results

The full dataset included 149 identified species or genera (Appendix B), but 78 of which were rare species.

Pre-2000 community

There was significant similarity in community composition in 1994 due to spatial autocorrelation ($r = 0.33$, Mantel test $p < 0.01$). Sites that were closer to each other were more similar than sites farther away. Part of this difference is accounted for by grouping because abiotic clustering revealed two strong groups, primarily determined by soil type, with elevation and HLI making very little difference. The soils below 400 m are sandy loams while the soils above 400 m are either loams or stony loams (Figure 2).

The elevation and soil type gradients allowed classification of vegetation into two broader groups. In 1994, plots in vegetation clusters matched abiotic cluster groups. These groups were used throughout the analysis and represent a "high elevation" group and a "low elevation" group (Table 1).

Community groups

Composition was significantly related to year, plot, and group × year. Year had the largest pseudo-F statistic for explaining differences in composition, though plot identity was a significant main effect reflecting the repeated measures design (Table 2). Group × year was significant, indicating low and high elevation communities had different responses by year, with the low elevation community tending to have higher dissimilarity than the high elevation community among years. Within the low elevation group, all pairwise comparisons between years were significant except between 2009 and 2010. Within the high elevation groups, all pairwise comparisons between years were significant except between 2003 and 2004.

The three dimensional NMDS gave a stress of 18.19, indicating a fair fit given the large sample size. Although the stress declined to 14.65 with a four dimensional model, the three dimensional model was selected for ease of display and interpretation. Axis 1 was correlated with the elevation and soil texture gradients. Axis 2 was correlated with the gradient of shrub cover, *B. tectorum* cover, and annual species cover (Figure 3a).

The plots within the low elevation and high elevation community groups were generally non-overlapping throughout the dataset though there was variation within the groups (Figure 3b) Elevational groups became similar after the first fire (Figure 3c). The second fire re-separated the two groups (Figure 3d). Overall, there was a compression in the ordination space occupied by the plots, indicating a reduction in heterogeneity of composition over the years of recovery from multiple fires.

Magnitude of change in composition was significantly related to year and plot. Year had the largest pseudo-F statistic to explain magnitude of change in composition, and plot was significant reflecting the repeated measures design (Table 3). The interval had a greater impact on vegetation community than the identity of the plot because the same plot did not remain close together in subsequent years, rather dramatic shifts were common (Figure 4, Figure 5). Group × year was not significant indicating that the magnitude of change within a year was similar between low and high elevation groups. Pairwise tests for year showed significant differences between all pairs of distances except between 2002 - 2003 to 2003 - 2004 and 2001 - 2002 to 2004 - 2009 (Table 4).

The low elevation plots most associated with *A. tridentata* ssp. *wyomingensis* shifted the furthest after the first fire and became most strongly associated with annual species cover (Figure 4a). Plots in the low elevation group moved dramatically after the first fire in ordination space (Figure 4b). A few plots started to stabilize in the amount of composition change each year by 2003 and 2004 and there was very little change between 2009 and 2010 (Figure 4c). Between 2001 and 2004, some shifts were greater than the shift from 1994, perhaps indicating perennials were resprouting after near removal of above ground biomass. By 2009 and 2010, the plots again became more tightly clustered and did not significantly change between those years (Figure 4d).

In 1994, plots in the high elevation group were fairly dispersed but were distinct from those in the low elevation group. The least shifts overall occurred at the highest elevations associated with species such as *A. tripartita* and *Chrysothamnus vicidiflorus* (Figure 5a). There was a large shift after the first fire but much less difference within the years of recovery after the first fire (Figure 5b, 5c). There was again a large shift after the second fire, but 2009 and 2010 were more homogeneous (Figure 5d).

Functional Groups

In low elevations, year and plot main effects were significant ($p < 0.05$) for every functional group, indicating at least one significant change in relative cover of a group in one of the years. Bunchgrasses declined slightly after the first and second fires but remained fairly stable over time (Figure 6a). Annual grasses increased after the first fire and declined after the second (Figure 6b). Shrubs declined in relative cover after the first fire but began to recover relative cover after the second (Figure 6e).

At high elevations, year and plot main effects were significant ($p < 0.05$) for every functional group except shrubs, where year was not significant. Bunchgrasses declined after the first fire and again after the second fire (Figure 7a). Annual grasses increased after the first fire and declined after the second but were a higher relative proportion than before the fires (Figure 7b). Shrub relative cover declined after the first fire and recovered after the second but was sparse on the landscape in all years (Figure 7e).

In both elevation community groups, both annual and perennial forbs increased relative cover after each fire (Figure 6c, 6d; Figure 7c, 7d).

Species Analysis

Species density (the number of species per plot) increased in both low and high elevation groups over time (Table 5). Only a subset of the total species were found on each plot in each year sampled. On average, only 4.3 species were found in all years in the low elevation plots, and 8.5 species were found in all years monitored in the high elevation plots indicating that there is relatively high turnover. However, 99 species were found in over half the years indicating that many species persist on the landscape.

Low and high elevations had 68 species in common in the dataset. 32 species were found in low elevations only, 49 in high elevations only. Of dominant and indicator species, nearly all species were found in both groups (Table 6). *A. hymenoides*, *A. tridentata* ssp. *wyomingensis*, and *Elymus elymoides* were only found in low elevation plots, and *A. tripartita*, *Castilleja thompsonii*, and *Lomatium triternatum* were only found in high elevation plots.

In both community groups over time, the five most dominant species totaled less of the total vegetation cover after the first fire and then decreased again after the second fire (Table 6). High elevation plots always had more species per plot and higher cover per plot in each year, but low elevation plots had a higher percentage cover occupied by the top five most dominant species compared to higher elevation plots.

In the low elevation community, many dominant species in 1994 remained dominant in other years. Before the first fire, bunchgrasses, *B. tectorum*, *A. tridentata* ssp. *wyomingensis*, and *Machaeranthera canescens* were indicator species. *A. tridentata* ssp. *wyomingensis* was removed or dramatically reduced from all but a single plot after the first fire and was no longer dominant nor an indicator. Plots were dominated by *P. secunda*, *P. spicata*, and *B. tectorum* in every year, *Phlox longifolia*, *M. canescens*, and *Vulpia* sp. depending on year, and *Hesperostipa comata* only in the first year (Table 6, Figure 6). After the first fire, *P. secunda* was fairly consistently indicative and was the only grass that was an indicator. Nearly all indicators in the low elevations after the first fire were annual species (*A. tessellata*, *Vulpia* sp.) and many were non-native (*Sisymbrium altissimum*, *Draba verna*). The only perennial native species found as indicators in multiple years after the first fire were *Astragalus caricinus* and *M. canescens* (Table 6).

The high elevation plots were dominated by *P. spicata*, *P. secunda*, and *F. idahoensis* every year, with *Poa cusickii*, *Balsamorhiza careyana*, and *B. tectorum* depending on year, and *A. tripartita* and *H. comata* only dominant in the first year (Table 6, Figure 7). At high elevations, *Crepis atribarba* was the only species found in all time periods before and after each fire. *Achillea millefolium*, *P. spicata*, *C. viscidiflorus*, and *F. idahoensis* were indicators before the second fire. *L. triternatum* and *Holosteum umbellatum* appeared as an indicator after both fires. *A. tripartita* was not an indicator in the first year but was an indicator in 2003 when there were four fewer high elevation plots surveyed. Other species were more ephemeral in their indicator status. All native indicators were perennial forbs or grasses (*Antennaria dimorpha*, *A.* cf. *conjunctus*, *C. thompsonii*, *B. careyana*, *P. cusickii*, *Nothocalais troximoides*, *Lupinus sulphureus*) except *D. verna* (Table 6). There were no non-native indicators in high elevations except *H. umbellatum*.

The reduced dominance of *A. tridentata* ssp. *wyomingensis* shrubs in the low elevations and the increase of *B. tectorum* in all plots corresponded to years and associated fires. In 1994, average total cover of low elevation plots with *A. tridentata* ssp. *wyomingensis* was 74.1% with *A. tridentata* ssp. *wyomingensis* 10 - 30% of the total. In 2010, *A. tridentata* ssp. *wyomingensis* was only present on 6 plots, and only one plot with more than trace amounts. *B. tectorum* was found on all 24 low elevation and 3 out of 18 high elevation plots in 1994. *B. tectorum* relative cover increased on nearly every plot after the first fire and many plots and higher elevations had B. tectorum recorded for the first time. After the second fire, in elevations under 800 m, *B. tectorum* relative cover declined in most plots, but in highest elevations tended to increase (Figure 7). By 2010, *B. tectorum* was present on 39 out of 42 plots.

Discussion

Community and Functional Groups

There were a variety of vegetation types represented in the dataset before the 2000 fire as illustrated by the amount of ordination space occupied (Figure 3c). All of the vegetation types within the elevational groups responded in generally similar ways following the fires, though the plots at the highest elevations changed less than the rest of the high elevation group. Though magnitudes of differences were not statistically different between low and high elevations, the low elevation tended to have higher magnitudes of changes and higher variability. Some plots were affected more than others by the fires resulting in increased homogeneity of vegetation, as illustrated by less ordination space occupied. After the fires the extent of some vegetation types was reduced. For example, plots that had been characterized by *A. tridentata* ssp. *wyomingensis* would now be characterized as another type dominated by *P. secunda* or *B. tectorum*. However, the low and high elevation communities remained separate even as the overall ordination space occupied was compressed.

At both elevations, perennial forbs that could resprout became more dominant, and annual species, both grasses and forbs, became more common, indicative, and even dominant. This dataset supports the general trend that disturbances favor annuals and small statured plants (McIntyre et al. 1999) while perennial grasses decline (Antos et al.

1983). The increase in number of species per plot may indicate that the decrease in the dominant species' proportional cover allowed other species to enter (Zouhar et al. 2008). Additional species added each year may indicate dispersal and colonization, but this effect may be ephemeral (Link et al. 2006) after disturbance released resources and the community is reassembling. The non-native species were present on the landscape but were not excluding native species. The functional group "annual grasses" is represented only by *B. tectorum* and the *Vulpia* group and therefore may not reflect more general trends that could be expected in that group elsewhere.

The magnitude of change in composition from before to after the first fire was greater than that from before to after the second fire. Although there were different numbers of years between observations, this indicates that the first fire had a greater impact on vegetation community perhaps because the fire may have burned at a higher severity or had abundant fuel from accumulated litter. *A. tridentata* ssp. *wyomingensis* burns with higher severity than bunchgrasses (Evans and Lih 2005). Areas where shrubs had been removed in a fire previous to the 2000 burn responded differently than areas with sagebrush burned in the 2000 fire. Previous disturbance history has been shown to have a large effect on the response of vegetation after a new disturbance (Davies et al. 2009). In the ordinations, plots associated with *A. tridentata* ssp. *wyomingensis* moved dramatically after the first fire. Time between successive disturbances can have significant effects on community response because species composition changes with time since disturbance (Hobbs and Huenneke 1992). Although the 2000 fire reduced vegetation cover over much of the reserve, this did not prevent another large fire from occurring just a few years later. The second fire burned with lower severity because most shrubs were gone. There had been little time to recover past an early seral state so communities showed less dramatic shifts with the less intense fire.

In the periods of recovery (2001 - 2004 and 2009 - 2010), there were dramatic compositional and relative cover changes over time after the first fire, but after the second fire, plots did not change significantly. The multiple fires may have acted as a filter to remove species that were not able to persist or disperse rapidly. The 2000 fire shifted the communities to early successional state, and the 2007 fire occurred with these species already present, so there was not as dramatic a change in composition.

Dominant and Indicator Species

P. secunda and *P. spicata* were found in all elevations before and after both fires. *P. secunda* has been shown to be a dominant colonizer on burned sites (Akinsoji 1988) and fire does not damage the root crown. *P. spicata* is a long-lived species with an extensive root system, allowing it to be tolerant of fire.

B. tectorum was found to be dominant in both communities after each fire, and in every year in low elevations. *B. tectorum* produces abundant seed and colonizes quickly after fire (Stewart and Hull 1949). *B. tectorum* can exploit the "islands of fertility" that shrubs provide (Zouhar 2003), allowing fire to travel between sagebrush patches, and then the seed is available immediately in the highly disturbed area.

Low elevation plots shifted toward annual and weedy species in composition following multiple fires. *A. tridentata* ssp. *wyomingensis* was lost from the dominant community, and it did not recover. *A. tridentata* ssp. *wyomingensis* does not resprout and is an obligate seeder (Akinsoji 1988) with low dispersal distances.

A. hymenoides, *E. elymoides*, and *H. comata* are all tolerant of low elevation, sandier soils and capable of recolonizing or resprouting after fire (USDA 2011), but only *E. elymoides* returned as an indicator after the second fire. Sandy soils that lost vegetation cover experienced intense wind erosion (Evans and Lih 2005) so recovery of initial composition on those plots may have been hampered. Both perennial and annual species could become exposed, have reduced establishment, or suffer from reduced water-holding capacity due to erosion.

Some native species in low elevations responded positively to fire. *P. longifolia* has been shown to have high vegetative and reproductive growth following fire (Wrobleski and Kauffman 2003). *M. canescens* is often found in early successional communities after fire (Koniak and Everett 1982). The grasses in the *Vulpia* genus, though small and annual, were found as dominants after each fire perhaps because they can maintain a seed bank through fire (Akinsoji 1988) or because total cover was so greatly reduced. The annual species *Amsinckia tessellata* appeared after the first fire and persisted. Other studies found it increased abundance over time but had no response to fire (Link et al. 2006).

Invasive species became relatively more common though native species (at least *P. secunda*) were always more dominant. *S. kali* and *S. altissimum* are noxious invasive annual forbs that easily colonize disturbed areas (USDA 2011), and *D. verna* is also invasive but is so small that it has less effect over a large area. Overall, both dominant and indicator species indicate that multiple fires push the low elevation community toward an early successional state characterized by fire tolerant native species with weedy invasives.

At high elevations, *A. tripartita* and *C. vicidiflorus* were able to resprout after the fire (Akinsoji 1988) and were indicator species even if not dominant. In addition to *P. spicata* and *P. secunda*, perennial grasses *F. idahoensis* and *P. cusickii* maintained dominance in all years, though fire affects them adversely (Antos et al. 1983). *P. secunda* was a smaller percentage of the perennial bunchgrass functional group at the high elevations and large bunchgrasses were more dominant. The high elevation group had a greater drop in bunchgrass cover after each fire than did the low elevation bunchgrass cover.

The high elevation sites had higher cover of resprouting species and was therefore more stable following multiple fires. The perennial forbs *B. careyana, C. atribarba, A. millefolium* and *L. triturnatum* increase in abundance after fire (Antos et al. 1983, Wrobleski and Kauffman 2003) perhaps due to reduced competition or release of nutrients.

Aside from *B. tectorum*, the only non-native species that became indicators after fire were *D. verna* and *H. umbellatum* which have been shown to increase in burned landscapes (Antos et al. 1983), but both are small species so likely have little impact overall. Although *B. tectorum* invaded many new areas with the niche space opened by the fire, it generally did not expand in the following years or even after the second fire, remaining at trace covers.

These results match well with a similar data set from ALE that used a different pre-fire year and scale (grain, extent) of sampling (Davies et al. 2010). High elevation communities showed resilience to composition change with resprouting shrubs, grasses, and forbs, while low elevation sites were homogenized after each successive fire, with annual species and forbs increasing in cover.

Sagebrush shrub-steppe has been hypothesized to be a stable community under shrub dominance (Anderson and Inouye 2001) but within-year variability cannot be directly assessed prior to the 2000 fire so no assumptions can be made about its stability. The 2009 and 2010 compositions were not significantly different from each other, but this short time interval is insufficient to indicate a stable community state. The extreme variation following the first fire compared with the decreased variability following the second suggests that multiple fires have shifted the species pool and relative dominance of functional species such that responses to multiple disturbance are different than responses to a single disturbance. Subsequent disturbances are expected to be similar or with less effect than the 2007 fire unless a very long fire-free interval allows a build up of shrubs, but this is highly unlikely.

Restoration effects

The observed changes in vegetation following fires were confounded by extensive restoration work on the reserve including aerially spraying herbicide, aerially seeding native species, drill seeding, and planting seedlings (Appendix E). Because nearly every plot in the low elevation group was treated, the general trends over years are comparable, but may be different compared to untreated areas. This may also affect comparisons with the high elevation plots that were not treated, but would likely increase differences between low and high elevation groups because restoration sought to ameliorate community changes.

Initial results of seeding and planting native species have been strongly dependent on year and amount of precipitation (Troy Wirth, unpublished data). Reduction in cover of the invasive species is likely attributed to herbicide treatments because a few low elevation areas of ALE that were not treated had nearly total cover of *B. tectorum* and *S. kali* (personal observation). Without restoration treatments, low elevation, sandy soils without high bunchgrass cover would likely be invaded because there is high propagule pressure from nearby invaded areas.

Future fires in this area are likely. Attempting to restore a previous disturbance regime simply by protecting the area from fire to reduce frequency will not guarantee a return to historical conditions due to other factors which affect community composition including anthropogenic activity such as habitat fragmentation, climate change, species invasions, and other forms of disturbance (Davies et al. 2009). To affect changes in fire regimes, fuel loads can be manipulated (Davies et al. 2009). There was a trend of increasing litter with time since fire (data not shown), and continued build up of fuels could enable larger future fires. Herbicide treatments reduced *B. tectorum* cover, reducing the amount of fine fuel on the landscape. Prescribed burns are not viable restoration treatments to reduce fuel on the landscape because there were two fires within a decade. Firebreaks have been maintained in parts of the reserve because high connectivity of annual grasslands may increase the likelihood that fires will spread (Knick and Rotenberry 1997). Care must be taken to prevent providing corridors of disturbance where noxious species can expand (Kevin Goldie, personal communication). Without restoration treatments, *B. tectorum* cover could increase across the lower elevations. *B. tectorum* can increase rapidly from patchy initial distribution, and can expand dramatically relative to perennial grasses (Blumenthal et al. 2006). Therefore, active management, including spraying herbicide and seeding native species is warranted to prevent conversion to nonnative communities.

Maintaining the character and functioning of the community requires the dominance of native species. The endangered Greater Sage Grouse (*Centrocercus urophasianus*) requires bunchgrasses, shrubs, and forbs for food and nesting throughout its life cycle (Crawford et al. 2004). Although species density in both low and high elevation communities increased over time, many of the additional species were small annual species. Cover of native species can be negatively related to invasives (Anderson and Inouye 2001) but cannot always prevent establishment (Young and Evans 1973). In several areas invaded by *B. tectorum*, bunchgrasses persisted by resprouting, but with increasingly frequent fires their reserves could gradually be depleted and they could be lost from the site. Due to short dispersal distances of *A. tridentata* ssp. *wyomingensis*, and the low persistence in the seed bank, sagebrush is not expected to return for a very long time without intervention. Seeding and out-planting native species provides propagules to areas where mature individuals may have been removed.

Land managers can use patterns of vegetation change in shrub-steppe, including structure (e.g. loss of shrubs in lower elevation), composition, ground cover, and condition (e.g. expansion of annuals or non-natives) for setting goals in restoration

(Miller and Hobbs 2007). The strong differences in response between the elevational communities must be considered and increased patchiness of remnant vegetation is a constraint that must be overcome (Miller and Hobbs 2007).

If multiple disturbances shift a community to an alternative state, changes in composition and functioning would not be reversible by altering the direction or intensity of the factors that produced the change (Bestelmeyer et al. 2003). Parts of the low elevations with sandy soils may have transitioned to an alternative state due to the extensive wind erosion observed (Evans and Lih, 2005). The low elevations may have constraints to returning to their initial community, including limited dispersal of desired species, neighbor effects, and site characteristics (Bestelmeyer et al. 2003). Active management, including seeding and planting locally sourced native species, removal of invasive species, and drift nets to trap soil all have tried to ameliorate these constraints. The short-term responses indicate much interannual variation that obscures the trajectory but future monitoring could determine whether these management steps have reversed the transition and turned community composition toward the trajectory of the pre-fire community.

Changes to a stable, undesirable state in one area may spread because ecosystem function in one site may affect an adjacent site (Bestelmeyer et al. 2003). The spread of *B. tectorum* following the wildfire and the increased dust erosion in low elevations may gradually degrade adjacent areas (Belnap and Eldridge 2001). However, there was a strong difference in the response to disturbance between the low and high elevation groups and thus changes in one will not necessarily trigger changes in the other. Dominant bunchgrasses are resilient because they were reduced to charred bases after the fires but resprouted. Multiple disturbances much be great enough in spatial and temporal scale that original state is disrupted for new species to gain foothold (Petraitis and Latham 1999). The non-native species already present on ALE expanded after each fire, but they have not outcompeted native species to create a new stable state

Sources of Error

Because the plots were not permanently marked in 1994, the least confident comparisons are from the pre-fire to any other year. However, although the plot location was not exact, there are several reasons that it can be used as the baseline to compare changes in the community over subsequent years. First, because there was significant correlation between plots that were closer in space than those farther away, it is likely that the location selected in 2001 was near enough to the original location in 1994 to be similar in composition. With the relatively large plot size, similar conditions were likely captured. When grouped into low and high elevation groups, small differences in placement are unlikely to change the overall conclusions. Additionally, although there was a relatively low proportion of species in common between pre-fire and 2001, the proportion is similar to the proportion of species in common between 2001 and 2004, and between 2004 and 2009, the years of post-fire recovery and before and after the second fire, respectively (Appendix D). All of these proportions are much lower than the number of species in common between the two sets of years with the least change in composition, 2003 - 2004 and 2009 – 2010, but within the range of the sample of other values observed. There was low proportion in common from 1994 - 2010 and 2001 - 2010, indicating that species turnover is common. However, this effect may also be attributed to a learning effect from observers who have prior knowledge of what is present on a plot and then can spot additional species. Although the uncertainty in spatial location likely accounts for some of the noise in the composition data before and after the first fire, the broader conclusions are sound.

Multiple years of pre-fire composition are lacking, preventing assessment of the inter-annual variability in composition before the fire. Due to the large extent of each fire, there are very few plots that remained unburned that could act as controls (Figure 1). Composition in unburned plots moved in similar ways to the burned plots over time (data not shown) but were not compared statistically. Therefore, direct assessment of whether the multiple disturbances have resulted in a novel state is impossible. However, high elevation communities responded less dramatically to the multiple fires than the low elevation communities. There is a higher likelihood of change to a new trajectory in low elevations which were less stable in overall composition, had significantly different functional group proportions with time, and shifted from shrub and perennial grass-dominated communities to grass and forb-dominated communities. However, most dominant species present before the fires persisted after both fires.

Because the fires were single large events, there is the possibility of pseudoreplication, where sample units are not independent. However, because each fire lasted multiple days and fire behavior depends on several factors, including temperature, wind, fuel size, moisture, and topography (Miller 2001), areas separated in space or burned on different days may have experienced very different fire behavior. However, fire behavior is also related to vegetation composition, so untangling these interacting factors is very complicated (Miller 2001, Turner 1989). Though pseudoreplication statistically limits the ability to make broad inferences, the biological insight gained is valid. The extent and frequency of fires in the sagebrush shrub-steppe is increasing, so having a detailed long-term understanding of a site with large fires may predict responses to multiple disturbances at similar sites at community, functional group, or individual species levels.

Change in composition across years was used to infer effects of fire, but climate is a strong confounding factor. Precipitation varied widely over the time period of this study. 1994 was used as a baseline to compare to other years but 1993 had high precipitation and 1994 had low precipitation (Figure 8a). This may have affected relative functional group abundance because growth of perennial grasses has been shown to be positively correlated with precipitation of two previous years (Anderson and Inouye 2001) and forb species numbers can fluctuate due to below-normal precipitation (Miller and Eddleman 2001). Response of the vegetation to inter-annual variation in climate is difficult to predict based on the individual species responses, but the multiple high rainfall years followed by several years of above-average temperatures (1996 - 1999) (Figure 8b) may have led to the large buildup of dry organic matter prior to the 2000 fire. There was also above-average precipitation prior to the 2007 fire, but not so large. These effects of precipitation may have compounded effects of the fire but distinguishing their individual effects is not possible.

Conclusion

There is not strong evidence of a shift to an alternative stable state following multiple fires in either low or high elevation communities due to the persistence of dominant native perennial shrub-steppe species. Rather, it indicates a shift between vegetation types within a relatively intact native-dominated state. Multiple large fires reduced heterogeneity across the landscape, preventing a mosaic of successional stages that would be present in response to smaller disturbances historically (Knapp 1996). Future fires are expected, but with resprouting perennials, the community may shift within the highly variable range of species present in the area while retaining dominant species.

This long-term dataset on an elevational gradient in sagebrush shrubsteppe allows assessment of both fire impacts and short-term successional changes in recovery periods. Investigation at different scales of the vegetation community, from general community group, to functional group, to individual species' characteristics shows that multiple disturbances affect some levels differently than others (Turner 1989). At low elevations, to add a shrub layer of *A. tridentata* ssp. *wyomingensis*, an input of seed or planted individuals is necessary. However, the wind erosion events in areas that lost vegetation cover indicate that there has been a change in functional state, and therefore establishment may be dramatically curtailed without active management. The low elevation group has shifted composition considerably in response to multiple fires but most dominant species are present throughout the years. High elevation communities demonstrated resilience to changes following fire, shifting composition among native perennial species without adverse effect from invasive annual species. The bunchgrass functional group cover has declined but most perennial species found there can resprout. This information can show which species or functional groups are driving changes to the community and be used to prioritize restoration efforts to the most susceptible areas.

Figures

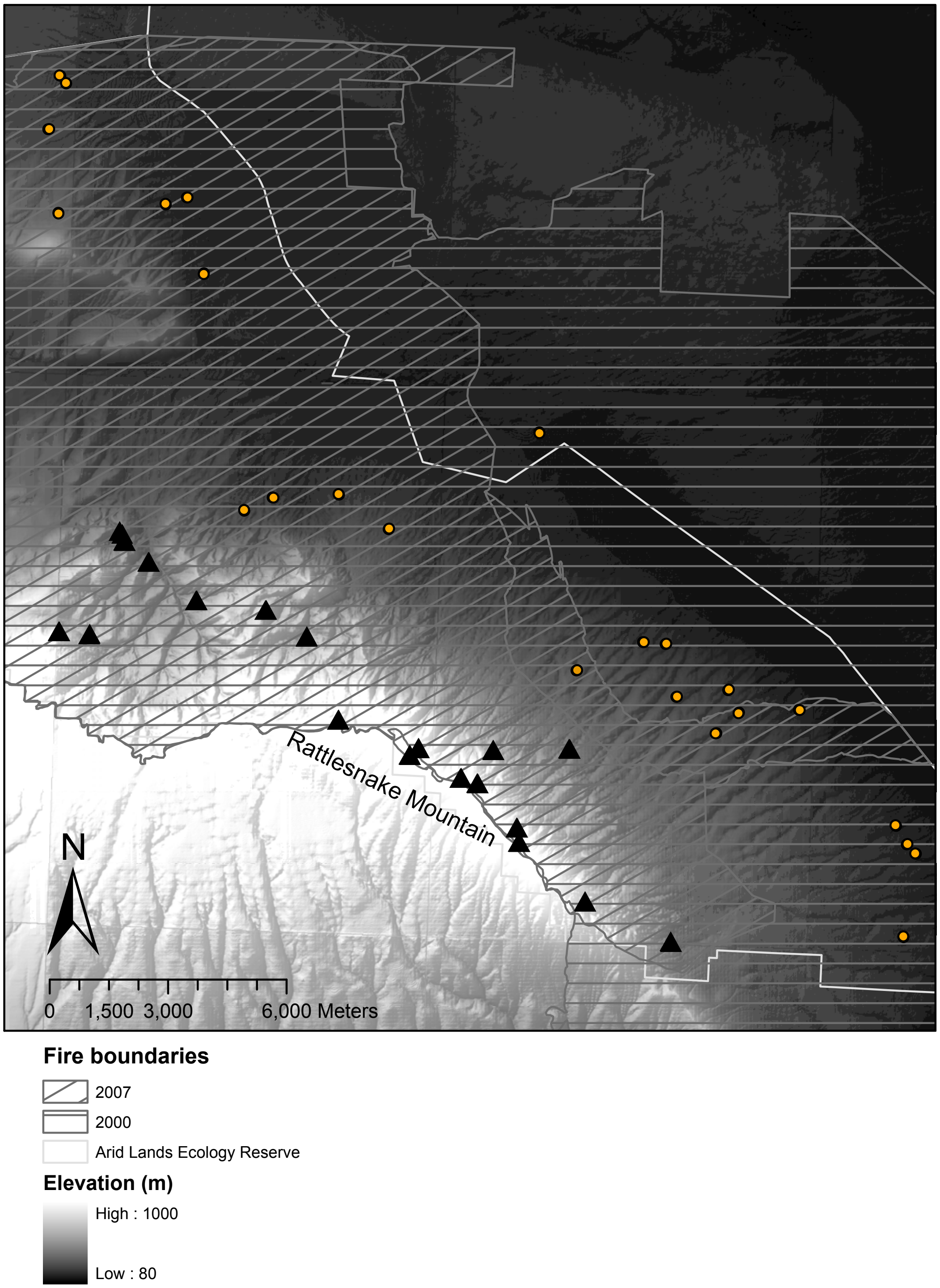

Figure 1: Biodiversity monitoring plots on the Arid Lands Ecology Reserve in low elevation group (circles) and high elevation group (triangles) with footprints of fires in 2000 and 2007.

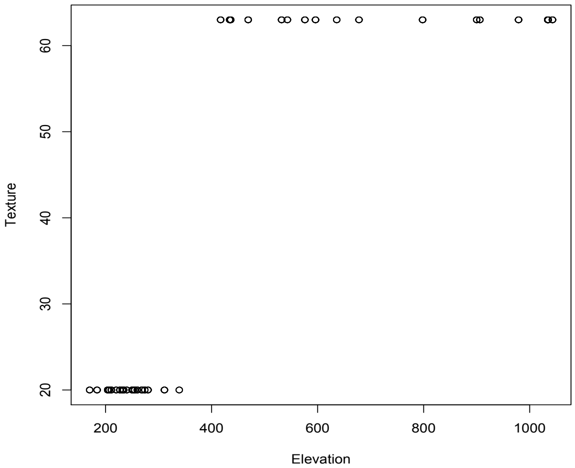

Figure 2: Texture (sum of percent silt and clay) by elevation (m) for 42 Biodiversity Monitoring plots on Arid Lands Ecology Reserve.

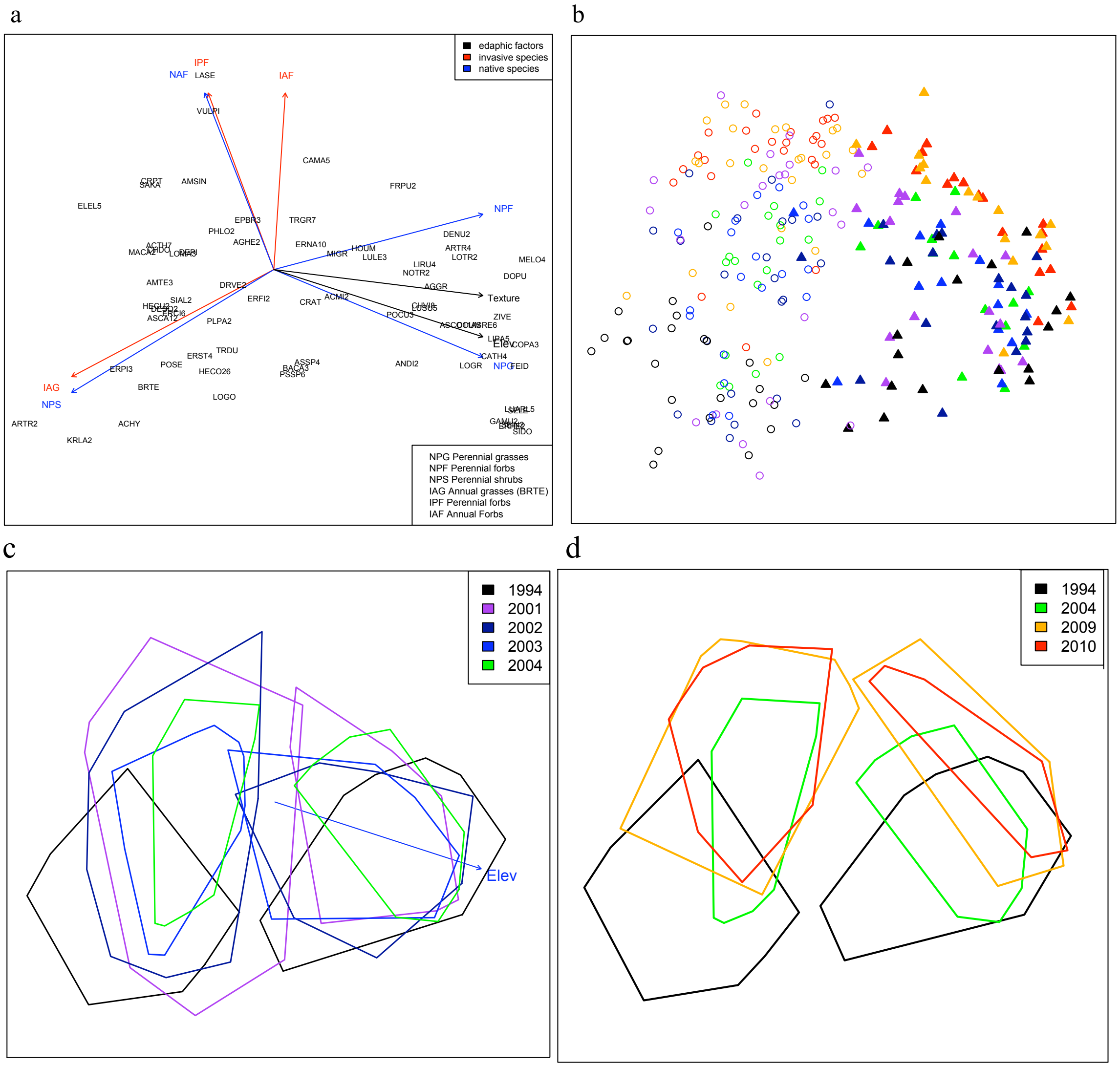

Figure 3: First two dimensions of three dimensional NMDS. a) Species codes with fitted environmental and functional group cover. b) All plots in ordination space. Triangles are in the high elevation group, circles are in the low elevation group, colors match polygons below. c) Polygons of total space occupied by high elevation and low elevation (with Elevation fitted) in years monitored before and after first fire. d) Polygons of total space occupied by high and low elevation in years monitored before first fire, before second fire, and after second fire. Fires were in 2000 and 2007.

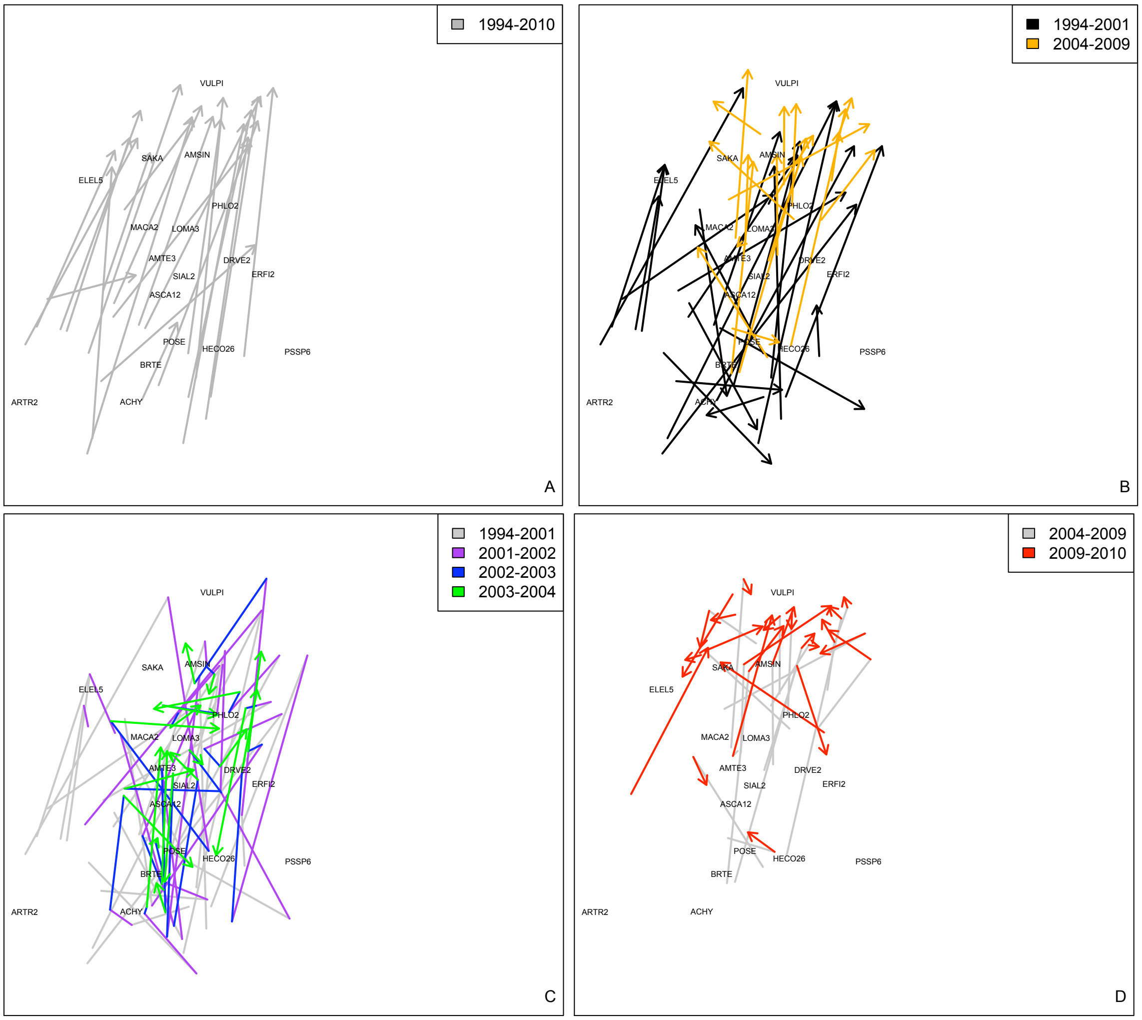

Figure 4: Ordination of low elevation plots with arrows connecting plot locations in years indicated by color. A) Change in ordination space over entire dataset (1994 – 2010). B) Change in ordination space over interval with the two large wildfires (2000 and 2007). C) Change in ordination space over interval following 2000 fire. D) Change in ordination space over interval following 2007 fire.

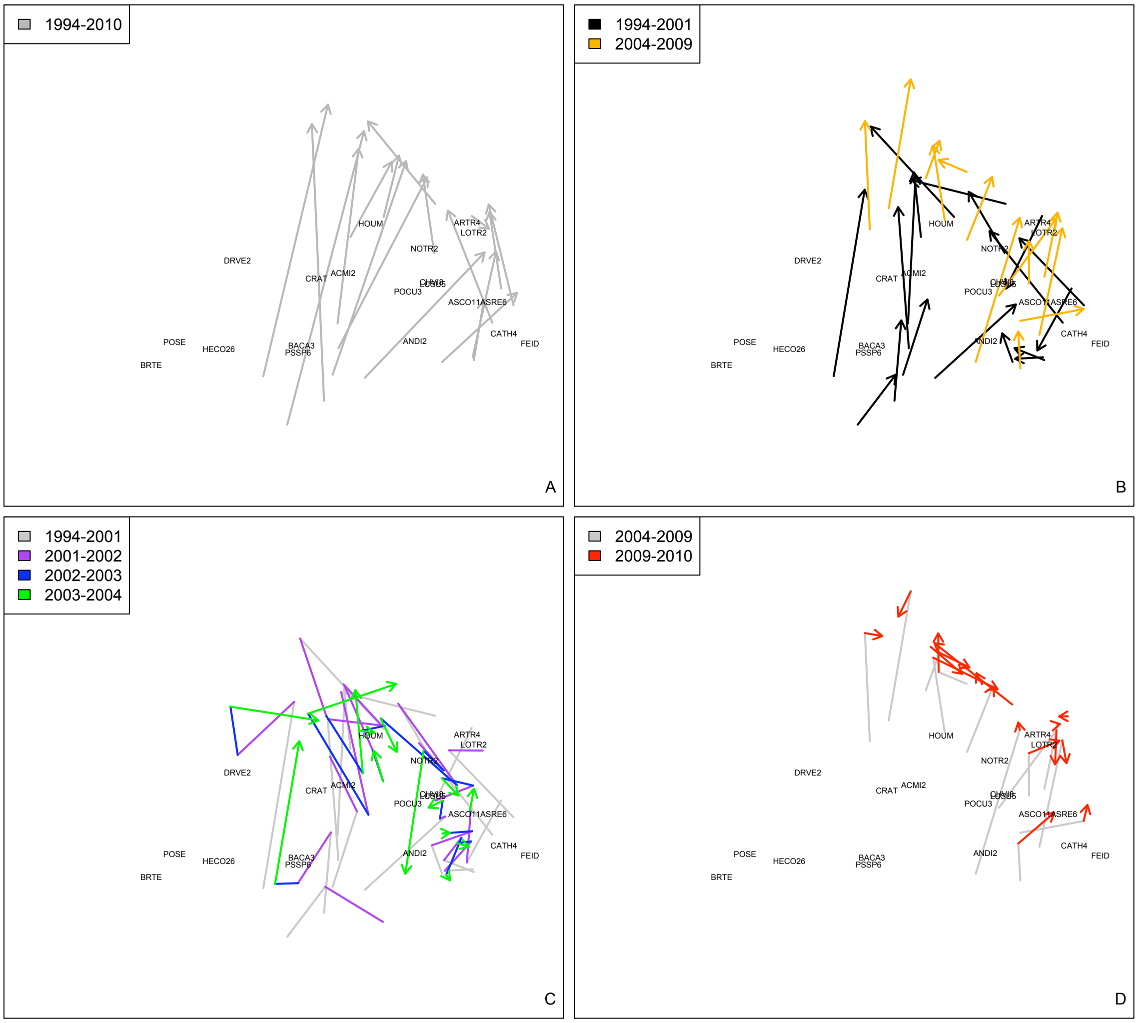

Figure 5: Ordination of high elevation plots with arrows connecting plot locations in years indicated by color. A) Change in ordination space over entire dataset (1994 – 2010). B) Change in ordination space over interval with the two large wildfires (2000 and 2007). C) Change in ordination space over interval following 2000 fire. D) Change in ordination space over interval following 2007 fire.

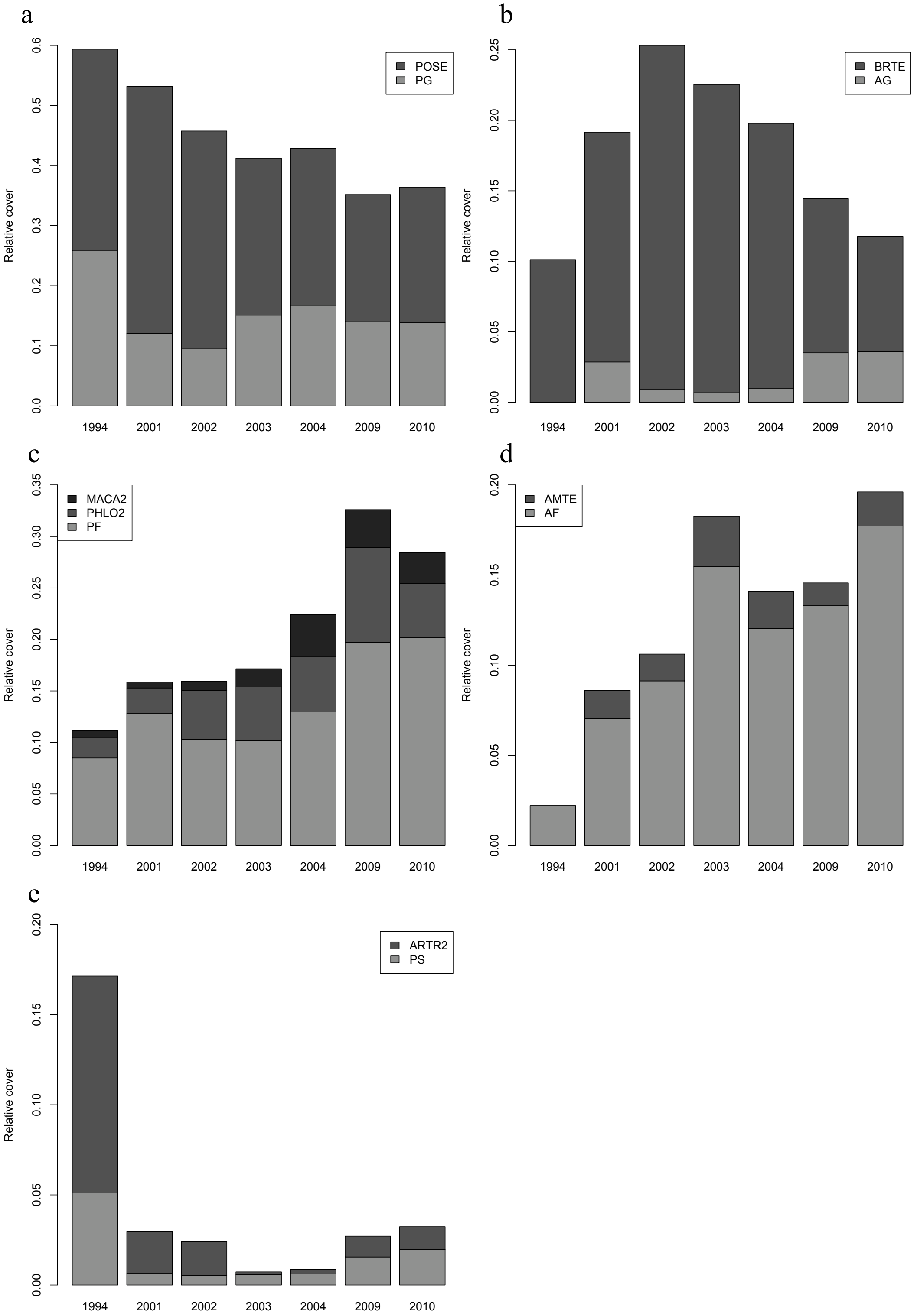

Figure 6: Mean relative cover on low elevation plots by functional group. Within each year, the columns of relative cover sum to 1.0 (<1.0 if species taxonomy did not allow determination of functional group). Important dominant or indicator species are separated from the sum of the rest of the group. a) Perennial grasses (PG). b) Annual grasses (AG). c) Perennial forbs (PF). d) Annual forbs (AF). e) Perennial shrubs (PS).

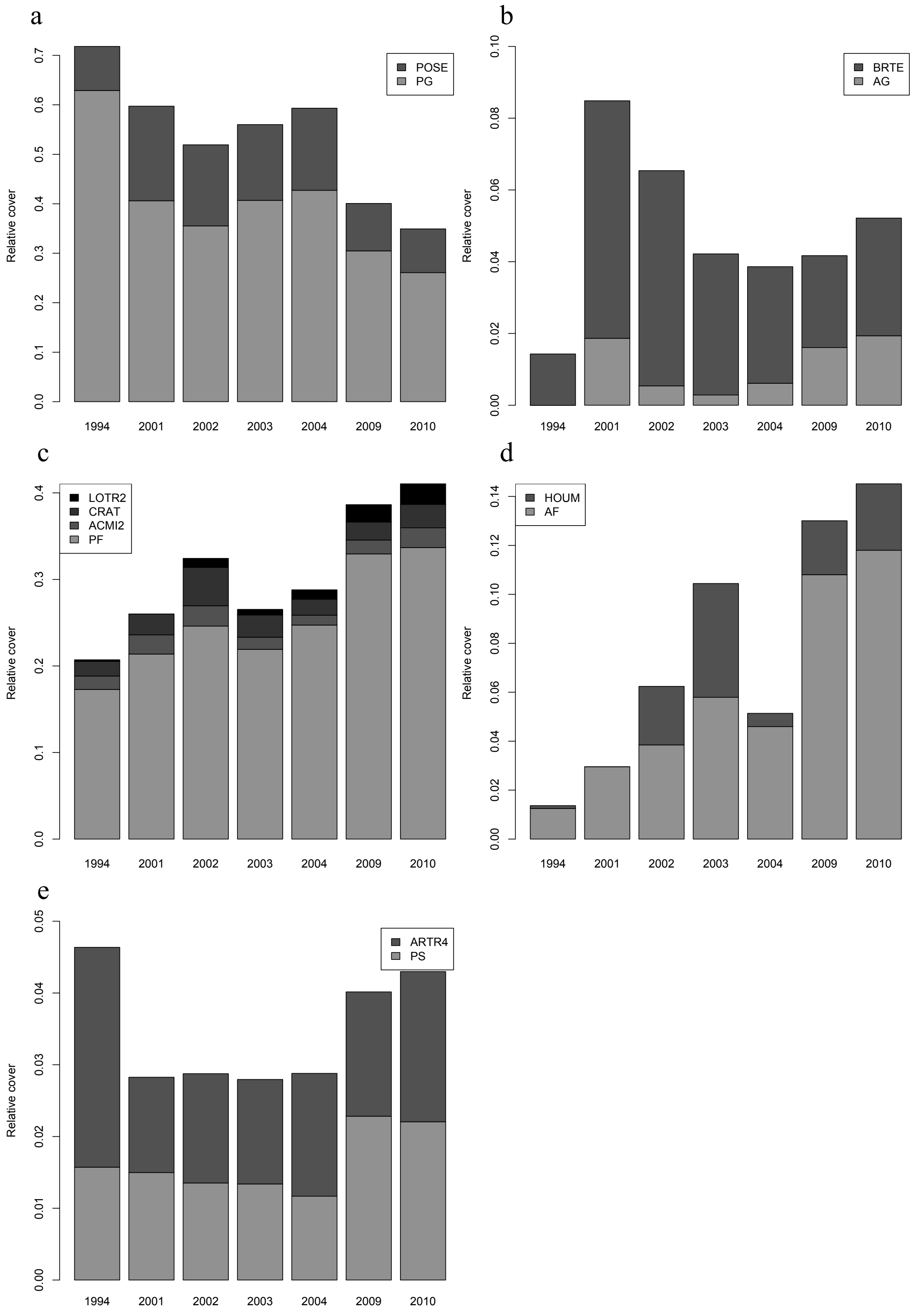

Figure 7: Mean relative cover on high elevation plots by functional group. Within each year, the columns of relative cover sum to 1.0 (<1.0 if species taxonomy did not allow determination of functional group). Important dominant or indicator species are separated from the sum of the rest of the group. a) Perennial grasses (PG). b) Annual grasses (AG). c) Perennial forbs (PF). d) Annual forbs (AF). e) Perennial shrubs (PS).

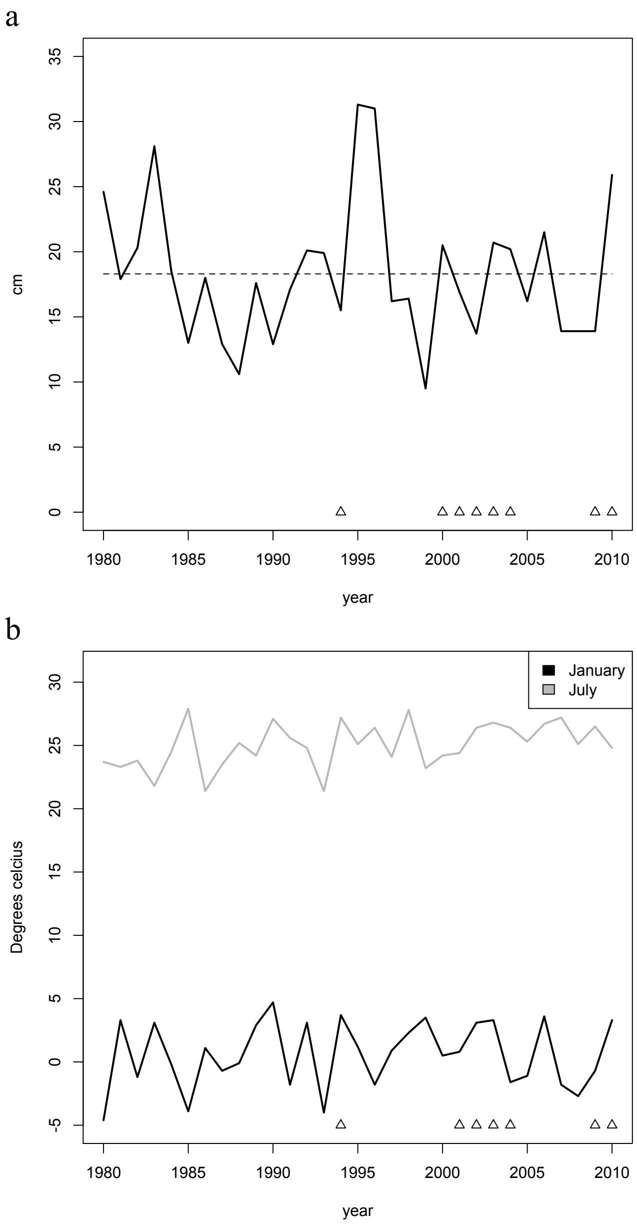

Figure 8: Summary of climatic factors, 1980 - 2010. Years with vegetation samples were 1994, 2001 – 2004, 2009 – 2010, shown with upward facing triangles. A) Total yearly precipitation (cm) with with long-term (1980-2010) average. B) Average July and average January temperature.

Tables

Table 1: Number of plots sampled and vegetation types classified in 1994 (Sackschewsky and Downs 2001). Canopy species are separated from understory species by "/". "Community group" was produced by cluster analysis of abiotic characteristics, and defined by low elevation community and high elevation community.

Number of plots sampled	Vegetation Type	Community group
5	Big Sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) / Bunchgrass Mosaic	Low
1	Big Sagebrush (*A. tridentata* ssp. *wyomingensis*) / Sandberg's Bluegrass (*Poa secunda*) - Cheatgrass (*Bromus tectorum*)	Low
2	Big Sagebrush - Spiny Hopsage (*Grayia spinosa*) / Sandberg's Bluegrass - Cheatgrass	Low
13	Bluebunch Wheatgrass (*Pseudoroegneria spicata*) – Sandberg's Bluegrass	8 are in Low 5 are in High
4	Winterfat (*Krascheninnikovia lanata*) / Bunchgrass Mosaic	Low
13	Threetip Sagebrush (*Artemisia tripartita*) / Bunchgrass Mosaic	High
1	Needle-and-Thread Grass (*Hesperostipa comata*) - Sandberg's Bluegrass	Low
1	Bunchgrass - Cheatgrass	Low
1	Needle-and-Thread Grass - Indian Ricegrass (*Achnatherum hymenoides*)	Low
1	Big Sagebrush / Bluebunch Wheatgrass	Low

Table 2: PERMANOVA table of factors affecting composition of vegetation for plots 1994-2010. There is not equal sample size at every year and group combination.

Source	df	SS	MS	Pseudo-F	P (perm)
Plot	41	471880	11509	10.569	0.001
Year	6	97253	16209	14.885	0.001
Group × Year	6	38113	6352.1	5.8332	0.001
Residual	219	238480	1089		
Total	272	855740			

Table 3: PERMANOVA table comparing magnitude of composition change (Bray-Curtis distances) between successive years ("Interval"), 1994 - 2001, 2001 - 2002, 2002 - 2003, 2003 - 2004, 2004 - 2009, and 2009 - 2010. There is not equal sample size at every year and group combination.

Source	df	SS	MS	Pseudo-F	P (perm)
Plot	41	2.1222	0.05176	4.6075	0.001
Interval	5	2.5966	0.51932	46.227	0.001
Group × Interval	5	0.0972	0.01944	1.7304	0.128
Residual	166	1.8649	0.01234		
Total	217	6.6138			

Table 4: Mean (SD) of Bray-Curtis distances indicating magnitude of composition change between subsequent years. Community group by year was not significantly different, but there were significant differences in years, indicated by different letters.

		Low community	High community
1994 - 2001	a	0.72 (0.15)	0.56 (0.10)
2001 - 2002	b	0.55 (0.18)	0.42 (0.08)
2002 - 2003	c	0.45 (0.14)	0.35 (0.10)
2003 - 2004	c	0.41 (0.10)	0.38 (0.11)
2004 - 2009	b	0.53 (0.16)	0.44 (0.11)
2009 - 2010	d	0.38 (0.12)	0.23 (0.10)

Table 5: Species density (average number of species per plot) by community group in each year.

	1994	2001	2002	2003	2004	2009	2010
Low	10.1	12.7	17.1	16.8	17.9	17.0	16.8
High	20.9	21.6	25	22.9	25.4	28.3	26.7

Table 6: Top five dominant species (proportion of species cover to total vegetation cover) and up to top five indicator species (Indicator value with $p < 0.01$) for each group in each year. Species codes in Appendix B. Non-native species are in bold.

	Low		High	
	Dominant Species	Indicator Species	Dominant Species	Indicator Species
1994	POSE (.33)	POSE (74.0)	PSSP6 (.33)	ACMI2 (84.0)
	PSSP6 (.14)	BRTE (62.2)	FEID (.20)	CRAT (77.3)
	ARTR2 (.13)	ELEL5 (50.0)	POSE (.08)	PSSP6 (77.0)
	BRTE (.11)	ACHY (41.7)	HECO26 (.07)	CHVI8 (65.8)
	HECO26 (.09)	ARTR2 (41.7)	ARTR4 (.03)	ANDI2 (61.1)
		MACA2 (41.7)		cf. ASCO11 (61.1)
				FEID (61.1)
2001	POSE (.39)	AMSIN (59.8)	PSSP6 (.18)	POCU3 (71.2)
	BRTE (.14)	AMTE (55.5)	POSE (.18)	ACMI2 (70.6)
	PSSP6 (.12)		FEID (.10)	PSSP6 (61.5)
	ARTR2 (.03)		POCU3 (.09)	CRAT (61.4)
	VULPI (.02)		**BRTE** (.06)	CATH4 (52.9)
				CHVI8 (52.9)
				FEID (52.9)
2002	POSE (.36)	**BRTE** (71.8)	PSSP6 (.19)	LOTR2 (100)
	BRTE (.22)	AMTE (68.2)	POSE (.15)	**HOUM** (85.0)
	PSSP6 (.10)	POSE (64.1)	FEID (.08)	ACMI2 (78.6)
	PHLO2 (.04)	ASCA12 (46.1)	**BRTE** (.06)	CRAT (73.1)
	ARTR2 (.02)		POCU3 (.04)	PSSP6 (72.7)
2003	POSE (.25)	**SIAL2** (69.0)	PSSP6 (.14)	LOTR2 (96.2)
	BRTE (.17)	POSE (66.3)	FEID (.14)	FEID (85.5)
	PSSP6 (.16)	AMTE (60.0)	POSE (.10)	CHVI8 (83.4)
	SIAL2 (.05)	VULPI (52.0)	BACA3 (.06)	BACA3 (77.0)
	PHLO2 (.05)	ERFI2 (48.0)	POCU3 (.06)	ARTR4 (71.4)
2004	POSE (.26)	MACA2 (85.5)	PSSP6 (.23)	LOTR2 (92.8)
	BRTE (.20)	**BRTE** (84.4)	POSE (.16)	POCU3 (87.2)
	PSSP6 (.12)	AMTE (80.7)	POCU3 (.09)	CRAT (71.5)
	PHLO2 (.04)	**SIAL2** (77.9)	FEID (.08)	PSSP6 (68.3)
	MACA2 (.04)	**DRVE2** (77.2)	BACA3 (.03)	FEID (64.3)
2009	POSE (.20)	**SAKA** (77.8)	PSSP6 (.12)	**HOUM** (88.9)
	BRTE (.13)	MACA2 (62.4)	POSE (.10)	LOTR2 (88.2)
	PSSP6 (.10)	LOMA3 (52.7)	FEID (.08)	POCU3 (85.5)
	PHLO2 (.10)	ELEL5 (37.5)	POCU3 (.04)	CRAT (70.5)
	MACA2 (.03)	AMTE (32.4)	BACA3 (.03)	**DRVE2** (66.3)
2010	POSE (.21)	**SAKA** (84.0)	FEID (.10)	LOTR2 (94.1)
	PSSP6 (.11)	MACA2 (72.0)	PSSP6 (.08)	POCU3 (88.9)
	BRTE (.08)	ASCA12 (59.2)	POSE (.08)	HOUM (86.2)
	PHLO2 (.06)	AMTE3 (44.0)	POCU3 (.05)	NOTR2 (78.5)
	VULPI (.03)		**BRTE** (.03)	LUSU5 (68.3)

Landscape, disturbance, and vegetation effects on biological soil crust in sagebrush shrub-steppe

Introduction

Biological Soil Crusts (BSC) are a feature of arid land ecosystems worldwide. BSC are composed of lichens, mosses, cyanobacteria, algae, and liverworts that live on the soil surface. BSC provide several functions, including soil stabilization and aggregation, photosynthetic activity, nutrient input to the soil, and aid in plant seedling establishment (Bowker 2007). Distribution of BSC is patchy across the landscape and has been shown to be related to physical and biological conditions as well as disturbance history.

Moss and lichen species vary in substrate, light, water, and nutrient requirements (Ponzetti et al. 2007) and growth rates (Furness and Grime 1982, Armstrong and Bradwell 2010). Landscape scale and microsite scale characteristics, vegetation, and disturbance history can be used to infer available resources for BSC growth and can therefore be used to assess the relative importance of direct and indirect factors to BSC growth.

The physical, biological, and disturbance conditions of a site can influence each other. The underlying elevation gradient can determine soil type and local available moisture (Chambers et al. 2007) through precipitation or condensation of fog. Soil characteristics that can determine BSC characteristics include texture, nutrient availability (Bowker et al. 2005), and acidity (Eldridge and Tozer 1997). Topographic position can affect soil characteristics and rates of change due to patterns of weathering, erosion, and heat load. The varying rates of organic matter decomposition in turn affect nutrient and organic material cycling needed by photosynthetic organisms.

BSC communities are more sensitive than plant communities to disturbance (Ponzetti and McCune 2001). Disturbances such as trampling, fire, and pollution can affect cover, composition, and physiological functioning of BSC (Belnap and Eldridge 2001). The successional trajectory following disturbance generally moves from microscopic algae and cyanobacteria to mosses then lichens (Belnap and Eldridge 2001). Effects of fire on BSC can vary dramatically by severity (Johansen et al. 1993). Elevation can directly affect fire because winds blowing up slope can carry flames, and preheating of upslope vegetation increases fire spread. Fire history can be related to elevation due to its effect on vegetation density and composition through available moisture (Chambers et al. 2007). Thus, topographic factors affect BSC through the effect on fire history and behavior.

Vascular plants affect BSC both through facilitation and inhibition. Plants can create favorable microsites, with enhanced water availability, temperature moderation, and nutrient availability (Bowker et al. 2005). However, dense foliage or thick litter can shade the surface and prevent photosynthesis. Plants can interact with fire because some drop their dead material while some maintain standing litter; the former may allow fire to directly burn BSC but in the latter case, fire may not directly touch the soil surface. Some plants burn with high severity, sterilizing soil around them due to high temperatures. Plants are affected by topography, soils, and disturbance, creating a network of effects on BSC cover that is more complicated than the net effects of explanatory factors.

The cool deserts of the American west are dominated by mosses and lichens (Belnap et al. 2001) and crust cover and composition varies across the landscape, vegetation type, and microsite (Ponzetti et al. 2007). The sagebrush shrub-steppe in the Columbia Basin is characterized by large shrubs (*Artemisia tridentata* ssp. *wyomingensis, Artemisia tripartita*) and bunchgrasses (*Pseudoroegneria spicata, Poa secunda, Festuca idahoensis*) grouped in habitat types determined by climate (Daubenmire 1970) and elevation. Bunchgrass and shrub cover in the Columbia Basin are positively correlated with moss and lichen cover (Muscha and Hild 2006, Ponzetti et al. 2007). Deeper soils with less erosional forces support higher crust cover (Ponzetti et al. 2007).

Much of the sagebrush steppe region has been converted to agriculture or grazing such that it no longer supports a native vegetation community (Noss et al. 1995). The expansion of the annual grass *Bromus tectorum* (cheatgrass) and anthropogenic ignitions have decreased the fire return interval (Brooks et al. 2002) and large fires have removed much of the mature sagebrush (Evans and Lih 2005). Invasive species such as *B. tectorum* can become dominant after disturbance and change the physical and chemical properties (e.g. bulk density, organic matter, and nitrogen content) of a site (Norton et al. 2004). *B. tectorum* can form dense monocultures and produce abundant litter.

Additionally, it reduces soil moisture close to the surface because of relatively shallow rooting depth (Morrow and Stahlman 1984). Thus, BSC development was negatively correlated to cover of *B. tectorum* (Hilty et al. 2004 and Ponzetti et al. 2007). Perennial grass clump cover has been shown to be negatively related to *B. tectorum* cover (Hilty et al. 2004), and may provide some resistance to invasion through competition (Chambers et al. 2007). The relative cover of bunchgrasses and *B. tectorum* may indicate light and water availability to BSC and affect the likelihood of fire to affect the soil organisms microsite.

I investigated the network of relationships among landscape factors, vegetation characteristics, and BSC in the sagebrush shrub-steppe habitat in the Columbia Basin. I hypothesized direct and indirect patterns of effects on BSC given the interactions across a range of elevations, soil types, fire history, and vegetation types (Figure 9). Because lichens have extremely slow growth rates, experimental manipulation was impractical, so statistical relationships were used to assess support for directed relationships between variables. Structural Equation Modeling (SEM) can account for simultaneous predictors and responses making it ideal to study networks of effects in systems.

Hypotheses

1. Elevation and other landscape-scale factors affect plants and BSC directly and also indirectly through their effects on soil texture and fire history.
2. Fire history can have direct effects on BSC through removing biomass or indirect effects by changing vegetation cover and structure.
3. Soil texture can affect plants directly and BSC directly and indirectly due to water holding capacity and nutrient availability.
4. Bunchgrass cover is negatively related to *B. tectorum* cover, with higher cover of established bunchgrasses able to prevent *B. tectorum* establishment.
5. Bunchgrasses can affect moss and lichen cover, either through amelioration of site characteristics or impeding growth by shading.
6. Moss cover affects lichen cover because fast-growing mosses provides a stable substrate for many lichens in succession after disturbance (Belnap and Eldridge 2001).

7. There is a negative relationship between *B. tectorum* and lichen cover, where lichen cover can inhibit *B. tectorum* establishment, but once established, *B. tectorum* can kill or prevent lichen recovery.
8. Microsite characteristics such as rock cover, available micronutrients, pH, and organic matter can affect moss and lichen cover.

Methods

Site

A range of elevations, aspects, soil types, fire history, and vegetation types were sampled on public and private land in the Benton County (46.33'N, 119.42'E) in southeastern Washington in the Columbia Basin. The climate is semi-arid, averaging 182 mm precipitation per year, with average January temperatures of 1°C and average July temperatures of 23.5°C. Most precipitation falls during the winter months (October – March) (Western Region Climate Center 2011). Elevation of plots range from 100 - 1110 m with generally northerly aspect (Figure 10). Soil types include Hezel sands, Quincy loamy sands, Esquatzel silt loams, Warden silt loams, Ritzville silt loams, Kiona very stony silt loams, and Lickskillet silt loams as elevation increases (NRCS 2011). Land use in the area includes agriculture, ranching, and conservation. The Arid Lands Ecology Reserve (ALE) is managed by the United States Fish and Wildlife Service and has been free of agriculture since 1943. In 1962, fencing was erected to exclude trespassing livestock and off-road vehicles (O'Connor and Rickard 2003), making it one of the largest remaining tracts of sagebrush shrub-steppe. Large fires burned the reserve in 1984, 2000, and 2007 removing much of the shrub cover. The Horse Heaven Hills complex is managed by the Bureau of Land Management and has been rested from grazing since 1986. Large fires occurred in the area in 1986, 2002, and 2007. Smaller fires have occurred across the landscape in other years. Several private landowners in the area have retained native vegetation on their property. Vegetation types include small remnant sagebrush-dominated sites, bunchgrass-dominated, and invasive annual-dominated sites. These sites provided variation in topography, soils, vegetation, and disturbance history.

Sampling Design

Transects 100 m in length were selected to overlap or be adjacent to existing monitoring plots established by Mike Marsh, Dave Wilderman, Pacific Northwest National Laboratories, Jeanne Ponzetti, and Terry McIntosh, all of whom had noted cover of BSC. Additionally, areas underrepresented by existing plots were surveyed by navigating to a point chosen from a map and then placing the transect parallel to the contour of the slope. Transects were no closer than 300 m to one another and were spread across an area of 100,000 hectares (Figure 10) with a range of elevation and fire history. Five quadrats, 20 × 50 cm in size, were placed 20 m apart on each transect. To compare sites with adequate potential growing space for BSC, the quadrat position was shifted 5 – 10m if the original location had > 20% pebble, gravel, or rocks < 1 cm in diameter.

Data collection

In each quadrat, vascular plants were identified to species and cover values recorded to the nearest percent. In addition, percent rock, litter, lichen and moss cover were recorded to the nearest percent. Functional group based on morphological type, life history duration, and nativity follows PLANTS database (USDA 2011). Litter cover in each quadrat was noted and then removed to observe BSCs. The surface of the quadrats was lightly sprayed with water to encourage photosynthetic activity of BSC organisms and make each group more visible.

Small soil samples (totaling approximately 200 g) were scraped from the top 1 cm of seven to ten points adjacent to the quadrats and placed in air-tight plastic bags. Forty samples were frozen until processing, while 44 were air-dried and stored at room temperature. For eleven of the samples, 400 g were collected, mixed thoroughly, and divided into separate bags to compare room temperature and frozen storage soil treatments. All soils were thoroughly mixed and passed through a 2 mm screen prior to processing. Soils were sent to Brookside Laboratories, Inc. (New Knoxville, OH 45871). Soils were tested for Mehlich III Extractable S, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, Al, and P, all measured in $mg*kg^{-1}$ (Mehlich 1984). pH was measured 1:1 in water (McLean 1982). Percent organic matter was measured by loss on ignition at 360°C (Schulte and Hopkins 1996). Soil texture (percent sand, silt, and clay) was determined using the hydrometer method (ASTM 2002).

Slope, aspect, and elevation were estimated from 10 m Digital Elevation Models (USGS 2011). Heat load index (HLI) was calculated (McCune and Keon 2002) keeping latitude constant because there was little variation in latitude across plots. Fire maps were compiled to determine fire history of each plot for the last 30 years, including total number of fires and years since last fire.

Statistical Methods

SEM is the use of two or more structural equations to model multivariate relationships that have simultaneous influences and responses. Unlike other multivariate methods, SEM can represent the model that best matches a situation and can discern networks of causal relationships instead of only net effects (Grace 2006).

Proposed relationships are represented in a path diagram with directed arrows indicating causal relationships based on published studies or reasonable inferences. Variance-covariance matrices are used for parameter estimation and model fit. The hypothesized model implies expectations for the observed covariance matrix. The observed matrix and model structure are then used to calculate maximum likelihood parameter estimates. Parameter estimates within the hypothesized model yield a model-implied covariance matrix which can be compared to the observed matrix to assess fit using Chi-square tests.

Structural coefficients are the regression coefficients in the structural equations and represent the structural effects of variables on other variables along the pathway. Standardized coefficients relate a change in one standard deviation of a predictor to the specified magnitude of change in standard deviation of the response. Standardized coefficients can be converted to unstandardized coefficients using the standard deviations of the variables. The total effect between two variables is the sum of the direct and indirect effect components.

In SEM, the objective is to minimize Chi-square difference (maximizing p-value) because this indicates that the observed matrix does not differ significantly from the proposed structure of the data. Parsimony is also preferred, so a path is generally removed if the elimination does not increase the Chi-square more than the critical value of Chi-square with one degree of freedom (Grace 2006).

To create a simple and functional model, many variables were considered but it is recommended that the ratio of sample size to number of parameters is at least 5:1. By investigating bivariate plots, only variables with apparent relationships were retained. HLI was excluded from the modeling due to the low variation in values (Table 7) and therefore low explanatory power. Total fires were strongly correlated with time since fire ($r = -0.88$). Time since fire was kept and total fires dropped from the model because the former had stronger linear relationships with the other variables so it was kept in the model. To reduce influence of large values, the maximum time since fire was set at 20 years so that 85% of the sample units were within the maximum.

Total bunchgrass and cheatgrass cover were the only vegetation characteristics included. Perennial forb and annual forb cover were excluded as they did not have as strong linear relationships with other variables as the grasses. Perennial grasses are dominant species in shrub-steppe communities and so are used as surrogates for vegetation type and condition. Shrub cover, though an important structural element to the system, was only present on 18 plots and fire history was a reasonable predictor of shrub cover ($r = .40$ with time since fire), so shrub cover was excluded. Litter was excluded because it was correlated with *B. tectorum* cover ($r = 0.48$).

Because the soil samples were stored differently (room temperature vs. frozen), any variable that differed significantly between the storage treatments was excluded. Therefore, only pH, organic matter, and eight extractable ions were used. Principal Components Analysis (PCA) reduced the dimensionality of the eight ions to a single variable to put into the model (Appendix G). The first Principal Component explained 28.6% of the variance. It is associated with B, Mn, Ca, and to a lesser extent Mg.

Box-Cox plots were used to determine appropriate transformations to approach normal distribution (Table 7, Appendix F) and linear relationships among variables. The inverse-square root transformation was used for elevation, *B. tectorum*, moss, and lichen cover data with the additional step of dividing by the exponent, which recovers the rank order of the untransformed data. Bunchgrass cover was square root transformed. Sum of percent silt and clay was used to indicate soil texture as a single variable.

The complete initial path diagram is presented in Figure 11. Though there may be additional hypothesized relationships among the variables, directed relationships are imposed from a landscape scale to small-scale processes because abiotic processes are hypothesized to be the main drivers of the biotic characteristics of these arid lands. It is possible to find the path diagram with the best possible fit through a specification search where all possible pathways between observed variables are allowed to float, but then the model responds to specific artifacts in a data set rather than finding support for a specific question. In this case, my question was focused on the factors that affect the distribution of BSC given hypothesized relationships from previous literature.

Analyses were run in AMOS Version 19.0.0 (Build 1376). Exploratory analysis was used until a structure was found that fit the data. Modification indices were examined for additional paths that had not initially been included but would have had a strong effect on the Chi-square statistic or that illuminated an overlooked relationship in the initial model. Then, pathways were removed in a stepwise fashion, beginning with the least significant. After reaching a model that fit, the order of those same pathways removed was altered several times to ensure that the final model was stable regardless of the order of alterations. Additionally, a sparse initial model was run with pathways added based on modification indices; the final model was identical to that obtained from the stepwise deletion process, suggesting that the final solution was robust. Bootstrapping was used to estimate standard errors of the maximum likelihood discrepancy and parameter estimates using 200 runs.

Because these factors were of secondary concern, after the stable model was reached, organic matter, pH, nutrients, and rock were added one at a time and a specification search was run for paths that would improve explanatory power for responses without significantly decreasing model fit. Directed relationships to bunchgrass or *B. tectorum* cover were not proposed because the soil samples were collected within two cm of the soil surface and most of the plants would be accessing deeper soils with their roots. The assumption is that these characteristics, especially nutrients and organic matter, would have developed over very long time scales because decomposition processes are very slow in arid lands, so the vegetation present was not the driver of the soil characteristics values that were observed. There were never any strong modification indices suggesting that pathways relating soil chemistry to BSC cover were warranted.

Results

The initial structure of the SEM linked elevation, soil texture, time since fire, native and invasive grasses, and BSC with a Chi-square of 0.75 (Figure 11). Several pathways were deleted but none were added. The final model fit adequately with Chi-square = 14.98, p = 0.13 (Figure 12). The mean maximum likelihood discrepancy was 25.59 with SE 0.71 indicating some degree of multivariate non-normality. The standard errors of the pathways show that some relationships are more robust than others, but most are within 20% of the mean, a broad rule of thumb for an acceptable model (McCune and Grace 2002). The model explained 39% of the variation in texture, 37% of the variation in bunchgrass cover, 28% of the variation in *B. tectorum* cover, 35% of the variation in moss cover, and 53% of the variation in lichen cover. There were significant linear relationships between all bivariate pairs in the final model (Figures 13-18).

Time since fire was not significantly related to elevation, but this may be due to the increase in large fires that burned at all elevations. The directed path from elevation to time since fire was retained, however, because if it were removed, a non-specified correlation would be put in place and it would not change parameter values nor affect model fit.

Bunchgrass cover was directly affected by elevation and soil texture but not by time since fire. Elevation had a high directed and total effect on bunchgrass cover.

Moss cover was nearly equally affected by bunchgrass cover and time since fire. *B. tectorum* cover likewise was affected only slightly more by bunchgrass cover than time since fire. Lichen cover was much more affected by moss cover than by bunchgrass cover. Lichen had significant undirected correlation with *B. tectorum.*

Standardized total effects indicate that elevation is a driver of every aspect of this system (Table 8). Time since fire affected lichen cover indirectly through its impact on moss cover. Other total effects indicate that net effects can be broken into direct and indirect effects through the network of relationships.

None of the microsite characters improved fit or explanatory power, and none were therefore included in the final model.

Discussion

The network of relationships in the final SEM path diagram confirms findings of individual effects of landscape scale factors (Ponzetti et al. 2007), vegetation community (Bowker et al 2005), and disturbance history (Belnap and Eldridge 2001) on BSC cover. Rather than using each factor as a predictor for net effects, this study integrated them in a mediator-driven model which enabled assessment of direct and indirect effects among variables. Though it is possible to over-fit a model so that it reflects anomalies in a given dataset rather than broad, underlying trends, the data reasonably fit model assumptions and each path has support from previous literature.

The relationships between landscape scale factors, vegetation, and BSC in Columbia Basin strongly resemble findings from the hot deserts of southern Utah which are dominated by cyanobacterial crusts (Chaudhary et al. 2009). This suggests that these hierarchical relationships affecting BSC may be broadly applicable. However, Chaudhary et al. (2009) grouped all vegetation cover together and found a negative relationship to BSC, whereas by splitting native bunchgrasses and noxious annual species, native vegetation cover is shown to be positively related to BSC cover, perhaps by mediating temperature and irradiance levels, increasing available water, or by impeding invasion by *B. tectorum*.

Soil surface characteristics (rock cover, organic matter, pH, and nutrient availability) were not found to drive BSC cover. Some possible explanations are that by averaging across quadrats, fine-scale patterns were lost (Turner 1989) or that there was not sufficient range in observed predictor values to show a response. Factors such as pH may be more important in structuring community composition (Ponzetti and McCune 2001) than explaining broad patterns of cover because some species tolerant of certain conditions may not form large colonies. Soil nutrient availability may be less important because lichens absorb nutrients deposited on the soil surface or dissolved in rainwater (Nieboer et al. 1978), and mosses can absorb nutrients through both their root-like rhizoids and their leaves. Organic matter may not have had a large impact because the water holding effect may be swamped by soil texture.

The high directed and total effect of elevation on bunchgrass cover supports the hypothesis that available water is limiting to vegetation at lower elevations (Chambers et al. 2007). There is a net negative relationship between elevation and *B. tectorum*. The relationship between *B. tectorum* and fire has been well established (Shinneman and Baker 2009), supporting the inclusion of the directed relationship between elevation and fire even though it is not significant based on this data set. The nonsignificant observed relationship between elevation and time since fire is an artifact of the plot selection in areas that have experienced multiple large fires. Higher cover of *B. tectorum* was negatively associated with lichens because *B. tectorum* can continuously produce fine litter that can accumulate and either shade the soil surface or allow the fire to travel along the surface. BSC can inhibit *B. tectorum* germination (Deines et al. 2007), so there is likely a negative reciprocal relationship resulting in a strong net negative relationship.

There may be different biological effects between total number of fires and time since fire because repeated disturbances may have a greater effect than a single disturbance (Paine, Tegner, and Johnson 1998), but this is beyond the scope of this project and thus only time since fire was retained in the model.

Mosses and lichens responded to different direct effects. Mosses can have a taller, upright stature that can catch fire whereas most soil lichens are strongly appressed to the substrate and can be passed over in a low intensity burn (Bowker et al. 2004) though they can be top-killed by high temperatures. Mosses are generally faster growing and cover values can show a relationship with time since disturbance.

Lichen establishment and growth rate is slow so the interval investigated may be insufficient to show differences in lichen cover in relation to time-since fire. The strongest direct predictor of lichen cover was moss cover. Some lichens grow directly on soil mosses, but this strong relationship also supports the hypothesis of a successional pathway where mosses disperse and grow in a disturbed area more quickly and stabilize substrate allowing slow-growing lichens to establish and grow.

Other disturbances, such as trampling and herbivory associated with ungulates, have been shown to affect vegetation, moss, and lichen cover and successional state (Kaltenecker et al. 1999). Evidence of deer, elk, or cattle were found on every transect, though species' effects may differ depending on their behavior.

These exploratory analyses indicate that in the cool desert habitat of sagebrush shrub-steppe, mosses and lichens are responding to different levels of environmental effects, with effects of elevation and texture mediated through native vegetation cover. This allows land managers to predict fairly well that if there is high perennial bunchgrass cover, BSC cover is likely also fairly high. This network of relationships also allows prioritization of higher elevations with good bunchgrass cover for protecting extant BSC cover or prioritization of low elevations with poor bunchgrass cover for removing invasive species that are negatively related with BSC recovery. Maintaining an area free of invasive species and protecting from fire improves conditions for high BSC cover.

Understanding factors affecting BSC cover can predict broader ecosystem functioning. BSC cover increases soil surface stability (Chaudhary et al. 2009) and soil water retention time (Belnap 2006). Disturbance can affect cover and therefore rates of photosynthesis of BSC (Grote et al. 2010). Factors affecting BSC affect the potential for wind and water erosion and primary production and are therefore important for maintaining a functional ecosystem. This study found support for biotic and soil processes affecting BSC mediated through higher order effects of elevation and disturbance.

Figures

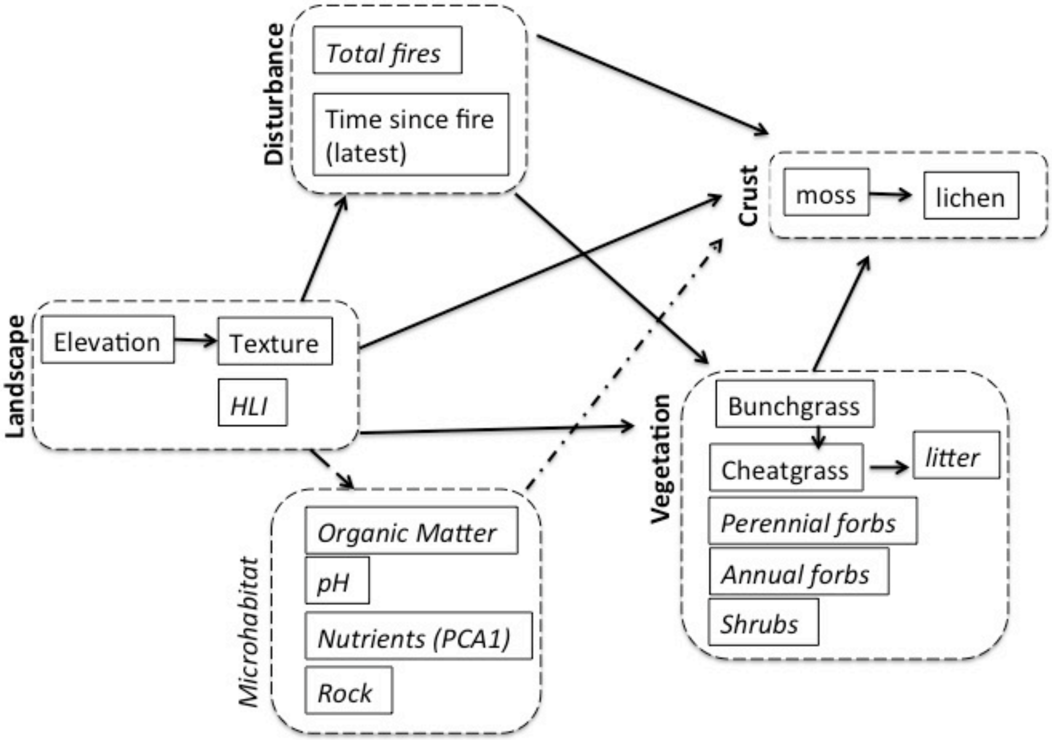

Figure 9: Conceptual diagram of hypothesized relationships between unobserved factors (dotted boxes) and observed variables (rectangles). Arrows indicate directed relationships. Observed variables in italics and dotted paths are considered nonessential and are assessed for importance only in relation to the rest of the model. Potential feedback relationships are not modeled.

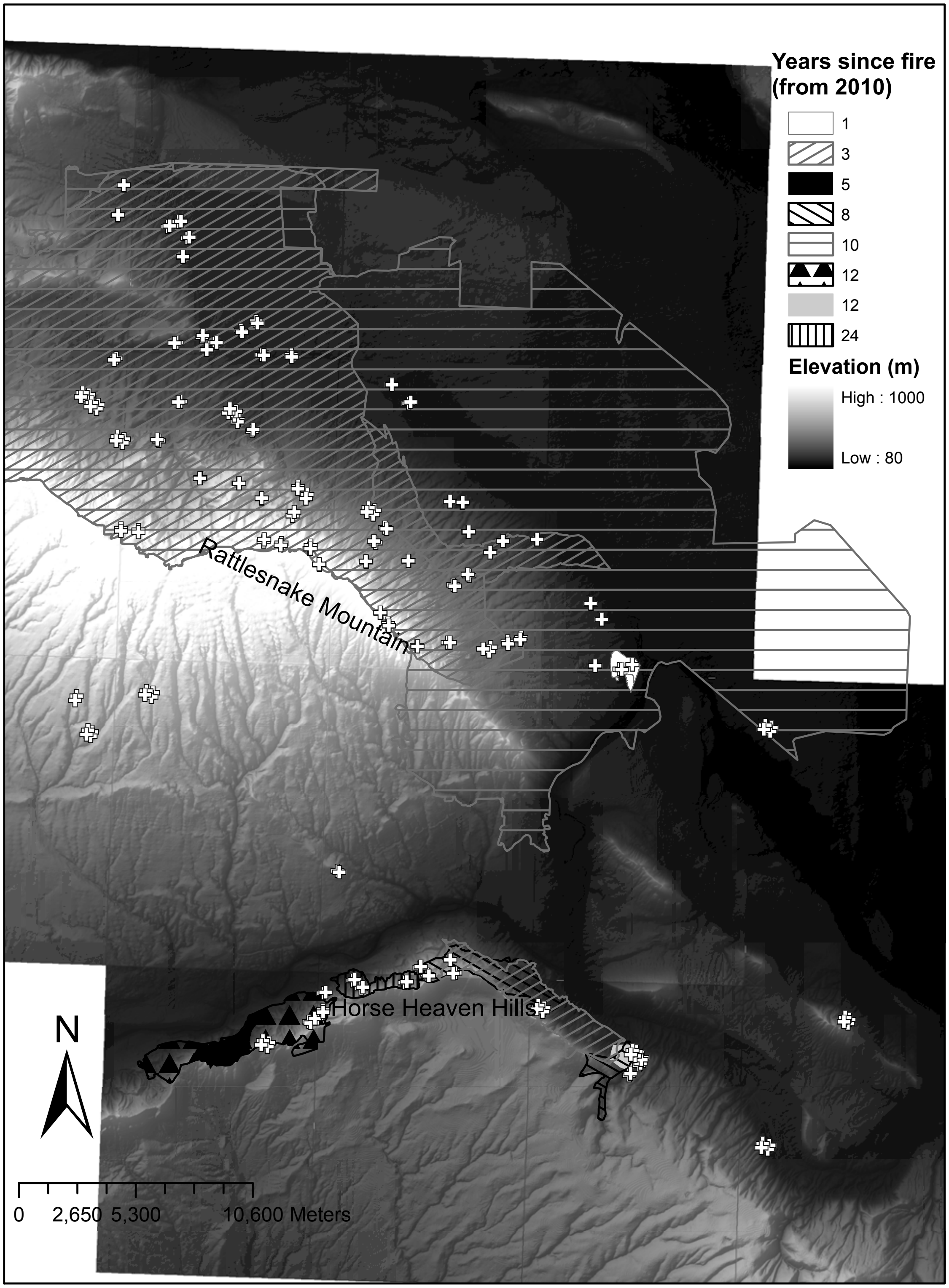

Figure 10: Transects (start and end points indicated by crosses) across elevation gradient in Benton County WA monitored for BSC with footprints of most recent fires since 1980. Note that maximum time since fire is set at 20 years.

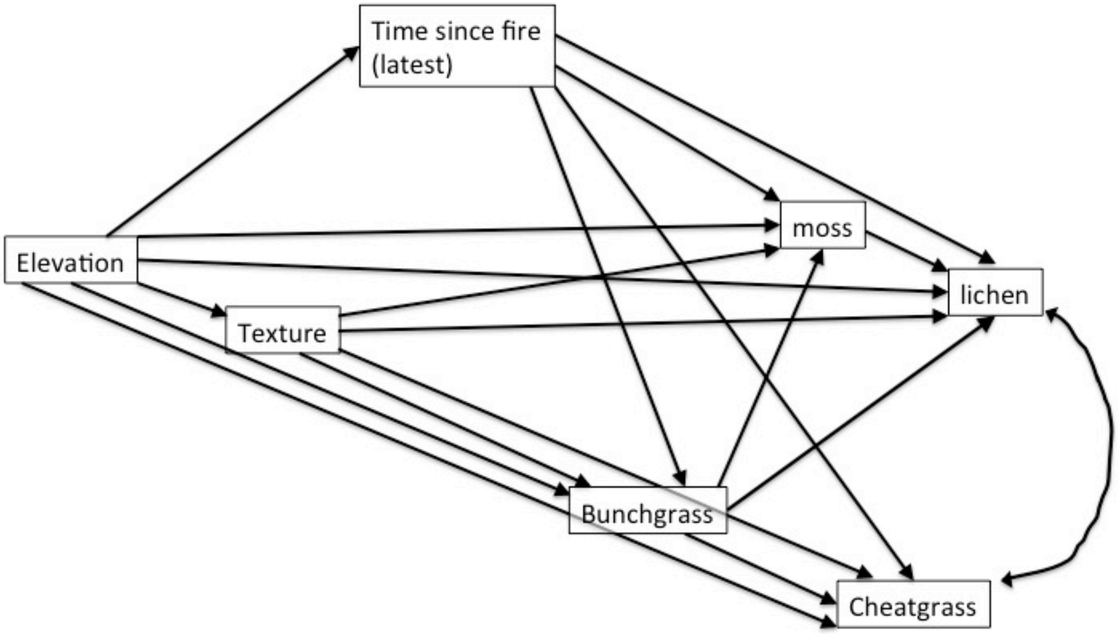

Figure 11: Proposed pathways from landscape, disturbance, and vegetation pathways to biological soil crust cover. Variables are defined in Table 7. Double-headed curved arrow indicates unresolved correlation between the errors of *B. tectorum* and lichen cover. Single headed arrows indicate directed relationships between variables. Error terms for endogenous variables are not shown.

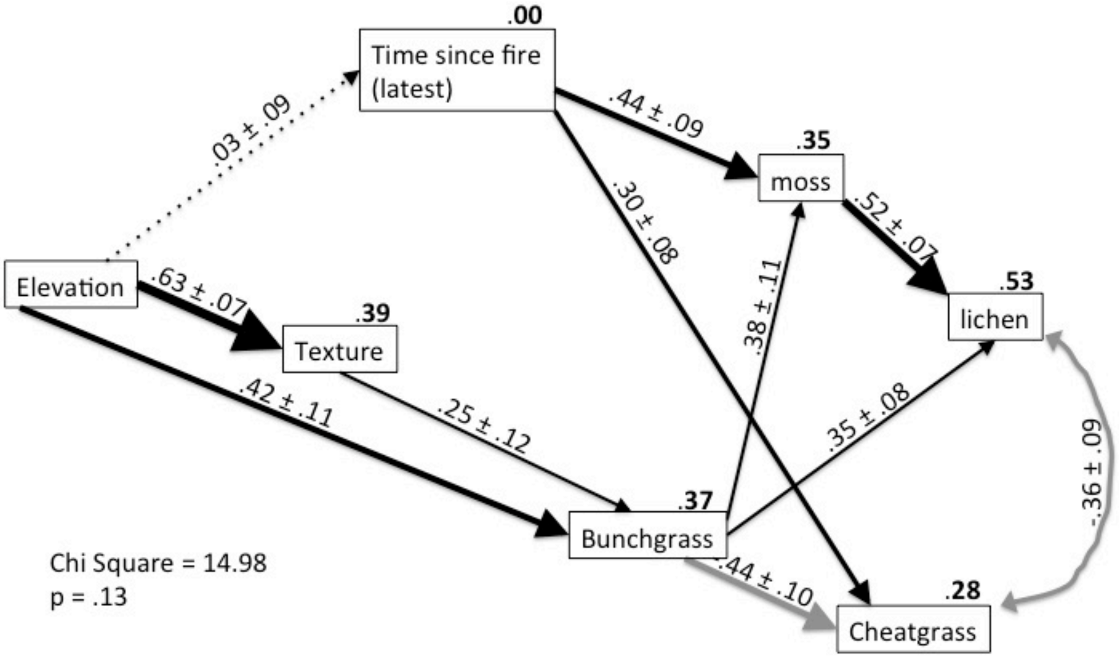

Figure 12: Final model with fit, Chi-square = 14.98, p = 0.13, df = 10. Arrows are drawn proportional to standardized regression weight and values are displayed with bootstrap estimates of standard error. Positive correlations are in black and negative correlations in grey. Error terms for endogenous variables are not shown. Dotted line is nonsignificant. R^2 values are displayed in bold above each variable.

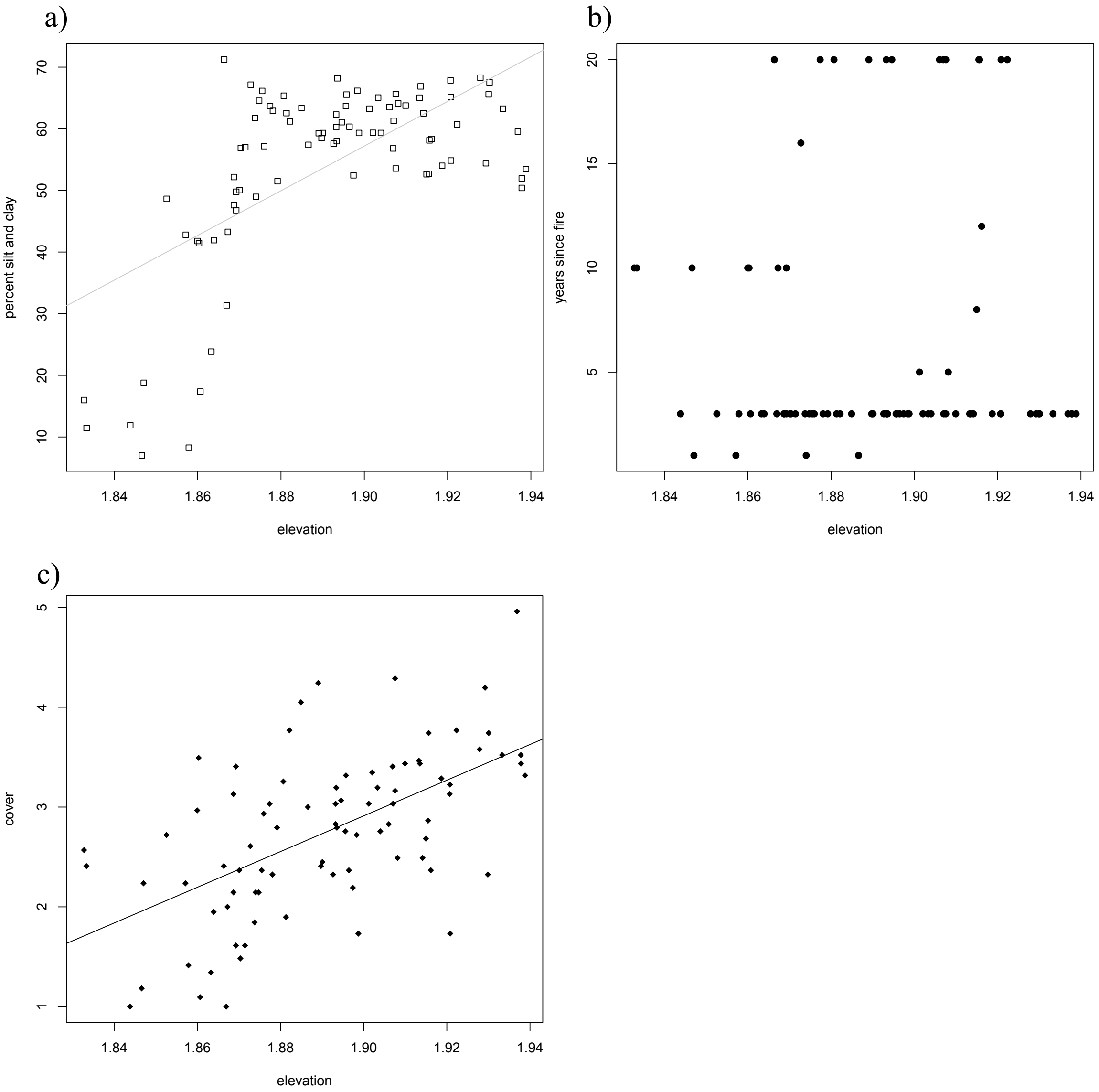

Figure 13: Elevation as predictor of a) texture (percent silt and clay) (r = 0.63), b) time since fire (r = 0.03), and c) bunchgrass cover (r = 0.58). Slope of linear relationships with texture and of bunchgrass cover were significant ($p < 0.05$). Variables were transformed as in Table 7.

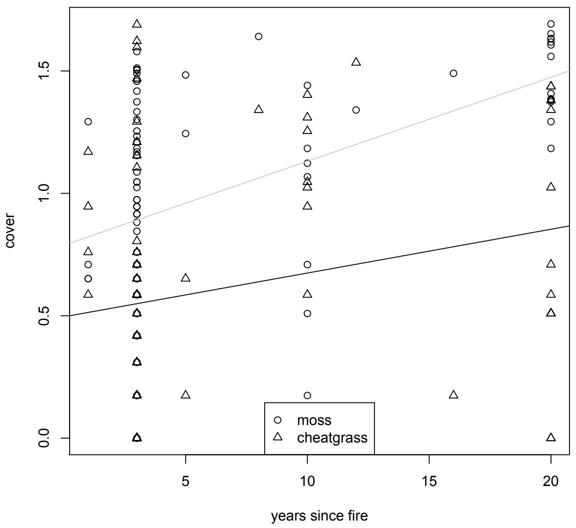

Figure 14: Time since fire as predictor of moss (r = 0.50) and *Bromus tectorum* cover (r = 0.23). Slope of linear relationships with moss (light grey line) and bunchgrass cover (dark grey line) were significant ($p < 0.05$). Variables were transformed as in Table 7.

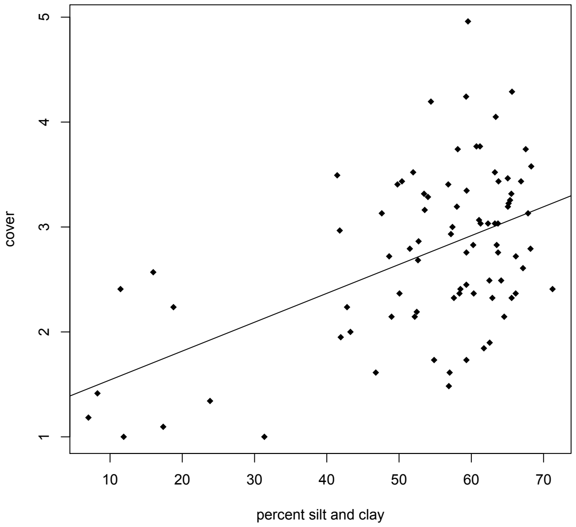

Figure 15: Soil texture as predictor of bunchgrass cover (r = 0.51). Slope of relationship was significant ($p < 0.05$). Variables were transformed as in Table 7.

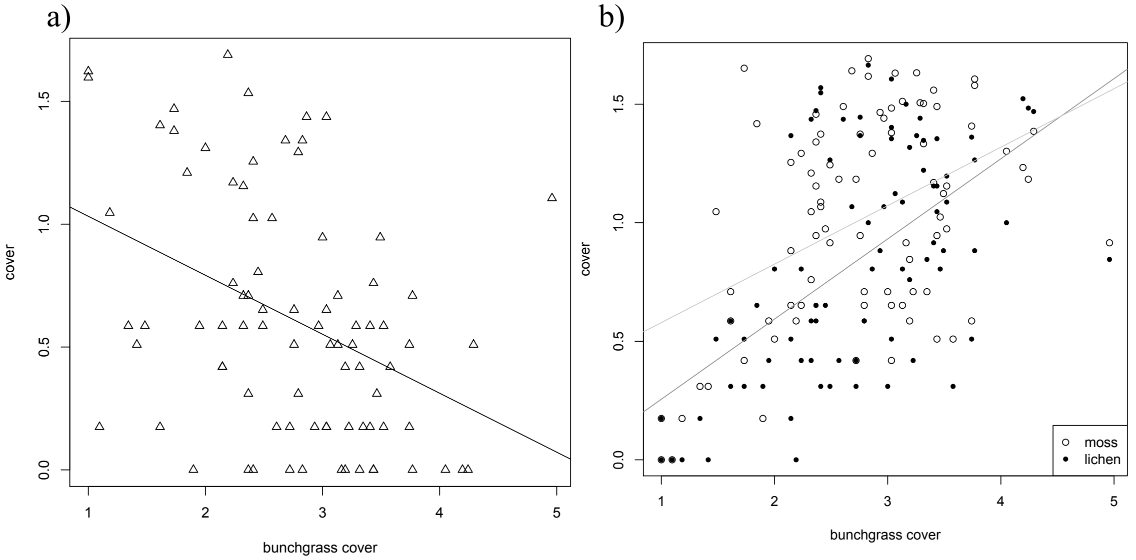

Figure 16: Bunchgrass cover as predictor of a) *Bromus tectorum* (r = -0.39), b) moss (r = 0.45), and lichen cover (r = 0.57). Slopes of linear relationships with *B. tectorum* (dark grey), lichen (medium grey), and moss (light grey) were significant ($p < 0.05$). Variables were transformed as in Table 7.

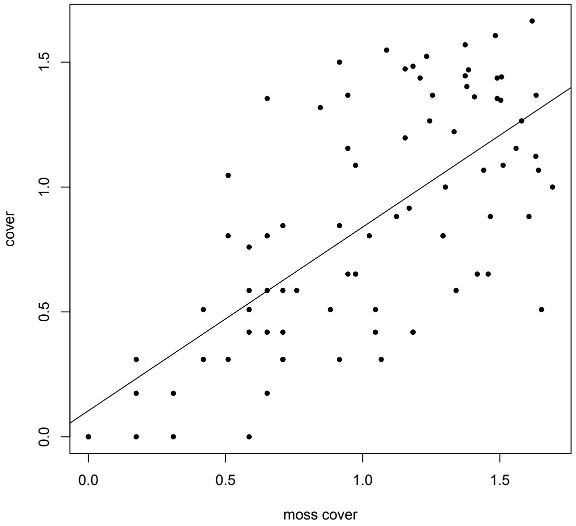

Figure 17: Moss cover as predictor of lichen cover (r = 0.68). Slope of linear relationship was significant ($p < 0.05$). Variables were transformed as in Table 7.

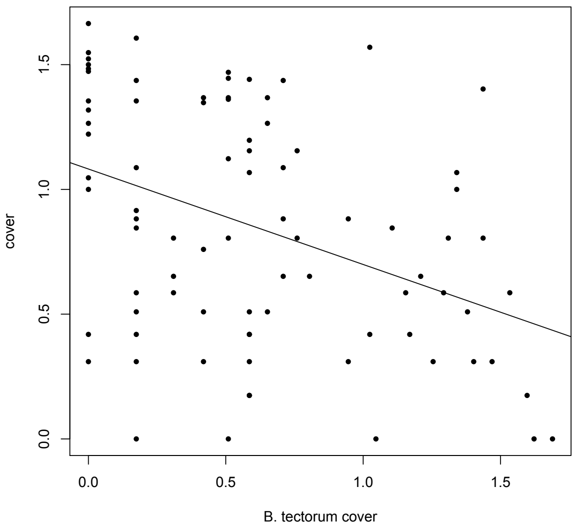

Figure 18: *Bromus tectorum* cover is negatively correlated to lichen cover (r = -0.39). Slope of linear relationship was significant ($p < 0.05$). Variables were transformed as in Table 7.

Tables

Table 7: Mean and standard deviations for all variables and transformations of selected variables for Structural Equation model of biological soil crust cover.

	Raw data	Transformation	Transformed
Elevation	406 (222) m	(((x+1)^-0.5)-1)/-0.5	1.89 (0.03)
Texture	53.9 (15.0) %		
Time since fire	6.49 (6.38) years	Maximum value set at 20 years to reduce influence of large predictor values.	
Bunchgrass cover	7.2 (4.4) %	(x+1)^0.5	2.75 (0.80)
Cheatgrass (*B. tectorum*) cover	3.2 (6.4) %	(((x+1)^-0.5)-1)/-0.5	0.61 (0.49)
Moss cover	7.1 (8.6) %	(((x+1)^-0.5)-1)/-0.5	1.01 (0.44)
Lichen cover	4.8 (6.3) %	(((x+1)^-0.5)-1)/-0.5	0.85 (0.47)
Organic matter	3.9 (1.6) %		
Nutrients	0 (1.5)		
Rock cover	0.9 (2.8) %		
pH	6.8 (0.5)		
Heat load Index	0.85 (0.07)		
Total fires	2.01 (1.11)		

Table 8: Standardized total effects for final structural equation model of factors affecting biological soil crust.

	Elevation	Texture	Time since fire	Bunchgrass cover
Bunchgrass cover	0.58			
Bromus tectorum cover	-0.24	-0.11	0.30	
Moss cover	0.24	0.10	0.44	
Lichen cover	0.32	0.14	0.23	0.55

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Appendix A: Number of plots in each community group in each year.

	low	high
1994	24	18
2001	23	17
2002	24	18
2003	19	14
2004	19	14
2009	24	17
2010	24	18

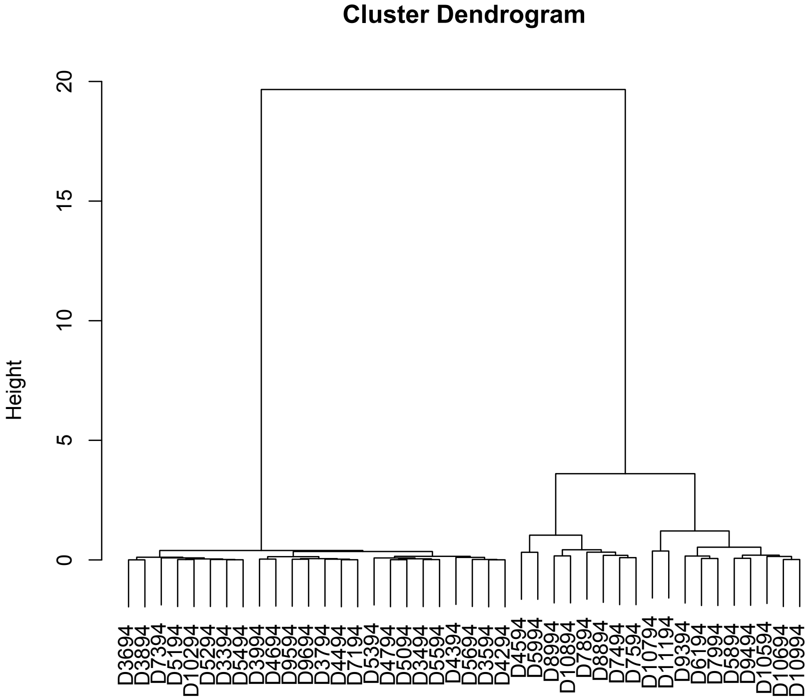
Appendix B: Species codes and scientific names. Codes are from USDA PLANTS Database (2011) with name if known.

Code	Scientific name	Code	Scientific name
ACHY	*Achnatherum hymenoides*	CIIN	*Cichorium intybus*
ACMI2	*Achillea millefolium*	CLAYT	*Claytonia*
ACTH7	*Achnatherum thurberianum*	COGR4	*Collomia grandiflora*
AGGL	*Agoseris glauca*	COLI2	*Collomia linearis*
AGGR	*Agoseris grandiflora*	COPA3	*Collinsia parviflora*
AGHE2	*Agoseris heterophylla*	COUM	*Comandra umbellata*
AGOC	*Ageratina occidentalis*	CRAT	*Crepis atrabarba*
AGOSE	*Agoseris*	CREPI	*Crepis*
ALLIU	*Allium*	CRMO4	*Crepis modocensis*
AMAC2	*Ambrosia acanthicarpa*	CRPT	*Cryptantha pterocarya*
AMLY	*Amsinckia lycopsoides*	CRYPT	*Cryptantha*
AMSIN	*Amsinckia*	DENU2	*Delphinium nuttalianum*
AMTE3	*Amsinckia tessellata*	DEPI	*Descurainia pinnata*
ANDI2	*Antennaria dimorpha*	DESO2	*Descurainia sophia*
ANMI3	*Antennaria microphylla*	DOPU	*Docecatheon pulchellum*
ARFR	*Arenaria franklinii*	DRVE2	*Draba verna*
ARRU4	*Armoracia rusticana*	ELEL5	*Elymus elymoides*
ARTR2	*Artemisia tridentata* ssp. *wyomingensis*	EPBR3	*Epilobium brachycarpum*
ARTR4	*Artemisia tripartita*	EPILO	*Epilobium*
ASCA12	*Astragalus caricinus*	ERAS2	*Erysimum asperum*
ASPU9	*Astragalus purshii*	ERCI6	*Erodiumcicutarium*
ASRE6	*Astragalus reventiformis*	ERCO5	*Erigeron corymbosus*
ASSC6	*Astragalus sclerocarpus*	ERFI2	*Erigeron filifolius*
ASSP4	*Astragalus spaldingii*	ERHE2	*Eriogonum heracleoides*
ASSU7	*Astragalus succumbens*	ERIGE2	*Erigeron*
ASTRA	*Astragalus*	ERLA6	*Eriophyllum lanatum*
BACA3	*Balsamorhiza careyana*	ERNA10	*Ericameria nauseosus*
BRCI2	*Bromus ciliatus*	ERPI3	*Erigeron piperianus*
BRTE	*Bromus tectorum*	ERPO2	*Erigeron poliospermus*
CADO2	*Carex douglasii*	ERPU2	*Erigeron pumilus*
CAMA5	*Calochortus macrocarpus*	ERST4	*Eriogonum strictum*
CATH4	*Castilleja thompsonii*	FEID	*Festuca idahoensis*
CEDI3	*Centaurea diffusa*	FRPU2	*Fritillaria pudica*
CHDO	*Chaenactis douglasii*	GAAP2	*Galium aparine*
CHLE4	*Chenopodium leptophyllum*	GALIU	*Galium*
CHVI8	*Chrysothamnus viscidiflorus*	GAMU2	*Galium multiflorum*

Appendix B (continued)

Code	Species name	Code	Species name
GISI	*Gilia sinuata*	PEAC	*Penstemon acuminatus*
GRSP	*Grayia spinosa*	PEGL4	*Penstemon glandulosus*
HADIA	*Hackelia diffusa*	PENST	*Penstemon*
HECO26	*Hesperostipa comata*	PHHA	*Phacelia hastata*
HECU2	*Helianthus cusickii*	PHHO	*Phlox hoodii*
HECY2	*Heuchera cylindrica*	PHLI	*Phacelia linearis*
HOUM	*Holosteum umbellatum*	PHLO2	*Phlox longifolia*
KOMA	*Koeleria macrantha*	PLMA4	*Plectritis macrocera*
KRLA2	*Kraschneninnikovia lanata*	PLPA2	*Plantago patagonica*
LAGL5	*Layia glandulosa*	POA	*Poa*
LAOC3	*Lappula occidentalis*	POBU	*Poa bulbosa*
LARA	*Lagophylla ramosissima*	POCU3	*Poa cusickii*
LASE	*Lactuca serriola*	POSE	*Poa secunda*
LECI4	*Leymus cinereus*	PSSP6	*Pseudoroegneria spicata*
LIBU2	*Lithophragma glabrum*	PTTE	*Pteryxia terebinthina*
LIGL2	*Lithophragma glabrum*	RAGL	*Ranunculus glaberrimus*
LIPA5	*Lithophragma parviflorum*	RANUN	*Ranunculus*
LIPE	unknown	SAKA	*Salsola kali*
LIRU4	*Lithospermum ruderale*	SEID	unknown
LODI	*Lomatium dissectum*	SEIN2	*Senecio integerrimus*
LOGO	*Lomatium gormanii*	SELE	*Sedum leibergii*
LOGR	*Lomatium grayi*	SIAL2	*Sisymbrium altissimum*
LOMA3	*Lomatium macrocarpum*	SIDO	*Silene douglasii*
LOMAT	*Lomatium*	SOCA	unknown
LOTR2	*Lomatium triternatum*	SPMU2	*Sphaeralcea munroana*
LUARL5	*Lupinus argenteus*	STLO4	*Streptanthella longirostris*
LULE3	*Lupinus leucophyllus*	STMI13	*Stephanomeria minor*
LUPIN	*Lupinus*	SYMPH4	*Symphyotrichum*
LUPU	*Lupinus pusillus*	SYOR2	unknown
LUSE	unknown	TECA2	*Tetradymia canescens*
LUSU5	*Lupinus sulfureus*	TOFL5	*Townsendia florifer*
MACA2	*Machaeranthera canescens*	TRDU	*Tragopogon dubius*
MEAL6	*Mentzelia albicaulis*	VUBR	*Vulpia bromoides*
MELO4	*Mertensia longiflora*	VUMI	*Vulpia microstachys*
MIGR	*Microsteris gracilis*	VUOC	*Vulpia octoflora*
MOPA	unknown	ZIVE	*Zigadenus venenosus*
MYST2	*Myosotis stricta*		
NALEL2	*Navarretia leptalea*		
NEST5	*Nestotus stenophyllus*		
NOTR2	*Nothocalais troximoides*		
OEPA	*Oenothera pallida*		

Appendix C: Dendrogram of plot elevation, soil texture (percent silt and clay), and heat load index using agglomerative clustering.



Appendix D: Proportion of species in common (based on presence/absence) between earlier and latter year by community group.

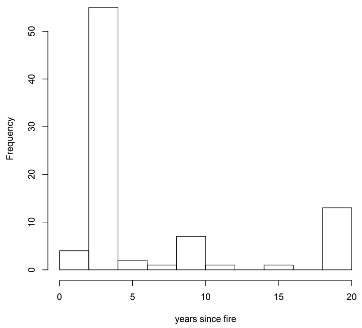
		1994	2001	2002	2003	2004	2009
2001	Low	.54					
	High	.58					
2003	Low			.73			
	High			.76			
2004	Low		.65				
	High		.76				
2009	Low					.46	
	High					.64	
2010	Low	.69	.71				.74
	High	.56	.75				.81

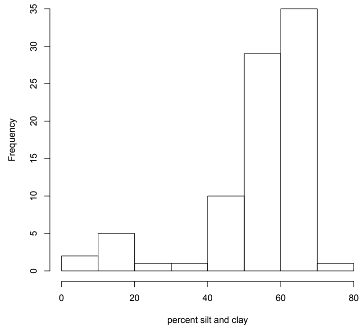
Appendix E: Timeline of restoration treatments following 2000 and 2007 fire on ALE with number of plots and average Bray-Curtis distance of plots with given treatment.

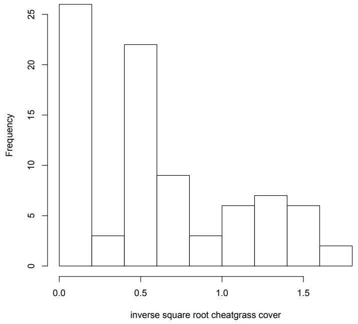
Year	Treatment	n	Average Bray-Curtis distance
2001-2002	No treatment	18	.54
	Locally sourced *Artemisia tridentata* ssp. *wyomingensis* planting	2	.47
2002-2003	No treatment	15	.45
	Aerial spray "Roundup" (glyphosate), aerial seed low elevation mix (*Elymus lanceolatus, Achnatherum hymenoides, Poa secunda, Elymus elymoides, Achillea millefolium*)	3	.37
	Aerial spray "Roundup", aerial seed high elevation mix (*Pseudoroegneria spicata, P. secunda, E. elymoides, A. millefolium*)	1	.54
	Aerial seed high elevation mix	1	.33
2003-2004	No treatment	17	.44
	Aerial spray "Roundup"	2	.49
2004-2009	No treatment	10	.51
	Aerial spray "Journey" (Glycine), drill mix 2 (*A. hymenoides, P. secunda, E. elymoides, A. millefolium, Sporobolus cryptandrus, Linum* sp.)	1	.47
	Aerial spray "Journey"	1	.93
	Aerial spray "Journey," aerial seed mix 1 (*A. hymenoides, P. secunda, E. elymoides, A. millefolium, Sporobolus cryptandrus, Linum* sp.)	3	.56
	Fire, aerial spray "Plateau" (Ammonium salt of imazapic), aerial seed mix 3 (*A. hymenoides, P. secunda, E. elymoides, Hesperostipa comata, P. spicata, A. millefolium, Sporobolus cryptandrus, Linum* sp., *Krascheninnikovia lanata, A. tridentata* ssp. *wyomingensis*)	5	.48
2009-2010	No treatment	22	.38
	A. tridentata ssp. *wyomingensis* bare root planting	2	.40
	Aerial spray "Strikezone" (Saccharide and polysaccharide ethers and alkyl polyethoxylated alcohols) and "Roundup," bare root planting	1	.18
	Bare root planting and aerial seeding mix 8 (*A. hymenoides, H. comata, P. secunda, P. spicata, A. tridentata* ssp. *wyomingensis, E. elymoides, A. millefolium, Sporobolus cryptandrus, Linum* sp., *Krascheninnikovia lanata, Purshia tridentata, Chrysothamnus viscidiflorus*)	1	.16

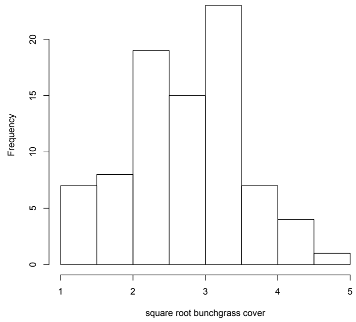
Note: No statistical comparisons were made due to lack of replication.

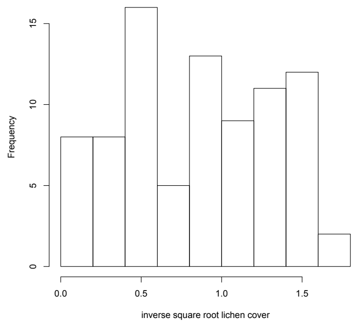
Appendix F: Histograms of transformed variables used in Structural Equation Model.

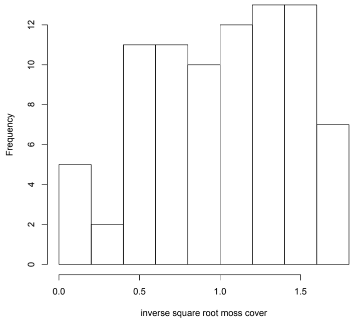


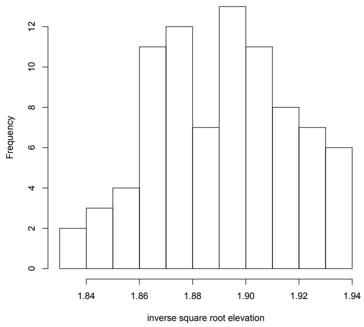












Appendix G: Loadings for soil nutrient variables on the principal component axes 1-5, and the amount of variation explained by each axis.

	PC1	PC2	PC3	PC4	PC5
B	.542	.269	.110	-.093	.005
Mn	.512	.135	-.259	.297	.242
Zn	.103	-.511	-.229	-.443	0.576
Al	.153	-.481	.468	-.092	-.509
P	.284	.006	-.622	-.019	-.538
Ca	.429	.196	.510	.012	.182
Mg	.379	.485	-.043	-.058	-.079
Na	.024	.379	-.009	-.833	-.145
% variation explained	28.6%	19.7%	17.4%	12.8%	8.3%