Department of Defense
Legacy Resource Management Program

PROJECT NUMBER 13-623

Leveraging Land Condition Trend Analysis (LCTA) Data to Understand Vegetation Change on Military Installations: Phase I Report

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August 13, 2015

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DoD Legacy Project 13-623

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Table of Contents

Non-Technical Summary 1

Introduction 2

State and Transition Models (STMs): Theory 2

The Sagebrush Steppe Ecosystem 3

State and Transition Models (STMs): Applications in the Sagebrush Steppe 4

Objectives 6

Methods 8

Study Site 8

Field Collection of Vegetation Data 8

Vegetation Response Variables 9

Environmental Variables 10

Disturbance Variables 11

Statistical Analysis 13

Community Classification 13

Identifying Transitions Among Communities 14

Quantifying the Role of Disturbance 15

Updating and Extending the State-and-Transition Model 16

Results 18

Communities in 1989 18

Communities in 2002 23

Transitions Among Communities 26

Transitions from the "Big Sagebrush/Grass" Community 31

Transitions from the "Big Sagebrush/Exotic" Community 31

Transitions from the "Dwarf Shrub" Community 32
Disturbance Impacts 35
Disturbance Effects on Vegetation Metrics 35
Disturbance-Related Indicator Species 39
State and Transition Model 41
Discussion 43
Vegetation Communities and Transitions at YTC 43
Disturbances as Drivers of Vegetation Dynamics 44
Relation to other Vegetation Classifications 46
Strengthening Current State and Transition Models 47
Implications for Military Training and Management 48
Future Research Directions 49
Acknowledgements 50
Bibliography 51
Appendix 1: Species retained for compositional analyses. 56
Appendix 2: Environmental cluster analysis 57
Appendix 3: Dendrograms and scree plots for plant communities in 1989 and 2002. 61
Appendix 4: Analysis results. 63
Additional Materials 68

Non-Technical Summary

Sagebrush steppe ecosystems are a unique feature of the American west, providing high quality land for military training and critical habitat for threatened and endangered wildlife. Disturbances, including fire, livestock grazing, and military training, can cause large changes in vegetation composition. Such changes can directly impact the utility of areas for military training, and could indirectly threaten military training if, for example, they contribute to the listing of endangered species and associated restrictions on activities within critical habitat. Vegetation change is often summarized in a state-and-transition model (STM). We analyzed vegetation data collected in 1989 and 2002 from 201 plots established as part of the Department of Defense Land Condition Trend Analysis (LCTA) program on the Yakima Training Center (YTC). We had four main objectives: 1) Identify and classify plant communities at YTC in 1989 and 2002; 2) Identify and quantify areas of greatest and least change between 1989 and 2002; 3) Evaluate the impact of disturbance on vegetation communities; and 4) Refine the current STM so that it is more directly relevant for YTC land management. Data on plant cover and composition were collected, along with disturbance histories. We combined vegetation data with information about the environmental characteristics and disturbance histories of each plot. Based on the vegetation, we identified three communities in 1989 (big sagebrush/grass; big sagebrush/exotic; dwarf shrub), and four communities in 2002 (grass steppe; exotic; big sagebrush/grass; dwarf shrub). Most of the plots classified in the same community in 1989 were also in the same community in 2002, though most transitions (10 of 12 possible) were detected. The dynamics of individual plots were related to their specific disturbance histories, especially in terms of military training intensity, livestock grazing, and fire. We synthesized these results into an updated STM for the shrub-steppe ecosystem at YTC. Future work will examine interim dates to distinguish short- and long-term effects of disturbances and will incorporate plant functional traits into analyses.

Introduction

Natural resource managers make many decisions about when, where, and which actions to take to meet their management objectives. Understanding how and why vegetation changes over time can help natural resource managers make more informed decisions. Many of these actions are disturbances that alter resource availability and shape plant communities, and are necessary because ecosystems and species are reliant on disturbance for maintenance and reproduction. Long-term studies of permanent plots are particularly valuable for providing insights about vegetation change and its drivers. This knowledge is often summarized in state and transition models (STMs).

State and Transition Models (STMs): Theory

Classical succession models are linear and deterministic (e.g., Clements 1916; Dyksterhuis 1958), but work in recent decades has shown that these models are insufficient in many systems. State and Transition Models (STMs) are a powerful way of integrating multiple sources of empirical knowledge in a visual summary of the dynamics of an ecosystem. In a STM, plant communities are identified and categorized into states, thresholds between states are delineated, and the drivers of transitions are described (Westoby et al. 1989; Allen-Diaz & Bartolome 1998).

A **state** is defined as a combination of vegetation structure and soil that is resilient to disturbance and able to remain at equilibrium (Stringham et al. 2003). Numerous studies have documented instances where vegetation can stably exist in a number of different states (configurations) within an ecosystem. For example, shallow lakes in Sweden either have clear water and abundant submerged vegetation, or are turbid with very high phytoplankton densities (Blindow et al. 1993). Similarly, plant communities in the shrub-steppe are assumed to exist in multiple stable states ranging from exotic-grass dominated to native-shrub dominated. Stability in this sense means that once the ecosystem has achieved this configuration, self-stabilizing mechanisms could maintain that state into perpetuity. Although states are generally considered to be stable, disturbances can also cause relatively small changes in the community such as changes in the relative abundance of species, creating temporary "transitional communities" or **phases**.

Some disturbances, or alterations to the disturbance regime, can cause the community to cross a **threshold** and shift from one state to another. In addition, multiple disturbances can synergistically drive state change. For example, Chambers et al. (2013) hypothesized that interactions between environmental conditions (e.g., temperature change), nutrient availability, and grazing disturbance interact to drive state changes from cold desert shrublands to annual systems dominated by *Bromus tectorum* through expansion of *Bromus'* realized niche**.**

The combination of initial community, final community, and the drivers that led to this change represents a **transition**. It is important to develop STMs from real data to verify which transitions actually occur and to document their probability of occurrence. Some transitions are passive, such as natural successional dynamics, while others require active intervention. A key example of the latter is a transition to re-establish a community after a threshold has been crossed. In an instance like this, restoring the prior community may require large and expensive restoration and maintenance efforts.

The Sagebrush Steppe Ecosystem

The sagebrush steppe ecosystem extends from the Great Basin region of the American west through the Columbia Plateau into British Columbia, Canada (Map 1). Historically dominated by a mixture of sagebrush (*Artemisia* spp.) and perennial bunchgrasses and forbs, these systems provide critical habitat for rare species like the greater sage grouse (*Centrocercus urophasianus*) and the Columbia basin pygmy rabbit (*Brachylagus idahoensis*). Sagebrush steppe ecosystems are relatively unique in that, historically, there were no large ungulate grazers until livestock were introduced.

Cheatgrass (*Bromus tectorum*), an exotic annual grass, has significantly altered the sagebrush steppe by altering fire regimes and converting perennial shrub steppe to annual dominated grasslands (Knapp 1996, Chambers et al. 2007). Invasion by exotic grasses like *Bromus* increases fire frequency and intensity, which in turn fragments sagebrush dominated communities and reduces overall shrub cover where species lack the ability to resprout (D'Antonio & Vitousek 1992). *Bromus* also alters the timing of fire in the system, drying earlier in the growing season (i.e., June) and thus supporting fires at times when the

native bunchgrasses are most susceptible to fire (Wright and Klemmedson 1965). In addition, the presence of exotic species has been demonstrated to be tied to the loss of dominant, foundational species in the ecosystem. Loss of the shrub canopy, for example, can alter water availability, allowing short-rooted exotic species to establish and dominate in disturbed shrub steppe (Prevéy et al. 2009, 2010). Finally, physical disturbances such as roads can strongly impact vascular plant diversity in the sagebrush steppe (Lavin et al. 2013).

State and Transition Models (STMs): Applications in the Sagebrush Steppe

STMs are of great utility in applied management, particularly in semi-arid and rangeland ecosystems (Stringham et al. 2003). Early models of arid-land response to disturbance and management relied on Clementsian concepts of succession wherein communities deterministically and linearly develop toward a "climax" community (Clements 1916). Models which built upon this foundation were used for arid-lands management for several decades (e.g., Dyksterhuis 1958) until Westoby et al. (1989) introduced a non-linear model describing rangeland responses at non-equilibrium, using a STM framework and focusing on a few key species. This model, considered to be more precise and useful than classical models (Allen-Diaz and Bartolome 1998), has become the basis for arid-lands and rangeland management in the sagebrush steppe.

Additional STMs have been developed for the shrub-steppe in recent years (e.g., Kachergis et al. 2012). Some STMs describe changes in communities without defined thresholds (e.g., Allen-Diaz & Bartolome 1998), while others have clearly delineated thresholds (Hemstrom et al. 2002, Bestelmeyer & Brown 2003, Wisdom et al. 2005, Bestelmeyer et al. 2010). In 2012, Davies et al. proposed a new STM that incorporates the impacts of multiple disturbances and restoration activities on the entire vegetation community. This model organized sagebrush-steppe states and transitions along two axes: shrub/grass cover, and native/exotic cover. This development represents a significant step forward, as previous models had focused on responses to single disturbance events, of individual species, or of broad functional groups (e.g. shrubs, grasses) to construct STMs. The model proposed by

Davies et al. (2012) was developed on the Arid Lands Ecology Reserve, near the Yakima Training Center, but has not been validated with data not used in its development.

Common disturbances such as fire and livestock grazing have been incorporated into STMs in the sagebrush steppe, but other activities such as military training and restoration or habitat maintenance activities may also be important. As is often the case, the specifics of the disturbance matter. For example, the effect of a fire may depend on its timing during the calendar year, the time since the last fire, and the size of the fire.

Davies et al. (2012) found that multiple wildfires caused widespread loss of shrub canopy in sagebrush steppe with a subsequent transition to domination by low-growing, resprouting forbs. Shrubs and forbs with the ability to resprout after fire were more abundant, while those that reestablished solely through seeding were essentially removed from the community by repeated wildfire. Unfortunately, efforts to restore the shrub canopy of recently burned sagebrush steppe through reseeding have been found to be mostly unsuccessful, highlighting the difficulty of restoring these communities to a previous state (Knutson et al. 2014).

Livestock grazing is a common type of land use throughout western North America. The type of livestock, as well as the timing and intensity of grazing, can strongly shape vegetation responses. For example, when managed appropriately, livestock grazing can improve habitat for endangered species (e.g., the greater sage grouse (*Centrocercus urophasianus*)) through removal of dense annual grasses and increased access to food plants (Boyd et al. 2014).

Military training activities can have large and long-lasting impacts on ecosystems (Belnap & Warren 2002). For example, tracked-vehicles have been demonstrated to have impacts lasting >4 years on invertebrate and vegetation communities in tall grass prairie ecosystems (Althoff & Thien 2005, Althoff et al. 2009) and can lead to decreased woody plant abundance and loss of native bunchgrasses (Thurow et al. 1993). In the shrub-steppe ecosystems of Idaho, tank tracks and divots created by tanks increased the cover of bare ground, litter, and exotic annuals, and decreased the cover of desirable native species, shrubs, and biotic soil crusts (Watts 1998). Studies performed on shrub-steppe ecosystems

located at Yakima Training Center in Yakima, Washington have demonstrated that training activities involving off-road maneuvers increase negative vegetation impacts, particularly for those vehicles with narrow turn-radii (Haugen et al. 2003).

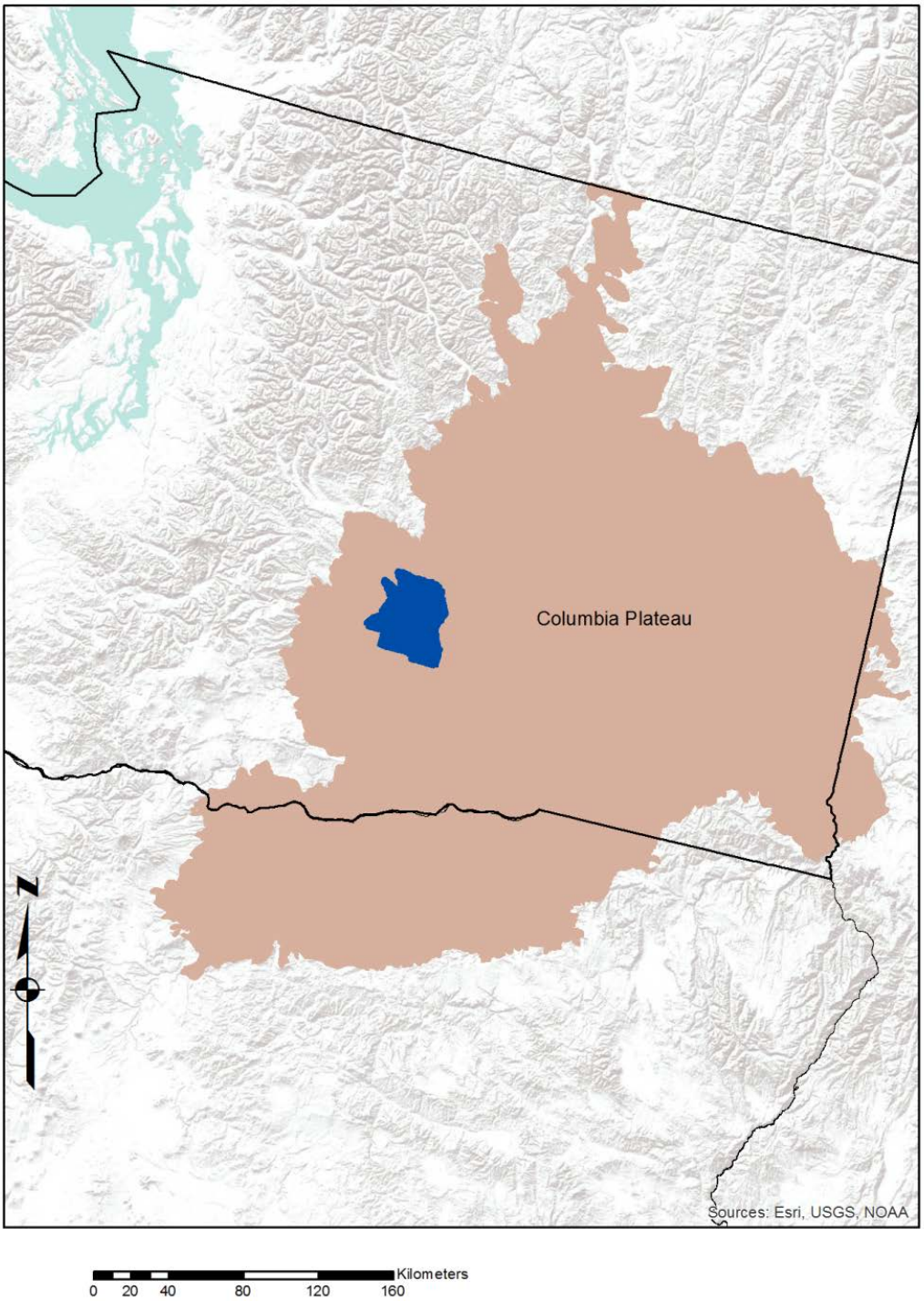
Restoration activities can also impact vegetation state. These activities include chemical and other methods of controlling undesirable vegetation and the establishment of desired species through activities such as seeding. Challenges to these efforts include the logistics of restoring large tracts of degraded land and the narrow windows of opportunity for establishing native species.

Objectives

In this study, we use data from 201 permanent plots located on the Yakima Training Center (YTC) to examine vegetation dynamics and to relate those dynamics to drivers such as fire, livestock grazing, military training, roads, and maintenance activities. The plots were established in 1989 as part of the United States Army Land Condition Trend Analysis (LCTA) program and re-measured multiple times through 2002, though this analysis focuses only on 1989 and 2002. These data are from more plots and spanning a wider range of environmental variables and disturbance conditions than those used by Davies et al. (2012). Therefore, our overall goal was to use these data to validate and strengthen the STM proposed by Davies et al (2012).

In this project, we had four specific objectives:

1) To identify and classify plant communities at YTC in 1989 and 2002;
2) To identify and quantify areas of greatest and least change between 1989 and 2002;
3) To evaluate the impact of disturbance on vegetation communities; and
4) To refine the current STM so that it is more directly relevant for YTC land management.



Map 1. Location of Yakima Training Center within the Columbia Plateau ecoregion.

Methods

Study Site

The Yakima Training Center (YTC) occupies about 133,000 ha in Washington state, on the western border of the sagebrush-steppe ecological zone (Map 1). Historic human activities in the YTC region include Native American occupation, ranching, and diatomaceous earth extraction (Jones & Kunze 2003). The site has been continuously used for military training since 1942. During the LCTA project (1989-2002), military training activities occurred in pulses tied to military mission needs, with large training activities occurring in 1989-1991 in preparation for Operation Desert Storm, and again in 1995 as YTC staged large-scale military training maneuver exercises (Jones & Kunze 2003). In addition, moderate intensity grazing by cattle and sheep occurred across YTC from 1960-1995. Non-military recreation also occurs at the site, including low impact activities such as hiking, horseback riding, and hunting.

This study focused on 202 permanent plots established in 1989 as part of the United States Army Land Condition Trend Analysis (LCTA) program (Map 2). Commonly occurring species on these plots include shrubs such as *Artemisia* spp., perennial bunchgrasses such as *Poa secunda, P. fendleriana*, *Festuca idahoensis*, and *Pseudoroegneria spicata*, and perennial forbs such as *Phlox* spp. The site has a semi-arid climate characterized by cold, wet winters and hot, dry summers. Thirty-year averages for mean annual temperature at the plots range from 7 - 12°C, and for annual precipitation range from 189 - 374 mm. Plot elevations range from 163 - 1247 m. Soil-types include glacial outwash, loess, residuum, alluvium and basaltic colluvium (Jones & Kunze 2003). YTC has experienced both small and large fires during the study period; individual plots burned from zero to three times between 1984 and 2002.

Field Collection of Vegetation Data

Each LCTA plot is a 100-m long transect. Data were collected periodically between 1989 and 2004. This analysis examines changes from 1989 to 2002 and is based on the 201 plots that were monitored in both years (plot 57 was not re-sampled in 2002).

Vegetation was sampled using the point intercept method (Jones & Kunze 2003). At each plot, a 100 m tape was stretched between permanent metal stakes and the vegetation was assessed every meter, from 0.5 to 99.5 m (n = 100 points) along the tape. At each point, a one-meter metal pin was lowered vertically to the ground and aerial plant cover was recorded at 0.10 cm height increments (Jones & Kunze 2003). For this analysis, we focused on the presence of each species at each point, and did not consider the height above the ground at which it was encountered. We calculated the frequency of each species in each plot as the number of points at which it occurred divided by the total number of points in the plot. For simplicity, we refer to these frequency values as 'cover' in this report.

Vegetation Response Variables

Vegetation dynamics between 1989 and 2002 were examined using composition and several univariate response variables.

Composition. Collectively, 131 species were recorded across the 201 plots measured in both 1989 and 2002. However, many of these species are too rare to differentiate among communities. For compositional analyses, we therefore removed all species that occurred on fewer than 5% of the 402 plot-year combinations. This resulted in the retention of 30 species for these analyses (Appendix 1). After removing these species, we relativized the reduced dataset by plot totals to focus on relative abundances.

Total cover. Total cover of all plants is sensitive to inter-observer differences but provides an indication of overall plant abundance. Total cover was calculated using all taxa (i.e., including rare species).

Species richness. Species richness provides a common and simple measure of the diversity of the community. Richness was calculated using all taxa (i.e., including rare species).

Bray-Curtis distance from 1989 to 2002. To quantify compositional change on each permanent plot, we calculated the Bray-Curtis distance (aka dissimilarity) between its composition in 1989 and 2002. These calculations were conducted on the reduced dataset used for compositional analyses. Bray-Curtis distances can range from 0 (no change; identical composition) to 1 (complete change; no species overlap).

Relative cover of functional groups. Species in the same functional group are more likely to have similar dynamics than those in other functional groups. We considered functional groups based upon the combination of life form (forb, grass, shrub) and nativity (native, exotic). However, the reduced dataset used for compositional analyses only included 3 exotic species (1 grass, 2 forbs) so we did not differentiate exotics by functional group. Species were therefore grouped into four functional groups: exotics, native forbs, native grasses, and shrubs (all native). The relative covers of all species in each group were summed to yield the total relative cover of that functional group in that plot-year combination. The STM model proposed by Davies *et al*. (2012) includes axes related to the abundance of shrubs and the abundance of exotic species. The functional groups included here thus are directly relatable to the STM model.

Environmental Variables

Elevation, slope, and aspect were measured for each plot, and the plot's UTM coordinates recorded. Soil texture (percent sand) was obtained from soil samples taken in each plot in 1989. Soil depth was identified as an important factor in determining the location of vegetation communities across the landscape in previous studies (Jones & Kunze 2003), so we obtained soil depths from the United States Department of Agriculture Soils Database (USDA NRCS; http://www.nrcs.usda.gov). Heat Load Index (HLI) was calculated based on aspect, slope, and latitude following McCune and Keon (2002; equation two). HLI is unitless, but larger values indicate warmer and drier conditions.

Climate data (mean annual precipitation (MAP), mean annual temperature (MAT)) were gathered for each plot from the PRISM database (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). However, these variables are highly correlated with elevation (MAP: R^2= 0.89; MAT: R^2 = -0.88) so these variables were not included in statistical models.

We explored the utility of grouping plots on the basis of their environmental similarity (Appendix 2). Clustering on the basis of 6 abiotic and climatic variables produced distinct groups, but preliminary analyses suggest that these groups were not helpful in understanding vegetation dynamics. Further investigation using additional variables might

be helpful in the future. For example, Trakhtenbrot & Kadmon (2005) successfully used 17 variables related to climate and lithology to identify sites that efficiently represented regional floristic diversity.

Disturbance Variables

One of our objectives was to relate compositional change to disturbance. We focused on six disturbance variables: military training activities, military training areas, roads, livestock grazing, fire, and maintenance activities. Data sources for each type of disturbance are described in this section. Disturbance categories differ in how they are expressed and whether they were constant during the study period (e.g., military training areas, roads, fire history) or varied from year to year (military training activities, livestock grazing, maintenance activities).

Military training. Military training varies among years and training areas (TAs). General information about the type and intensity of military training activities was obtained from Jones & Kunze (2003). Two variables related to military training were used. First, the YTC LCTA database contains information about activities around each plot in most years (1989-1998; 2002-2004). These *military training activities* were assigned relative intensities: foot-based training activities were assigned the lowest intensity while those involving ground disturbance were assigned the highest intensity (Table 1). For each plot, the relative intensities of all training activities in all years were summed (range = 0-61; mean = 17) and analyzed as a continuously distributed variable. These data are concentrated in 1989-1996 and 2002; information from 1997-2001 is available from YTC (Jones & Kunze 2003) and should be included in the next iteration of this analysis.

Table 1. Military training activities and the relative intensity (0 to 5) assigned to each.

Training Activity	Relative Intensity
No Mil.	0
Foot	1
Wheeled	2
Tracked	3
	4
Bivouac Demolition Excavation	5

Second, *military training areas* (TAs) were assigned relative off-road military usage ranks (low, moderate, high) by Jones & Kunze (2003; Table 5-1). All plots within a TA were assumed to have experienced the same intensity of activities. TA 11 was noted as 'moderate-high' usage ('overall disturbance moderate with areas of high'); this was changed to 'moderate' in our tally. In addition, a few areas were not included in the table; we assumed their usage intensities were as follows: TA 13 (high), Multi-Purpose Range Complex (MPRC; low), and MPRC surface danger zone (SDZ; low).

Roads. Roads were used as a proxy for other human-caused disturbances, and were assumed not to vary among years. Distance from each plot to the nearest road was calculated from GIS layers obtained from YTC. The distance to the nearest road ranged from 5 to 3762 feet (mean = 626 feet).

Livestock grazing. The YTC LCTA database contains land use notes about grazing by cattle, sheep, or other animals. Each plot in each year was classified as 'grazed' or 'ungrazed' based on whether evidence of livestock grazing was noted in the database. For these 201 plots, grazing was noted in 0 to 7 (mean = 3.8) of the 11 years in the database.

Fire. The fire history of each plot was compiled by overlaying the plot locations onto fire perimeter data provided by YTC staff and obtained from the MTBS (http://mtbs.gov) and GeoMAC (http://www.geomac.gov) databases. These data spanned the period from 1984, the earliest year for which MTBS data are available, to 2002. Fires impacting at least one research plot occurred in 1987, 1988, 1990, 1996, 1999, 2000, and 2001. For this analysis, we focused on fires that occurred between 1989 and 2002. Plots were classified as 'Unburned' unless they occurred within the perimeter of any fire during this period, in which case they were classified as 'Burned'. Using these criteria, 55 of the 201 plots were classified as 'Burned'.

Maintenance activities. We defined maintenance activities as intentional activities undertaken by managers to enhance or maintain vegetation. For the period from 1989-2002, the YTC LCTA database contains 8 maintenance categories: no maintenance, accidental burning older than one year, accidental burning less than one year old, prescribed burning older than one year, chemical application, mowing, other, and seeding.

We did not include 'no maintenance' or accidental burns in our summary of maintenance activities. Relatively few plots (39 of 201) were noted to have received maintenance during the study period, so we used a binary maintenance classification (Yes/No). The dominant activity noted was seeding (45 plot-year combinations, followed by prescribed burning and chemical application (16 and 4 plot-year combinations, respectively).

Statistical Analysis

Community Classification

To identify broad vegetation communities, we applied hierarchical cluster analysis to the compositional data, analyzing each year separately. We used Bray-Curtis distances and Ward's linkage method (the 'ward.D2' method) in the "hclust" function of the *vegan* package (v.2.2-0) in R (v.3.1.2). The number of communities was identified through examination of scree plots and visualized in dendrograms (Appendix 3). Compositional differences were visualized using non-metric multidimensional scaling (NMDS) with Bray-Curtis distances, 2 dimensions, and 1000 random starts.

Within each year, communities were described on the basis of key environmental characteristics (elevation, HLI, soil depth, percent sand), total cover, species richness, and the relative abundance of each functional group. Differences among communities were tested using ANOVA. Significant differences were followed by pairwise tests to determine which groups differed from one another. Pairwise tests were conducted using the *lsmeans* package (v.2.13); in figures and tables, lowercase letters identify these differences. In each comparison, values are identified beginning with 'a' for the lowest value.

Communities were also described on the basis of their dominant species (the five species with the highest mean relative abundance in the group) and indicator species (species strongly associated with that community). Indicator species were identified using Indicator Species Analysis (ISA; Dufrêne and Legendre 1997, De Cáceres et al. 2010). ISA is calculated separately for each species *i* in group *j*, where *j* is a single community or a combination of communities. By allowing for differences among combinations of communities, this ISA can distinguish species that occur in a single community, that occur

in multiple communities, or that are ubiquitous and occur in all communities. The relative abundance and relative frequency of species *i* in group *j* are multiplied to produce an Indicator Value (IV). IV ranges from 0 to 100; a value of 100 indicates that species *i* occurs in all plots of group *j* and does not occur in any other group. Statistical significance is assessed by permuting the group identities and recalculating IV for each permutation; the true IV is then compared to the IVs of the permutations. A separate ISA was conducted for each year. Species were considered to be indicators if IV > 25 and $P < 0.05$. ISAs were conducted with the "multipatt" function in the *indicspecies* package (v.1.7.4) in R.

Identifying Transitions Among Communities

We used several approaches to examine the extent and directions of change between 1989 and 2002. We began by cross-classifying the communities in 1989 and in 2002. Because we classified communities separately within each year, we refer to each combination of a community from 1989 and a community from 2002 as a 'transition' even though they may reflect communities where little actual change occurred. Since our analysis identified 3 communities in 1989 and 4 communities in 2002, there were 12 possible transitions. The number of plots that experienced each transition was tallied, and the transition probability calculated by dividing the number of plots in that transition by the total number of plots in that 1989 community.

A NMDS ordination of the compositional data (402 plot-year combinations × 30 species) was conducted and the locations of each plot in this compositional space in 1989 and 2002 were connected to visualize the extent and direction of change. This ordination used the same settings as the ordinations describe above for individual years.

Next, we calculated the compositional change in each plot as the Bray-Curtis distance between its composition in 1989 and its composition in 2002. The mean distance and range of distances were summarized for each transition. For each 1989 community, common transitions were analyzed using ANOVA to determine whether distance differed among the communities to which plots transitioned in 2002.

Third, we analyzed changes over time in total cover, species richness, and the relative cover of each functional group. Each 1989 community was analyzed separately, and uncommon

transitions (those represented by < 5 plots) were omitted from analyses. Explanatory variables in these analyses were the community to which each plot transitioned in 2002, year (1989 vs. 2002), and plot ID (included as a blocking term to account for temporal autocorrelation between re-measurements). The response variables were total cover, species richness, and the relative abundance of each functional group. Our key interest was the interaction between year and 2002 community; when this term was significant, it indicated that plots that ended up in different communities in 2002 differed in the amount of change that occurred from 1989 to 2002. If this term was significant, it was followed by pairwise comparisons of each 2002 community to identify which ones changed significantly from 1989 to 2002.

Finally, we focused on each transition separately and used ISA to determine whether any species were significant indicators of one year over the other.

Quantifying the Role of Disturbance

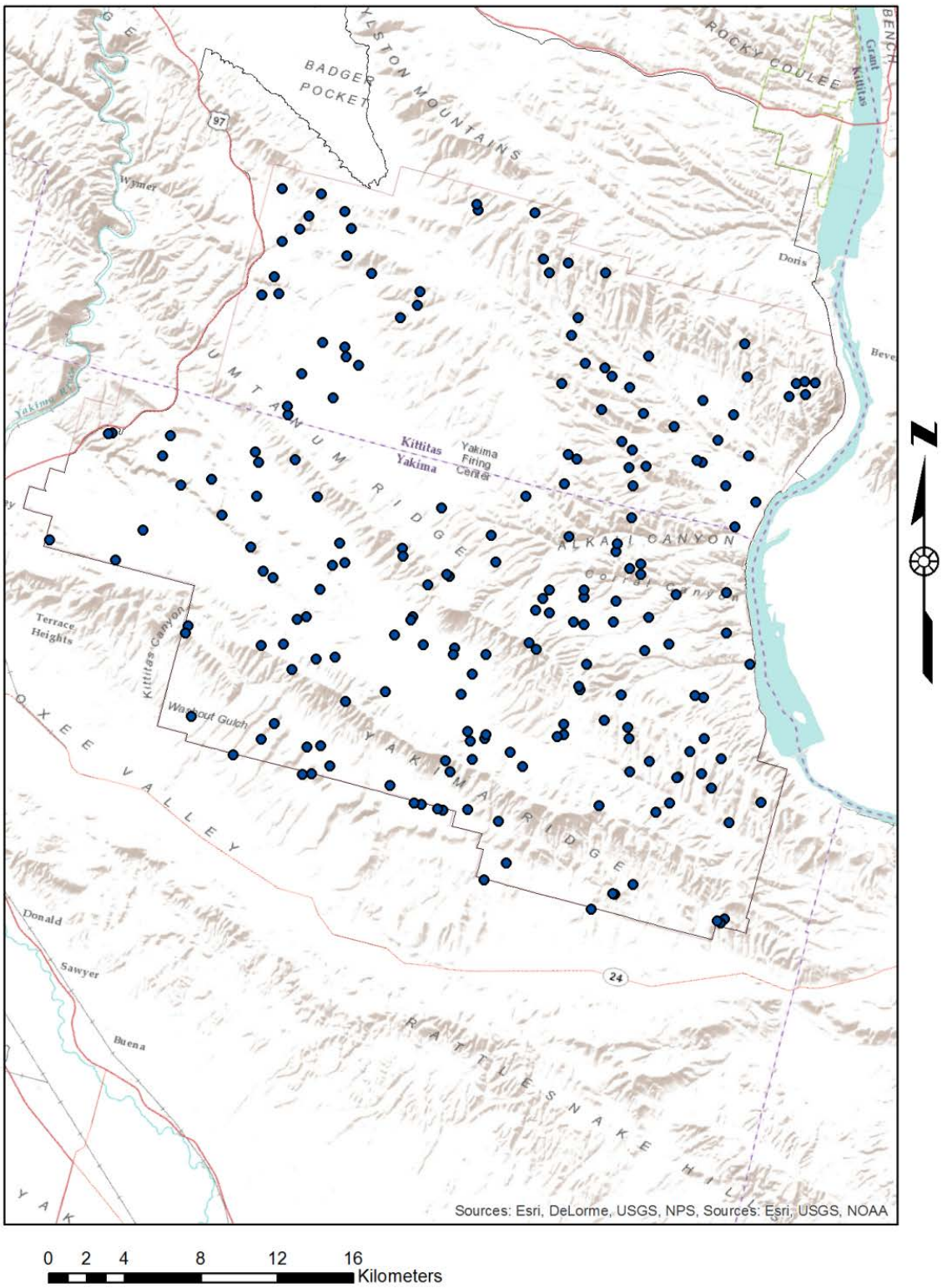
The role of disturbance as a driver of compositional change was explored by focusing on changes in vegetation composition from 1989 to 2002 (i.e., Bray-Curtis distance between a plot in each of these years) and on total cover, species richness, and the relative abundance of each functional group in 2002. Response variables were analyzed using stepwise regression with the "stepAIC" function in the *MASS* package (v.7.3-35). The explanatory variables considered for inclusion in these models were all possible interactions among the 1989 community that each plot originated from, the community that it transitioned to in 2002, and the disturbance variables (military training activities, military training areas, roads, livestock grazing, fire, maintenance activities). We used Bayesian Information Criterion (BIC) to select the model that best balanced complexity with explanatory power.

We also explored the degree to which individual species were associated with each disturbance variable. Categorical disturbance variables (usage of military training areas, fire, maintenance activities) were analyzed using ISA. Continuous disturbance variables (intensity of military training activities, roads, livestock grazing) were analyzed using Threshold Indicator Taxa Analysis (TITAN; Baker & King 2010). TITAN is an extension of ISA to continuously distributed data. It is conducted separately for each species,

identifying the value of a continuous variable – the change point – that partitions plots into two groups (high or low) such that the species is maximally associated with one of the groups. Association is determined using the same IV statistic as in ISA, the significance of which is assessed via 1000 permutations. In addition, 1000 bootstraps are used to assess the purity and reliability of the indicators, where purity is defined as the percentage of bootstraps in which the species was assigned to the same group (high or low) as in the actual data and reliability as the percentage of bootstraps in which the IV of the species was statistically significant at $P \leq 0.05$. We conducted TITAN analyses using the "titan" function provided by Baker & King (2010). We restricted our attention to taxa for which IV ≥ 25, $P \leq 0.05$, purity ≥ 95%, and reliability ≥ 90% as recommended by Baker & King (2010). Because each disturbance variable was analyzed separately, species could be identified as indicators for multiple disturbances.

Updating and Extending the State-and-Transition Model

Davies et al. (2012) proposed that plant states and transitions could be arrayed along an axis of shrub/grass cover and an axis of exotic/native cover. We expressed these axes as the relative cover of shrubs and the relative cover of exotics, respectively. Communities were placed qualitatively along these axes. Community stability was assessed by determining whether communities were identified in both years, and whether individual plots were classified in the same community in each year. Transition probabilities were determined as the number of plots that experienced a given transition divided by the number of plots in that community in 1989.



Map 2. LCTA plot locations within YTC. Note that plots in the northern expansion are not shown as they were not included in this analysis.

Results

Communities in 1989

Hierarchical cluster analysis indicated that there were 3 distinct communities in 1989 (Figure 1, Map 3). Although identified on the basis of their vegetation, these communities also differed in elevation, HLI, and the sandiness of their soils (Table 2).

Communities differed in total cover and species richness per plot (Table 3), as well as the relative abundance of most functional groups (Table 4). Dominant and indicator species of each community are identified in Table 5. Three species were particularly widespread: *Poa secunda*, which occurred in almost every plot regardless of community, *Poa fendleriana*, and *Achnatherum thurberianum*. Other species were common in two of the three communities or were indicative of a single community.

Table 2. Environmental characteristics of community types identified in 1989. For each variable, different lowercase letters after the mean (SE) indicate statistically significant differences among communities. Statistical results are reported in Appendix 3.

Community	N	Elevation (m)	HLI	Sand (%)	Soil Depth (cm)
Big Sagebrush/Grass	88	771 (18) c	0.73 (0.01) a	42 (1) a	60 (3) a
Big Sagebrush/Exotic	39	576 (28) a	0.76 (0.01) ab	52 (2) b	54 (5) a
Dwarf Shrub	74	680 (20) b	0.78 (0.01) b	50 (1) b	55 (4) a

Table 3. Mean total cover and species richness (SE) of each community in 1989. For each variable, different lowercase letters indicate statistically significant differences among communities. Statistical results are reported in Appendix 3.

Community	N	Total Cover (%)	Species Richness
Big sagebrush/Grass	88	84 (3) b	8.1 (0.3) b
Big sagebrush/Exotic	39	76 (4) b	6.4 (0.4) a
Dwarf Shrub	74	57 (3) a	7.1 (0.3) a

Table 4. Functional groups of each community in 1989. The abundance of each functional group is expressed as a percentage of the total cover. Within each functional group, different lowercase letters indicate statistically significant differences among communities. Statistical results are reported in Appendix 3.

Community	N	Exotic	Native Forb	Native Grass	Shrub
Big sagebrush/Grass	88	5.6 a	7.0 b	73.8 b	13.5 a
Big sagebrush/Exotic	39	46.5 b	2.1 a	40.0 a	11.4 a
Dwarf Shrub	74	4.3 a	12.9 c	70.7 b	12.2 a

Table 5. Dominant and indicator species of each community in 1989. Listed species are the 5 most abundant species in at least one community (shown in bold) and/or are statistically significant indicators (IV > 25, $P < 0.05$) of a community or combination of communities.

Community	Relative Cover (%)			IV	*P*
Species	Big Sagebrush /Grass	Big Sagebrush /Exotic	Dwarf Shrub		
Big Sagebrush/Grass					
None					
Big Sagebrush/Exotic					
Bromus tectorum	**5.6**	**43.7**	**4.1**	81.9	0.001
Salsola kali	-	**1.9**	<0.1	30.5	0.001
Dwarf Shrub					
Artemisia rigida	<0.1	0.4	**9.4**	52.9	0.001
Phlox hoodii	<0.1	-	1.3	32.8	0.001
Stenotus stenophyllus	0.4	0.1	**3.1**	32.0	0.001
Eriogonum thymoides	-	-	2.0	25.7	0.001
Big Sagebrush/Grass and Big Sagebrush/Exotic					
Artemisia tridentata	**9.2**	**9.4**	2.1	50.3	0.001
Lupinus sulphureus	1.9	0.9	0.8	29.6	0.006
Chrysothamnus viscidiflorus	1.9	0.7	0.3	27.1	0.001
Big Sagebrush/Grass and Dwarf Shrub					
Pseudoroegneria spicata	**36.7**	**3.7**	**11.2**	79.7	0.001
Phlox longifolia	1.4	0.3	1.3	31.9	0.002
Big Sagebrush/Exotic and Dwarf Shrub					
Elymus elymoides	0.2	1.7	1.4	30.8	0.001
All groups					
Poa secunda	**27.0**	**31.8**	**54.8**	99.6	-
Poa fendleriana	**4.8**	1.6	1.8	35.9	-
Achnatherum thurberianum	2.1	0.7	1.3	31.4	-

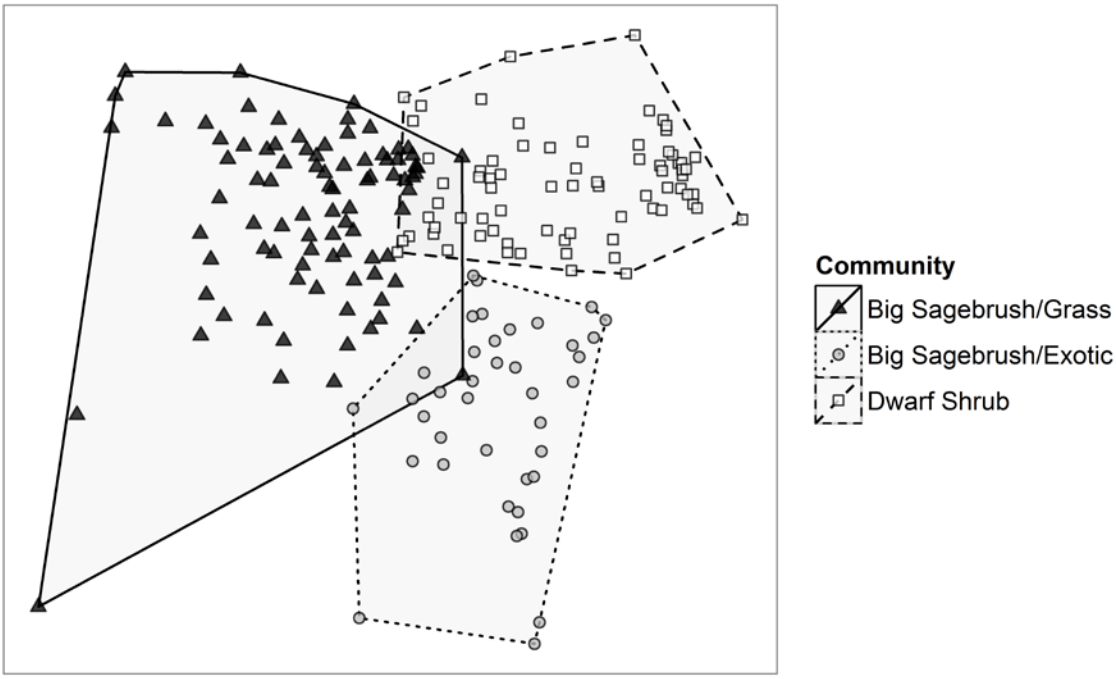


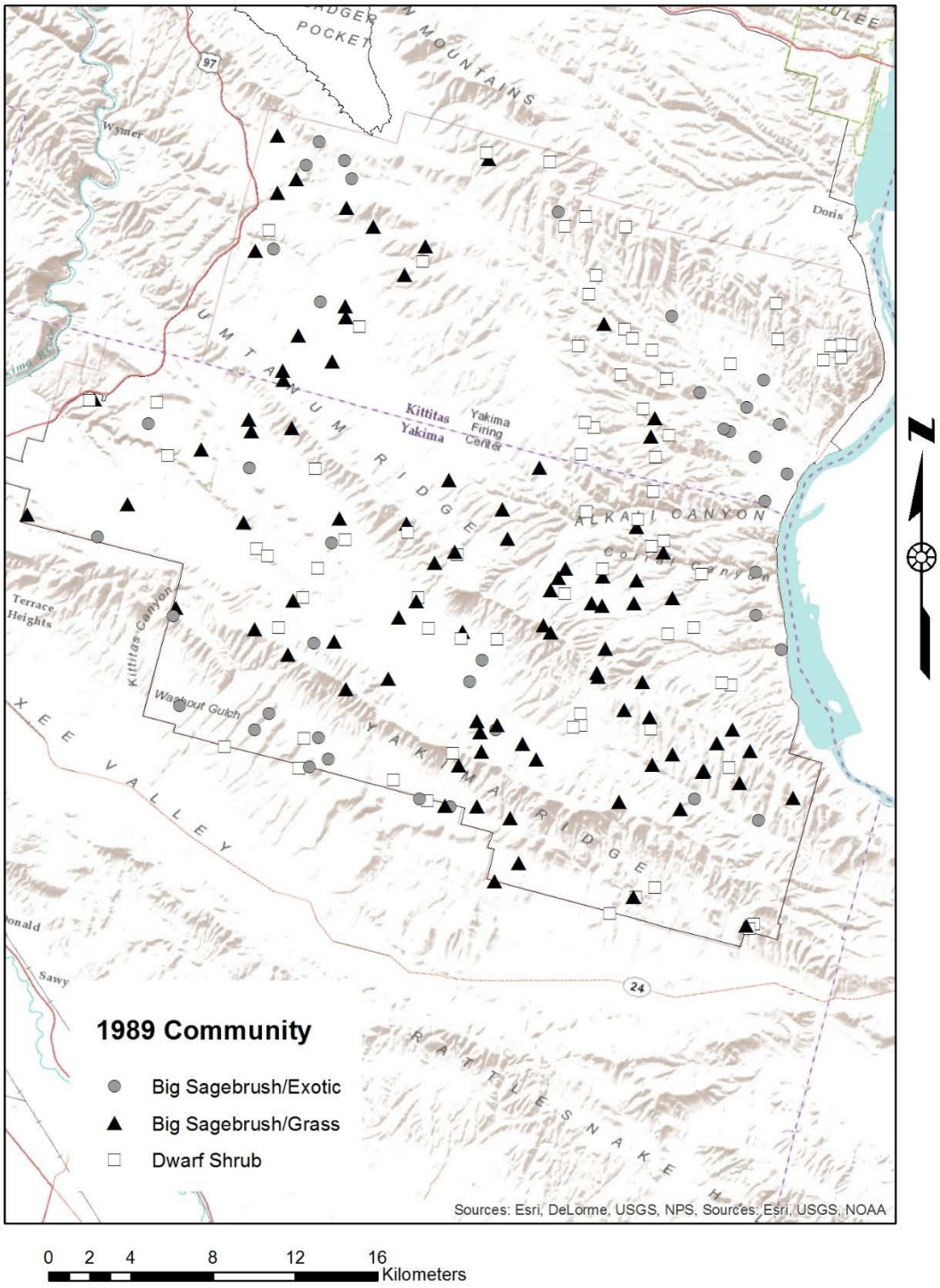
Figure 1. NMDS ordination of 1989 communities identified by hierarchical cluster analysis. This solution had a stress of 0.150.

The "Big Sagebrush/Grass" community was the largest in 1989 (88 plots). On average, plots in this community had the highest elevation, lowest HLI, and least sandy soils. The vegetation was dominated by native grasses (74% of the cover). The two most abundant species were *Pseudoroegneria spicata* and *Poa secunda*. No species were indicators of this community alone. *Artemisia tridentata* , *Lupinus sulphureus*, and *Chrysothamnus viscidiflorus* were indicators of plots in this or the Big Sagebrush/Exotic community, while Pseudoroegneria spicata and Phlox longifolia were indicators of plots in this or the Dwarf Shrub community. *Elymus elymoides* was an indicator of plots that were not in this community (i.e., were in one of the other two communities).

Thirty-nine plots were classified within the "Big Sagebrush/Exotic" community. This community occurred at the lowest average elevation but did not differ from the Dwarf Shrub community in other environmental variables. Total cover was relatively high while species richness was low. Exotic species, particularly *Bromus tectorum* and *Salsola kali*,

accounted for almost half of the cover in these plots, and *Bromus* and *Salsola* were significant indicators for this community. Native forbs were notably sparse in this community, accounting for only 2% of cover. However, on average the *Artemisia tridentata* canopy was the same here as in the Big Sagebrush/Grass community. *Lupinus sulphureus* and *Chrysothamnus viscidiflorus* were also indicators of either of these communities. *Elymus elymoides* was an indicator of plots that were part of this community or of the Dwarf Shrub community. *Pseudoroegneria spicata* and *Phlox longifolia* were indicators of plots that were not part of this community.

Seventy-four plots were classified within the "Dwarf Shrub" community. On average, these plots occurred at intermediate elevations and had the highest HLI. Total cover was lower in this community than either of the other two. This community was dominated by native grasses and native forbs. Shrub cover was similar to that in the other communities, though the dominant shrub was *Artemisia rigida* instead of *A. tridentata*. This community also had the most indicator species: *A. rigida*, *Phlox hoodii, Stenotus stenophyllus,* and *Eriogonum thymoides* were significant indicators of it, while *Pseudoroegneria spicata* and *Phlox longifolia* were indicators of plots that were part of this community or of the Big Sagebrush/Grass community and *Elymus elymoides* was an indicator of plots that were part of this community or of the Big Sagebrush/Exotic community. *Artemisia tridentata*, *Lupinus sulphureus*, and *Chrysothamnus viscidiflorus* were indicators of plots that were not in this community (i.e., were in one of the other two communities).



Map 3. LCTA plots coded by 1989 community.

Communities in 2002

Four distinct communities were identified in 2002 (Figure 2, Map 4), some of which differed in environmental characteristics (Table 6).

Communities differ in total cover and species richness (Table 7), and in the relative abundance of functional groups (Table 8). Dominant and indicator species of each community are identified in Table 9. *Poa secunda* occurred in almost every plot, regardless of community, and *Achnatherum thurberianum* was also widespread. Other species were indicators of combinations of communities or of single communities.

Table 6. Environmental characteristics of community types identified in 2002. For each variable, different lowercase letters after the mean (SE) values indicate statistically significant differences among communities. Statistical results are reported in Appendix 3.

Community	N	Elevation (m)	HLI	Sand (%)	Soil Depth (cm)
Grass Steppe	66	777 (22) b	0.73 (0.01) a	41 (1) a	61 (4) a
Exotic	54	631 (24) a	0.76 (0.01) b	50 (1) b	57 (4) a
Big Sagebrush/Grass	43	696 (27) a	0.74 (0.01) ab	48 (2) b	58 (5) a
Dwarf Shrub	38	669 (29) a	0.80 (0.01) c	52 (2) b	49 (5) a

Table 7. Mean total cover and species richness (SE) of each community in 2002. For each variable, different lowercase letters indicate statistically significant differences among communities. Statistical results are reported in Appendix 3.

Community	N	Total Cover (%)	Species Richness
Grass Steppe	66	73 (3) c	8.8 (0.4) c
Exotic	54	67 (3) bc	7.7 (0.4) ab
Big Sagebrush/Grass	43	62 (3) b	8.3 (0.4) bc
Dwarf Shrub	38	35 (4) a	6.6 (0.5) a

Table 8. Functional groups of each community in 2002. The abundance of each functional group is expressed as a percentage of the total cover. Within each functional group, different lowercase letters indicate statistically significant differences among communities. Statistical results are reported in Appendix 3.

Community	N	Exotic	Native Forb	Native Grass	Shrub
Grass Steppe	66	2.9 a	8.4 b	80.4 c	8.2 a
Exotic	54	39.3 b	3.7 a	50.5 a	6.5 a
Big Sagebrush/Grass	43	4.9 a	10.9 b	64.4 b	19.8 b
Dwarf Shrub	38	3.0 a	20.2 c	59.1 b	17.8 b

Table 9. Dominant and indicator species of each community in 2002. Listed species are among the 5 most abundant species in at least one community (shown in bold) and/or are statistically significant indicators (IV > 25, $P < 0.05$) of a community or combination of communities.

Community	Relative Cover (%)				IV	*P*
Species	Grass Steppe	Exotic	Big Sagebrush /Grass	Dwarf Shrub		
Grass Steppe						
Poa fendleriana	**12.4**	1.6	2.2	0.3	65.0	0.001
Festuca idahoensis	**3.1**	-	0.4	-	13.6	0.001
Exotic						
Bromus tectorum	2.5	**36.8**	**4.6**	3.0	78.5	0.001
Big Sagebrush/Grass						
None						
Dwarf Shrub						
Artemisia rigida	0.3	0.8	1.6	**16.5**	65.9	0.001
Eriogonum thymoides	<0.1	0.1	0.3	**5.1**	61.3	0.001
Stenotus stenophyllus	0.1	0.1	1.7	**6.7**	38.8	0.001
Grass Steppe and Big Sagebrush/Grass						
Phlox longifolia	1.9	0.4	1.1	0.6	31.8	0.008
Lupinus sericeus	1.9	0.5	1.6	-	31.4	0.001
Big Sagebrush/Grass and Dwarf Shrub						
Balsamorhiza hookeri	0.1	0.1	**2.6**	2.1	20.0	0.001
All but Dwarf Shrub						
Pseudoroegneria spicata	**44.0**	**15.1**	**24.7**	**3.3**	85.6	0.001
Artemisia tridentata	**4.2**	**3.8**	**15.6**	0.2	45.0	0.001
Chrysothamnus viscidiflorus	1.8	0.9	0.7	-	25.2	0.001
All groups						
Poa secunda	**18.1**	**30.7**	**34.9**	**53.3**	98.6	-
Achnatherum thurberianum	2.7	**2.1**	1.3	1.0	20.9	-

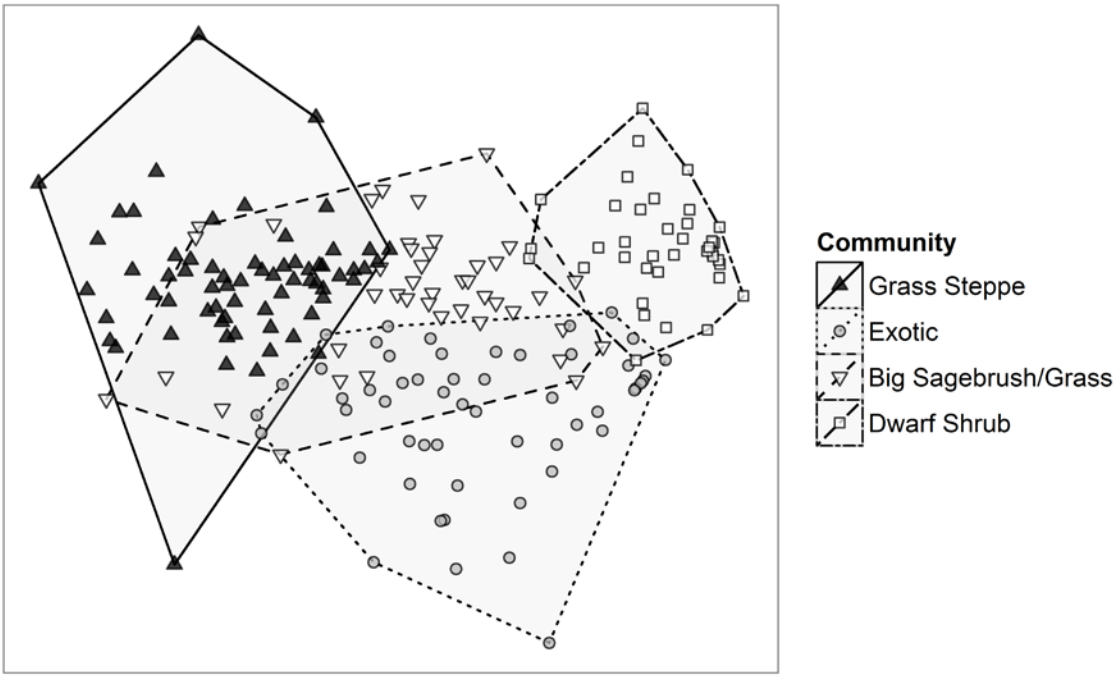


Figure 2. NMDS ordination of 2002 community types identified by hierarchical cluster analysis. This solution had a stress of 0.166.

The "Grass Steppe" community was the largest in 2002, comprising 66 plots. On average, plots in this community occurred at the highest elevations, had the lowest HLI, and had the least sandy soils. This community had the highest total cover and species richness. The vegetation was dominated by native grasses (80% of the cover), particularly *Pseudoroegneria spicata*, *Poa secunda*, and *Poa fendleriana*. *P. fendleriana* and *Festuca idahoensis* were indicators of this community, while *Phlox longifolia* and *Lupinus sericeus* were indicators of plots from this or the Big Sagebrush/Grass community.

Fifty-four plots were classified within the "Exotic" community. Plots in this group were not strongly differentiated from those of most other communities in environmental conditions, total cover, or species richness. The vegetation was dominated by exotic species (39% of the cover); native forbs and native grasses were sparse. *Bromus tectorum* was the only indicator of this community.

Forty-three plots were classified into the "Big Sagebrush/Grass" community in 2002. Plots in this group were not strongly differentiated from those of most other communities in environmental conditions, total cover, or species richness. Shrubs accounted for 20% of the cover on plots in this community. No species were indicators of this community, though *Phlox longifolia* and *Lupinus sericeus* were indicators of this or the Grass Steppe community, and *Balsamorhiza hookeri* was an indicator of this or the Dwarf Shrub community.

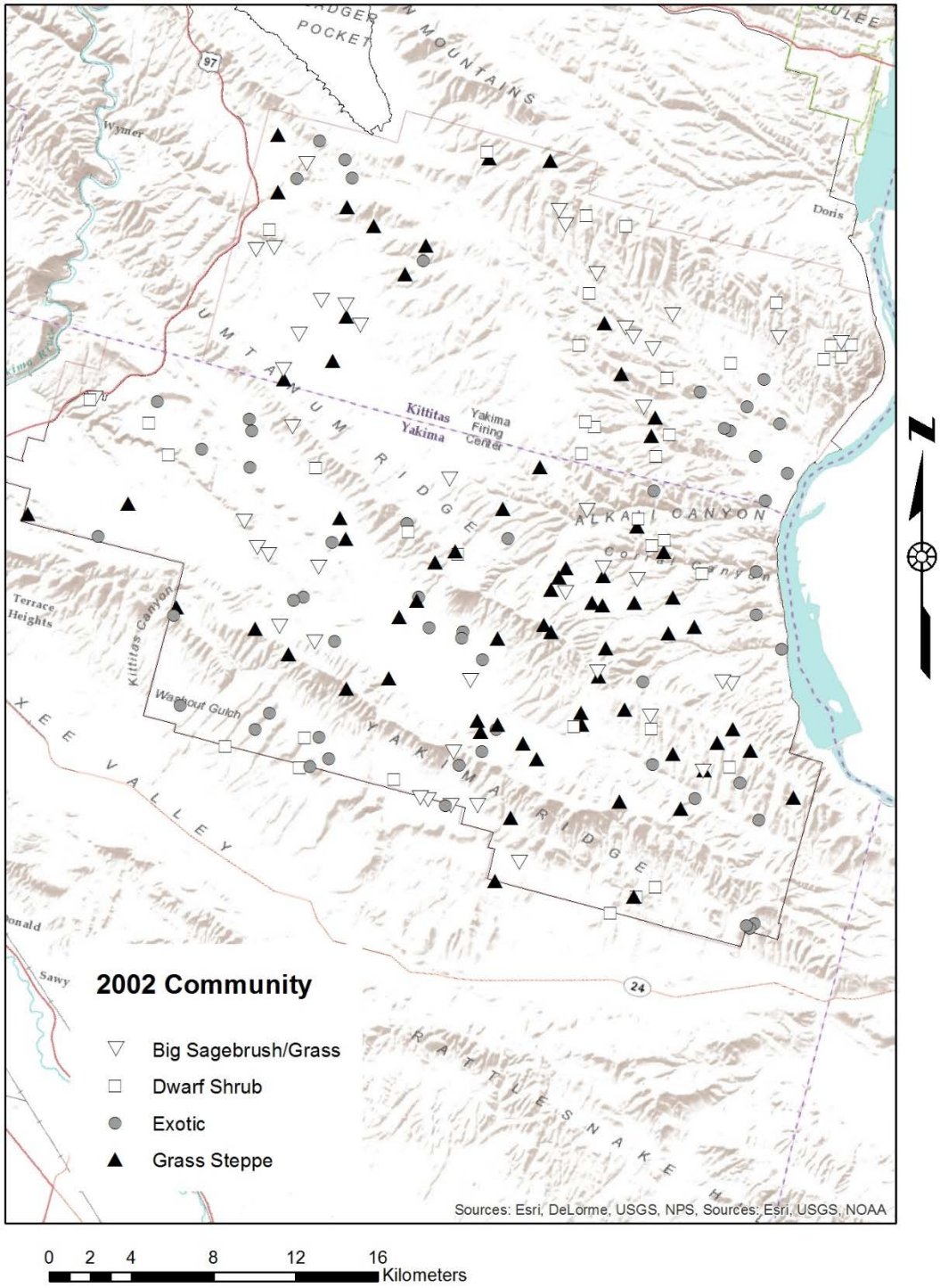
Finally, 38 plots were classified in the "Dwarf Shrub" community. This community had the highest mean HLI but did not differ from most other communities in other environmental characteristics. Total cover and species richness were lower in this community than the others. Native forbs were most abundant in this community (20% of the cover). *Artemisia rigida*, *Eriogonum thymoides*, and *Stenotus stenophyllus* were indicators of this community, while *Balsamorhiza hookeri* was an indicator of this or the Big Sagebrush/Grass community. *Pseudoroegneria spicata*, *Artemisia tridentata*, and *Chrysothamnus viscidiflorus* were indicators of plots that did not occur in this community.

Transitions Among Communities

Transitions were defined as the combination of a community in 1989 and a community in 2002. Since there were 3 communities in 1989 and 4 communities in 2002, there were 12 possible transitions. Every plot was assigned to one of these transitions. In total, 10 of the 12 possible transitions were documented (Tables 10 and 11). Most transitions were common; only one was represented by a single plot.

The amount of change spanned almost the full range possible (Map 5), from 0.06 to 1.00. On average, the Bray-Curtis distance was 0.31 indicating that the degree of similarity in composition over this 14-year period was 69%.

Transitions are visualized in compositional space in Figure 3 and in geographical space in Map 6. Changes in the relative abundance of functional groups are shown in Figure 4.



Map 4. LCTA plots coded by 2002 community.

Table 10. Summary of transitions between 1989 communities and 2002 communities. B-C: Bray-Curtis distance.

1989 Community	2002 Community	N	Mean (SD) B-C distance	Range
Big Sagebrush/Grass	Grass Steppe	58	0.31 (0.12)	0.14-0.70
Big Sagebrush/Grass	Exotic	16	0.36 (0.18)	0.23-1.00
Big Sagebrush/Grass	Big Sagebrush/Grass	14	0.25 (0.09)	0.06-0.44
Big Sagebrush/Grass	Dwarf Shrub	0	-	-
Big Sagebrush/Exotic	Grass Steppe	0	-	-
Big Sagebrush/Exotic	Exotic	29	0.28 (0.13)	0.07-0.51
Big Sagebrush/Exotic	Big Sagebrush/Grass	9	0.38 (0.16)	0.08-0.58
Big Sagebrush/Exotic	Dwarf Shrub	1	0.96	-
Dwarf Shrub	Grass Steppe	8	0.40 (0.14)	0.13-0.53
Dwarf Shrub	Exotic	9	0.42 (0.15)	0.18-0.65
Dwarf Shrub	Big Sagebrush/Grass	20	0.30 (0.14)	0.11-0.63
Dwarf Shrub	Dwarf Shrub	37	0.25 (0.12)	0.07-0.56
Total		201	0.31 (0.15)	0.06-1.00

Table 11. Percentage of plots within each 1989 community (row) that transitioned to each 2002 community (column).

		2002 Community			
		Grass Steppe	Exotic	Big Sagebrush /Grass	Dwarf Shrub
1989 Comm.	Big Sagebrush/Grass	66	18	16	0
	Big Sagebrush /Exotic	0	74	23	3
	Dwarf Shrub	11	12	27	50

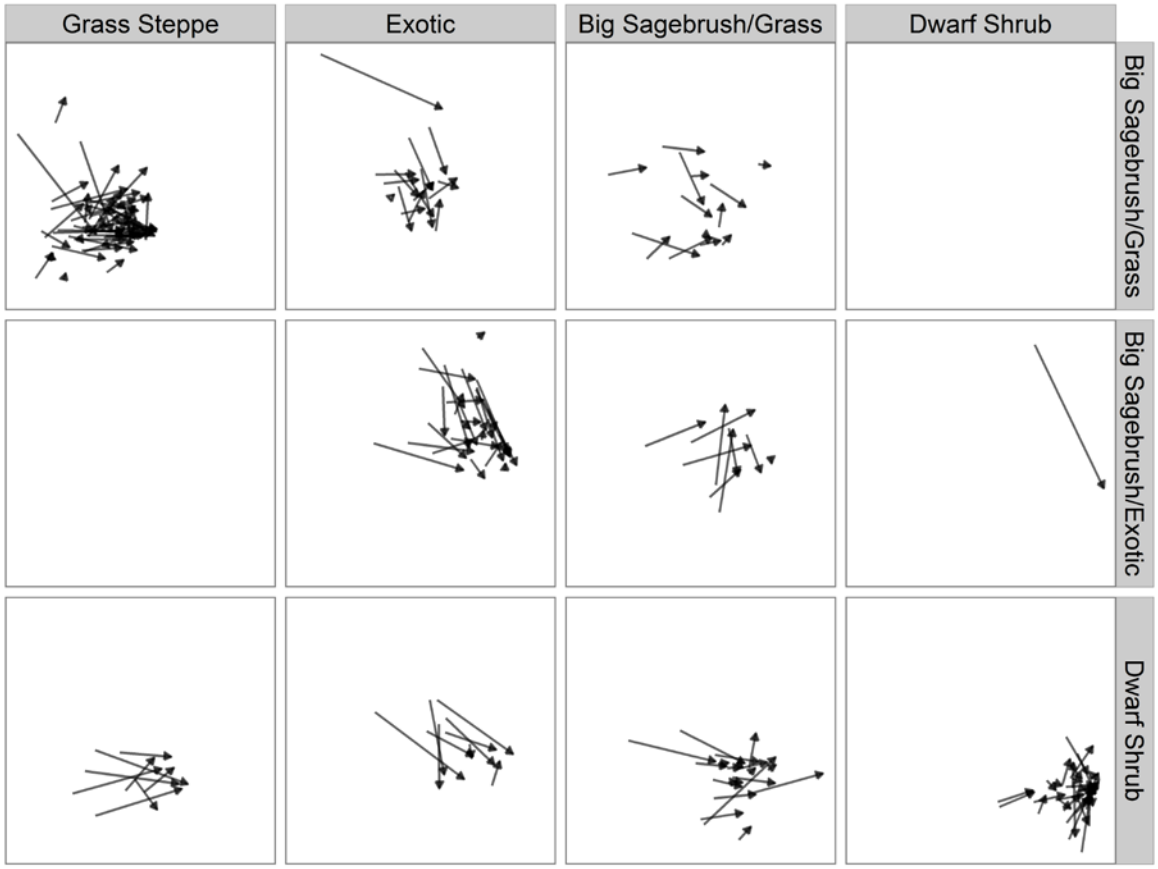
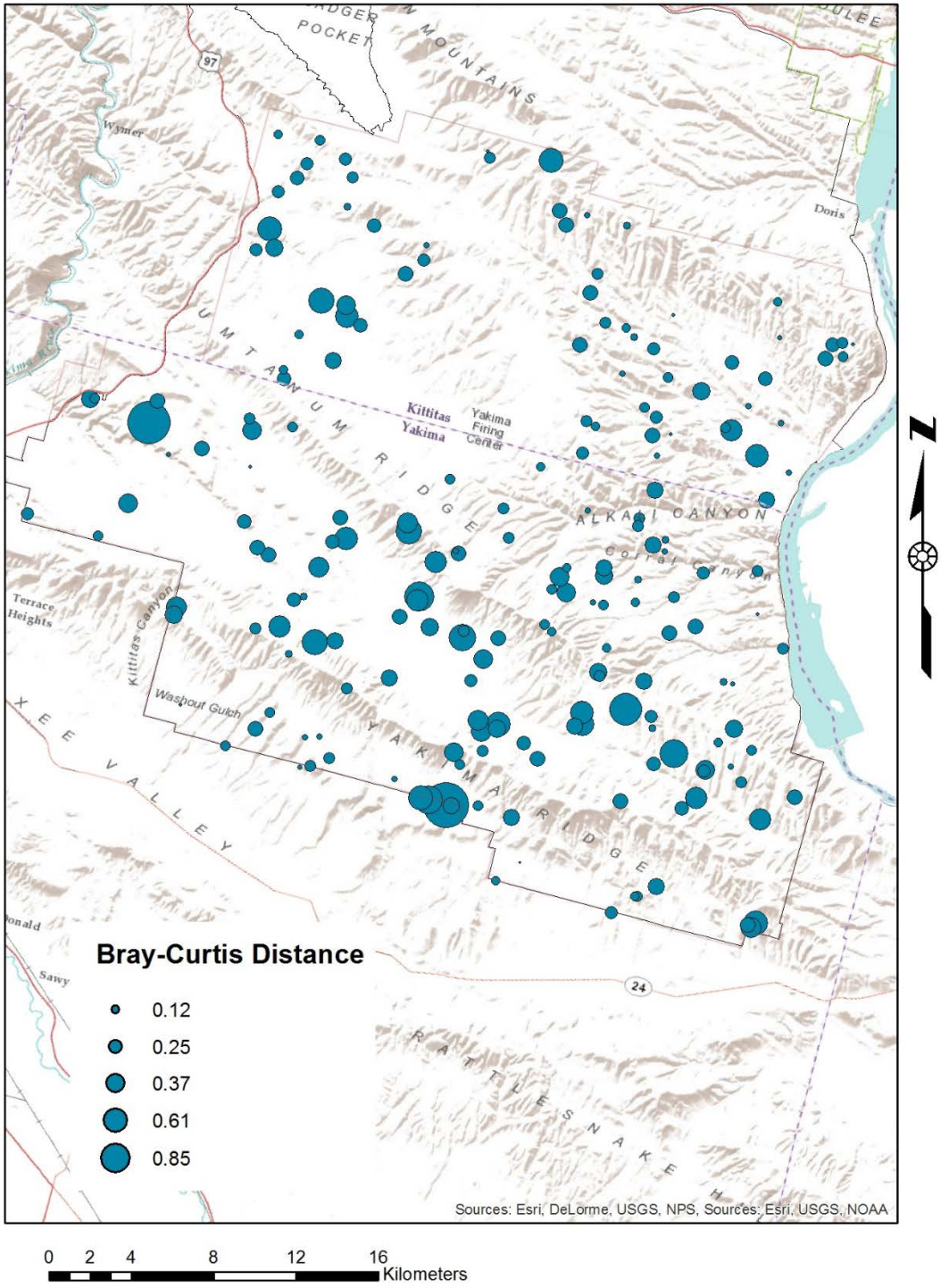


Figure 3. NMDS ordination showing the movement of plots in ordination space between 1989 and 2002. All plots were included in the same analysis (stress = 0.162), but each transition from a 1989 community (row) to a 2002 community (column) is shown separately for clarity. Each plot is shown as a vector, beginning at its location in 1989 and pointing to its location in 2002.



Map 5. Bray-Curtis distance for each LCTA plot. Point size is proportional to the amount of compositional change from 1989 to 2002; a sampling from the range of distances is shown in the legend.

Transitions from the "Big Sagebrush/Grass" Community

This community was the largest in 1989 (n = 88), and plots diverged into three communities in 2002. No plots transitioned from this community to the "Dwarf Shrub" community.

Compositional change, as measured by the Bray-Curtis distance between the composition of a plot in 1989 and that of the same plot in 2002, averaged 0.31. Transitions did not differ in Bray-Curtis distance, total cover, or species richness, but differed in the amount of change that occurred within functional groups (Appendix 4).

Two-thirds (n=58; 66%) of the plots in this community in 1989 were placed in the "Grass Steppe" community in 2002. Plots in this transition declined significantly in shrub cover (Figure 4). *Lupinus sericeus* was the only species that was an indicator of one year over the other in these plots (IV = 40.3; $P = 0.001$); its relative cover increased from 0.1% in 1989 to 2.0% in 2002.

The second-largest transition (n = 16; 18%) was to the "Exotic" community in 2002. Plots in this transition increased greatly in exotic cover and decreased in native grass cover. *Sisymbrium altissimum* was the only significant indicator (IV = 37.5, $P = 0.018$); it was absent in 1989 but accounted for 2.7% of the cover in 2002.

Finally, 14 plots (16%) transitioned to the "Big Sagebrush/Grass" community. As suggested by the fact that the names of these communities are the same, the relative cover of no functional groups varied significantly over time. *Lupinus sericeus* was the only species that was an indicator of one year over the other in these plots (IV = 35.8; $P = 0.037$); it was absent in 1989 but accounted for 1.1% of the cover in 2002.

Transitions from the "Big Sagebrush/Exotic" Community

This community was the smallest in 1989 (n = 39). Plots within this community were classified into three communities in 2002, though only one plot transitioned to the "Dwarf Shrub" community so that transition is not detailed here.

The average Bray-Curtis distance between a plot in 1989 and the same plot in 2002 was 0.32. Transitions did not differ in the amount of change that occurred in total cover or

species richness, but differed in the amount of change in exotic cover and native grass cover (Appendix 4).

Most plots (29; 74%) transitioned to the "Exotic" community, though cover of the various functional groups did not change significantly in these plot during this time. Somewhat counter-intuitively, the exotic species *Salsola kali* was a significant indicator of 1989 (IV = 45.6, P = 0.018), declining from 1.9% of the cover in 1989 to 0.4% in 2002.

Nine plots (23%) transitioned to the "Big Sagebrush/Grass" community. This transition was characterized by a very large decrease in cover of exotic species (35% in 1989, 6% in 2002) and by increases in the cover of native forbs and grasses (Figure 4). *Bromus tectorum* was a significant indicator of 1989 (IV = 84.8, P = 0.001), declining from 33% of the cover in 1989 to 6% of the cover in 2002.

Transitions from the "Dwarf Shrub" Community

This community was composed of 74 plots in 1989. Plots within this community diverged more than those in other communities, transitioning into all four communities in 2002. The average Bray-Curtis distance was 0.30, but transitions differed in how much composition changed over time. Transitions did not differ in the amount of change that occurred in total cover or species richness, but differed in the amount of change in exotic cover and native grass cover (Appendix 4).

Eight plots (11%) were classified in the "Grass Steppe" community in 2002. The relative covers of all functional groups in this transition were stable over time.

Nine plots (12%) were classified in the "Exotic" community in 2002. These plots experienced the largest transition (mean distance = 0.42). Exotic cover increased greatly in these plots over time (12% to 35%) while native grass cover decreased (77% to 54%).

20 plots (27%) were classified in the "Big Sagebrush/Grass" community in 2002. Native grass cover decreased in these plots over time (74% to 66%). *Erigeron linearis* was a significant indicator of 2002 in these plots (IV = 31.7, P = 0.037), increasing from 0.1% to 1.1% of the cover.

Half of these plots (n = 37%) were classified in the "Dwarf Shrub" community in 2002. Bray-Curtis distances averaged only 0.25 for this transition. Native grass cover decreased in these plots over time (65% to 59%).

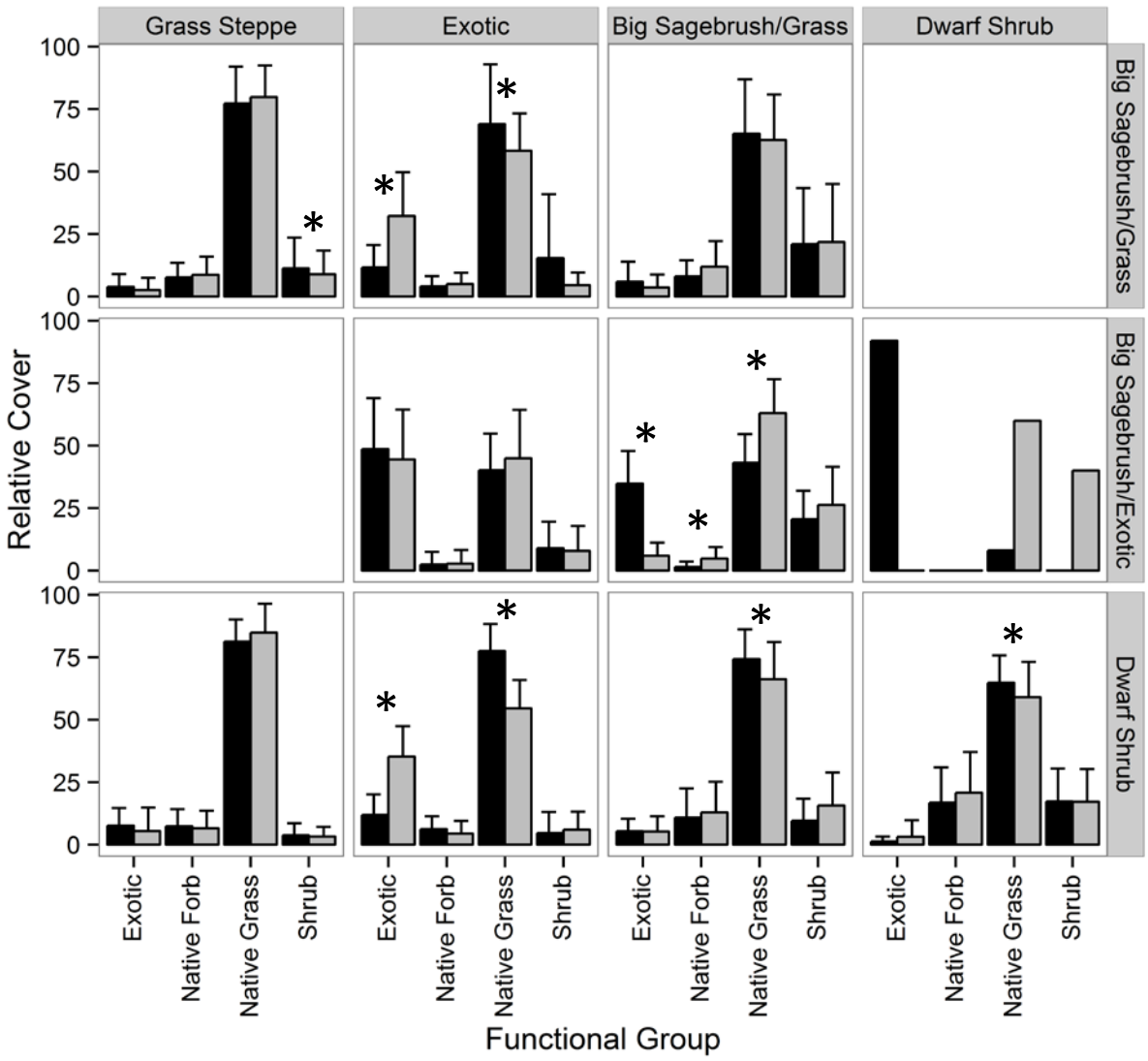
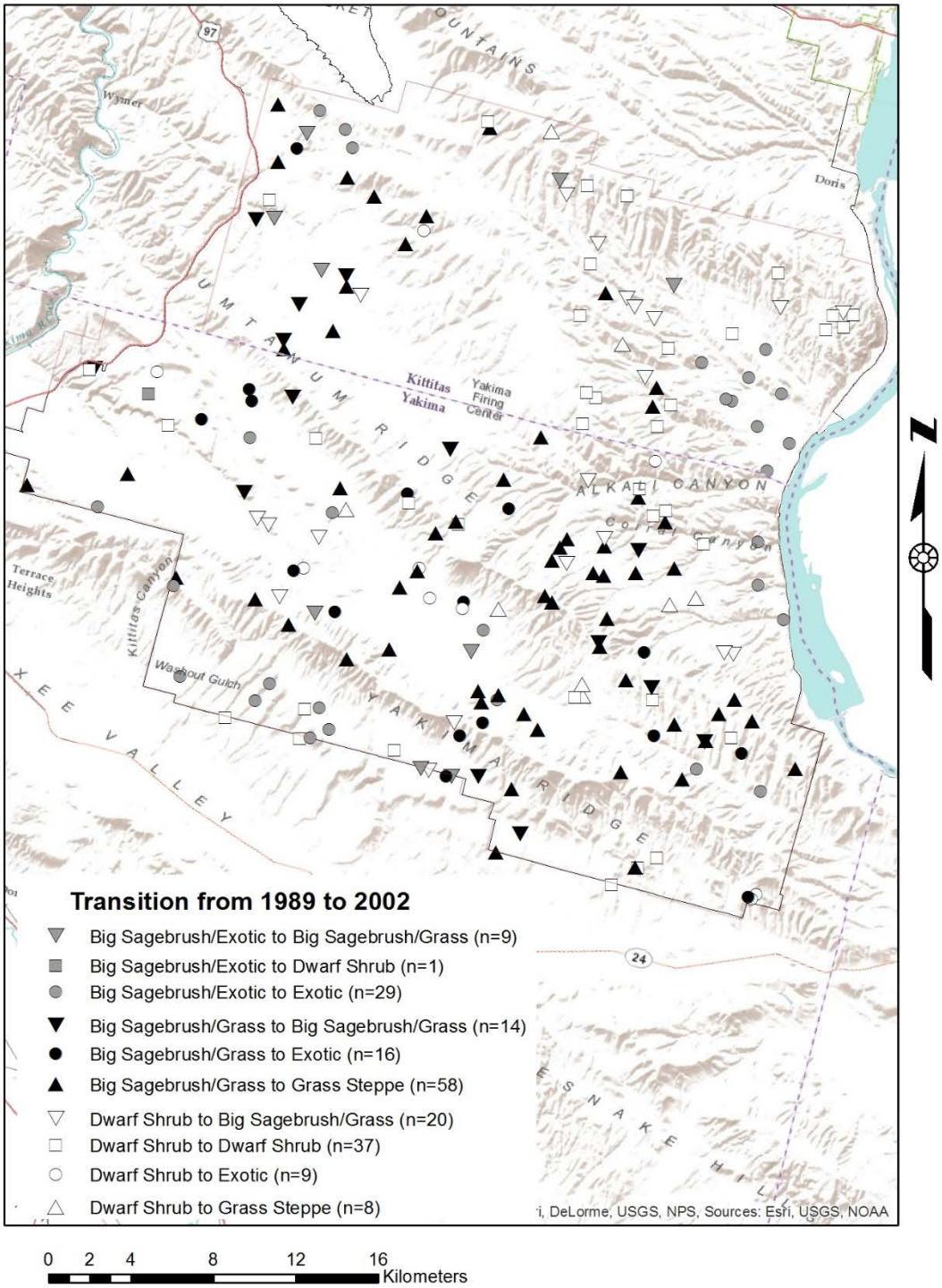


Figure 4. Changes in key functional groups between 1989 (black) and 2002 (grey) for each transition from a 1989 community (row) to a 2002 community (column). Significant differences ($P \leq 0.05$) between the 1989 and 2002 data for a given functional group in a given transition are indicated by an asterisk. Statistical results are reported in Appendix 3.



Map 6. Transitions between communities in 1989 (colors) and communities in 2002 (symbols). The number of LCTA plots associated with each transition is noted parenthetically in the legend.

Disturbance Impacts

Disturbance Effects on Vegetation Metrics

The results of the stepwise BIC model selection are shown in Table 12. Community classification in 1989 and/or 2002 was important for most variables. Variables that were related to one or more disturbance variables are highlighted here. Overall, grazing was the most commonly selected disturbance variable followed by military training intensity and fire. Training Area usage, distance to road, and maintenance were not selected for any of the response variables.

Compositional change, measured as the Bray-Curtis distance between a plot's composition in 1989 and its composition in 2002, was positively related to military training intensity and grazing. In other words, the more intense the training around a plot, and the more years of grazing that occurred around it, the greater its composition changed from 1989 to 2002 (Figure 5). This was the only variable that was not related to the group a plot was classified in in 1989 or 2002.

Total cover in 2002 was affected by military training intensity and grazing, and differed among 2002 communities. Plots that experienced more intense military training had lower cover, while those that experienced more years of grazing had higher cover (Figure 6).

Species richness in 2002 showed the same relationships with military training and grazing as did total cover, but differed more strongly with initial (1989) communities than with 2002 communities (Figure 7).

The relative abundances of exotic species and of native forbs did not vary with any disturbance variables. The relative abundance of native grasses declined as the number of years of grazing increased and was higher in burned than unburned plots (Figure 8). The relative abundance of shrubs showed the opposite pattern: it increased with the number of years of grazing and was lower in burned than unburned plots (Figure 9).

Table 12. Disturbance impacts on vegetation dynamics, as expressed by the Bray-Curtis distance between the vegetation composition of each plot in 1989 and 2002 and by various vegetation metrics in 2002. Explanatory variables included in the final model for each response, as determined via BIC, are highlighted in grey; for continuous variables, the direction of the relationship is also shown. Comm.: Community; Inten.: Intensity; TA: Training Area; Maint.: Maintenance; Distance: Bray-Curtis distance.

	1989 Comm.	2002 Comm.	Training Intens.	TA Usage	Road	Grazing	Fire	Maint.	R^2
Distance			+			+			0.11
Total Cover			-			+			0.34
Species Richness			-			+			0.15
Exotics									0.70
Native Forbs									0.24
Native Grasses						-	+		0.45
Shrubs						+	-		0.30

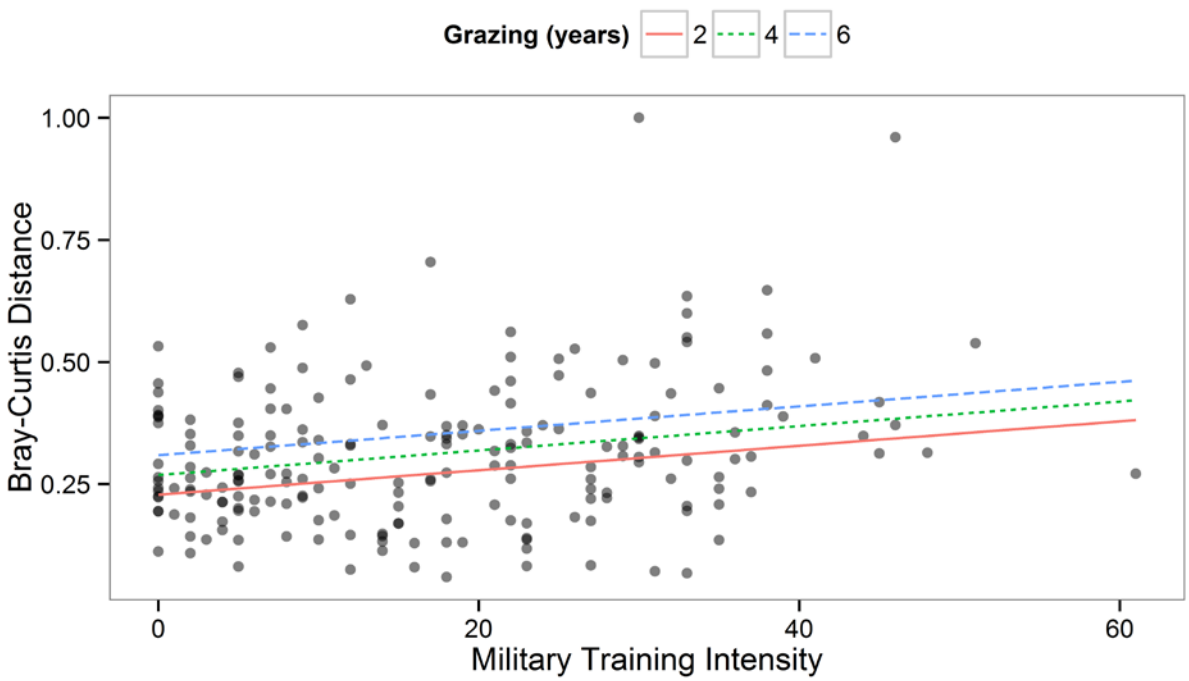


Figure 5. Changes in Bray-Curtis distance as a function of military training intensity and grazing. For simplicity, the fit line for grazing is only shown for 3 years.

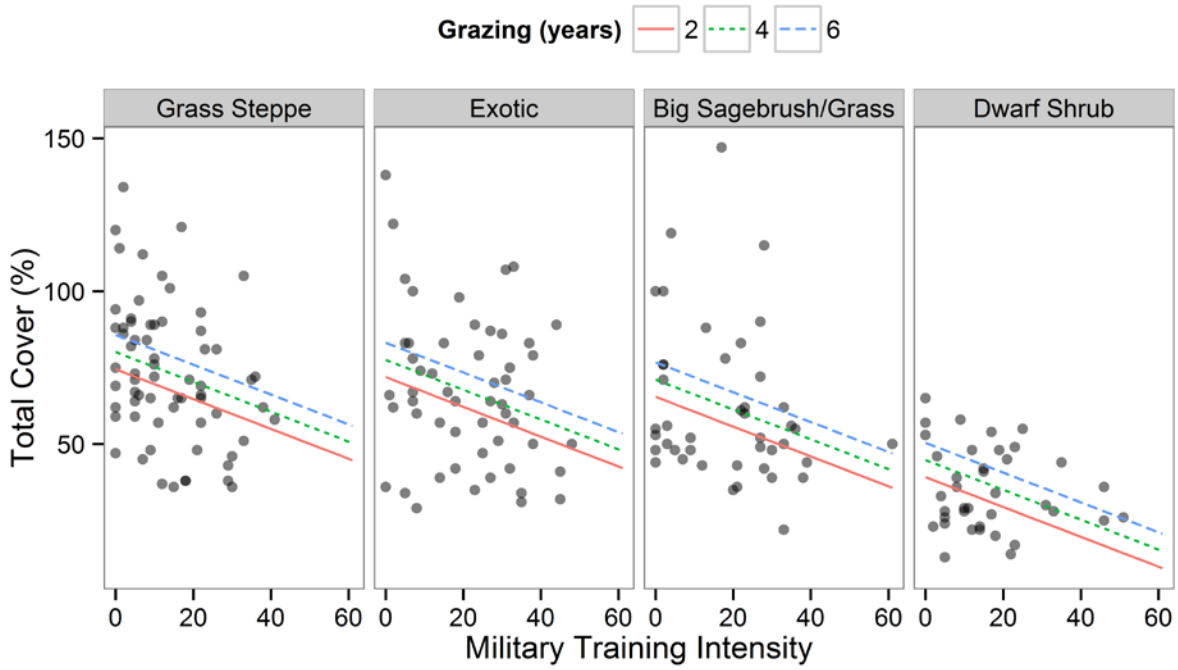


Figure 6. Total cover in 2002 as a function of military training intensity and grazing in the four communities identified in 2002. For simplicity, fit lines for grazing are only shown for 3 years.

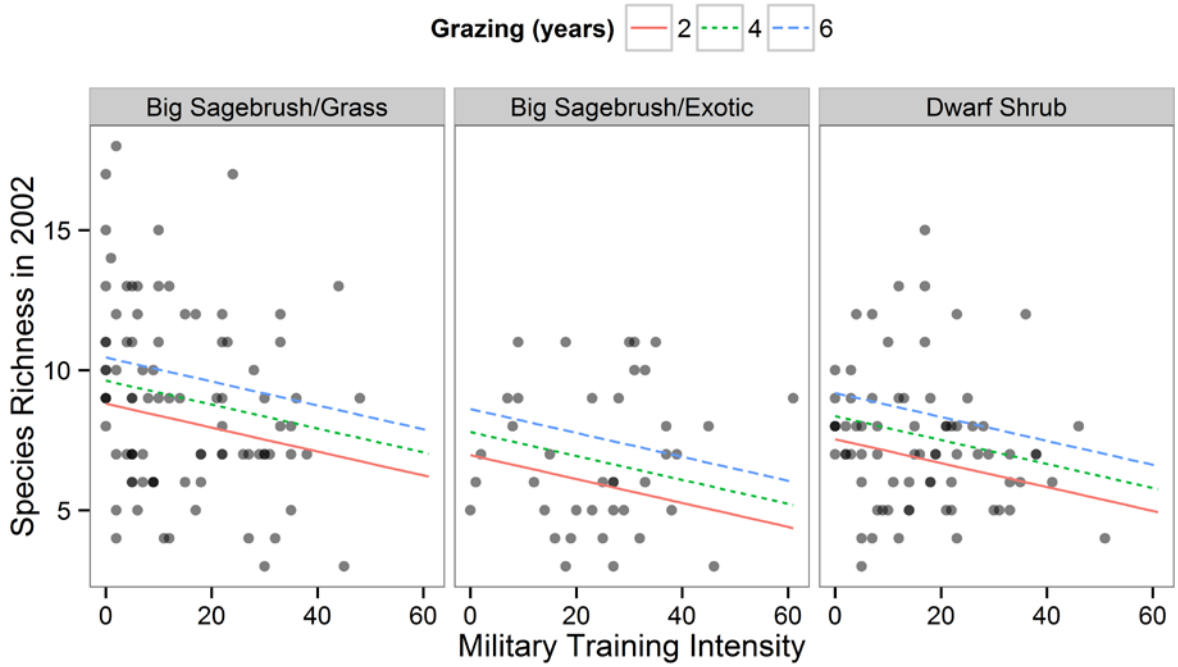


Figure 7. Species richness in 2002 as a function of military training intensity and grazing in the three communities identified in 1989. For simplicity, fit lines for grazing are only shown for 3 years.

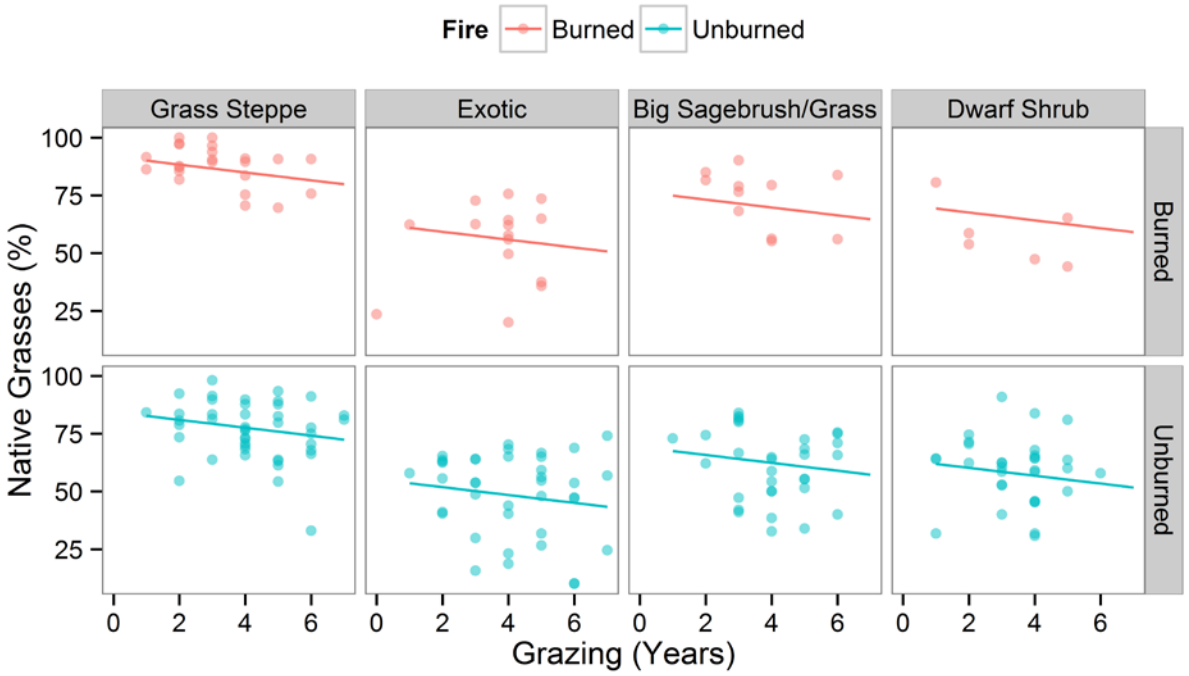


Figure 8. Relative abundance of native grasses in 2002 as a function of grazing and fire in the four communities identified in 2002.

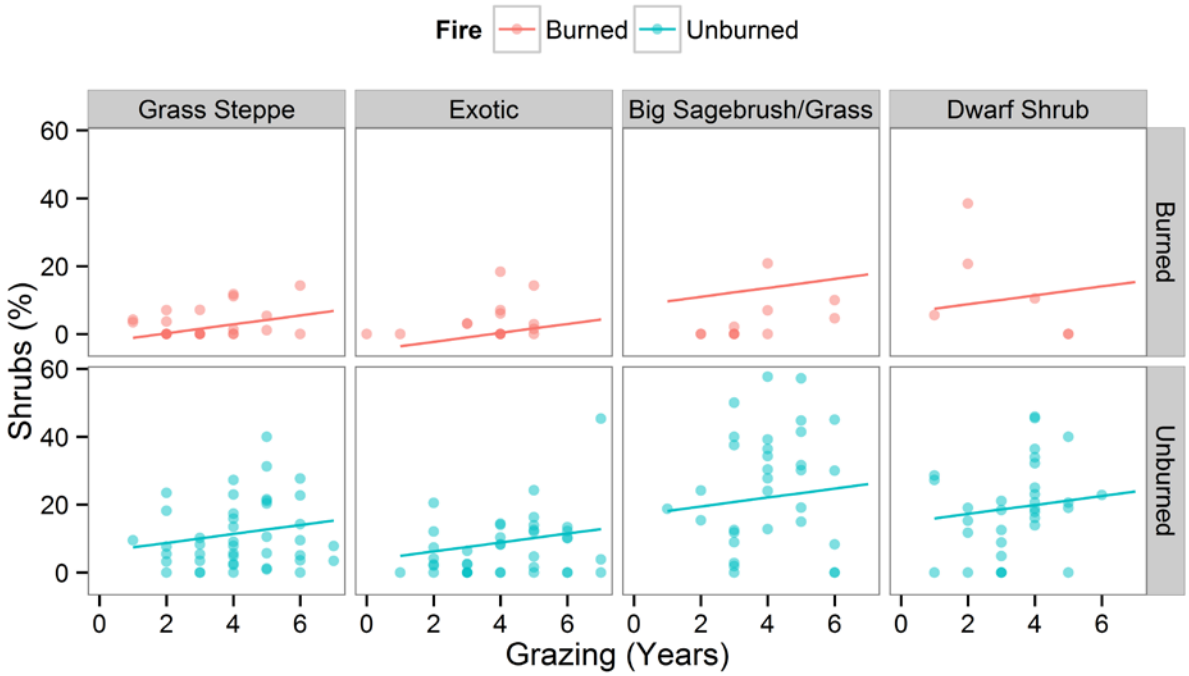


Figure 9. Relative abundance of shrubs in 2002 as a function of grazing and fire in the four communities identified in 2002.

Disturbance-Related Indicator Species

Indicator species associated with each disturbance metric are identified in Table 13.

Six species were identified as indicators of military training intensity. Three species (*Eriogonum sphaerocephalum*, *Festuca idahoensis*, *Poa fendleriana*) were more likely to be found in areas with low military training intensity, while three other species (*Artemisia tridentata*, *Bromus tectorum*, *Elymus elymoides*) were more likely to be found in areas with high military training intensity.

One species, *Elymus elymoides*, was an indicator of areas with High training area usage.

No species were indicators of areas close to roads, though three species (*Artemisia rigida*, *Balsamorhiza hookeri*, *Eriogonum thymoides*) were indicators of areas far from roads.

Two species (*Eriogonum sphaerocephalum*, *Poa secunda*) were indicators of plots that received little grazing while three species (*Artemisia tridentata*, *Artemisia tripartita*, *Lupinus sericeus*) were indicators of plots that received high amounts of grazing.

Two species were significant indicators of fire status. *Lupinus sericeus* was an indicator of areas that burned between 1989 and 2002, while *Artemisia tridentata* was an indicator of areas that did not burn during this period.

No species were indicators of maintenance activities.

Table 13. Indicator species associated with disturbance metrics. Continuously distributed metrics (military training intensity, distance to roads, grazing) were analyzed via TITAN (Baker & King 2010) while categorical metrics (training area usage, fire, maintenance activities) were analyzed via ISA (Dufrene & Legendre 1997). See text for details about these techniques.

Disturbance Metric Species	Change Point	IV	*P*	Purity	Reliability
Military Training Intensity (Low)					
Eriogonum sphaerocephalum	0.0	31.6	0.008	1.00	0.97
Festuca idahoensis	0.0	54.0	0.002	1.00	1.00
Poa fendleriana	12.0	45.9	0.002	1.00	1.00
Military Training Intensity (High)					
Artemisia tridentata	17.5	31.1	0.006	0.95	0.92
Bromus tectorum	26.0	48.9	0.002	0.99	0.99
Elymus elymoides	35.0	43.1	0.002	1.00	1.00
Training Area Usage (None)					
None					
Training Area Usage (Low)					
None					
Training Area Usage (Moderate)					
None					
Training Area Usage (High)					
Elymus elymoides		30.4	0.001		
Roads (Near)					
None					
Roads (Far)					
Artemisia rigida	1139.5	28.0	0.004	0.99	0.97
Balsamorhiza hookeri	1913.0	42.2	0.004	0.95	0.92
Eriogonum thymoides	1789.0	43.3	0.002	1.00	0.99
Grazing (Less)					
Eriogonum sphaerocephalum	1.0	44.6	0.004	0.97	0.84
Poa secunda	5.0	56.6	0.006	0.98	0.96
Grazing (More)					
Artemisia tridentata	4.0	34.9	0.002	1.00	1.00
Artemisia tripartita	6.0	36.6	0.002	1.00	0.99
Lupinus sericeus	6.0	44.3	0.002	1.00	1.00
Fire (Unburned)					
Artemisia tridentata		44.9	0.001		
Fire (Burned)					
Lupinus sericeus		27.1	0.003		
Maintenance (Yes)					
None					
Maintenance (No)					
None					

State and Transition Model

Disturbances can alter community composition, including the cover of dominant or indicator species, and cause transitions among communities. Furthermore, communities may be transient and short-lived or may be stable over longer time frames. We observed 10 transitions among vegetation communities from 1989 to 2002 though, as noted previously, not all of these transitions include changes in composition.

Integrating across 1989 and 2002, the vegetation on these plots can be described in five communities. One of these, the "Big Sagebrush/Exotic" community was only identified in 1989 and thus is transient. Two communities, the "Big Sagebrush/Grass" and "Dwarf Shrub" communities, were stable; some of the plots that were in these communities in 1989 persisted in them through 2002. The last two communities, "Exotic" and "Grass Steppe", were only observed in 2002. Further monitoring would be necessary to determine whether these communities are stable.

In part, these transitions relate to the amount of disturbance that plots experienced. For example, plots that were subject to heavy military training also experienced greater compositional change. Grazing and fire were also important disturbances.

Transitions may also be dependent on environmental characteristics; we have not yet evaluated this.

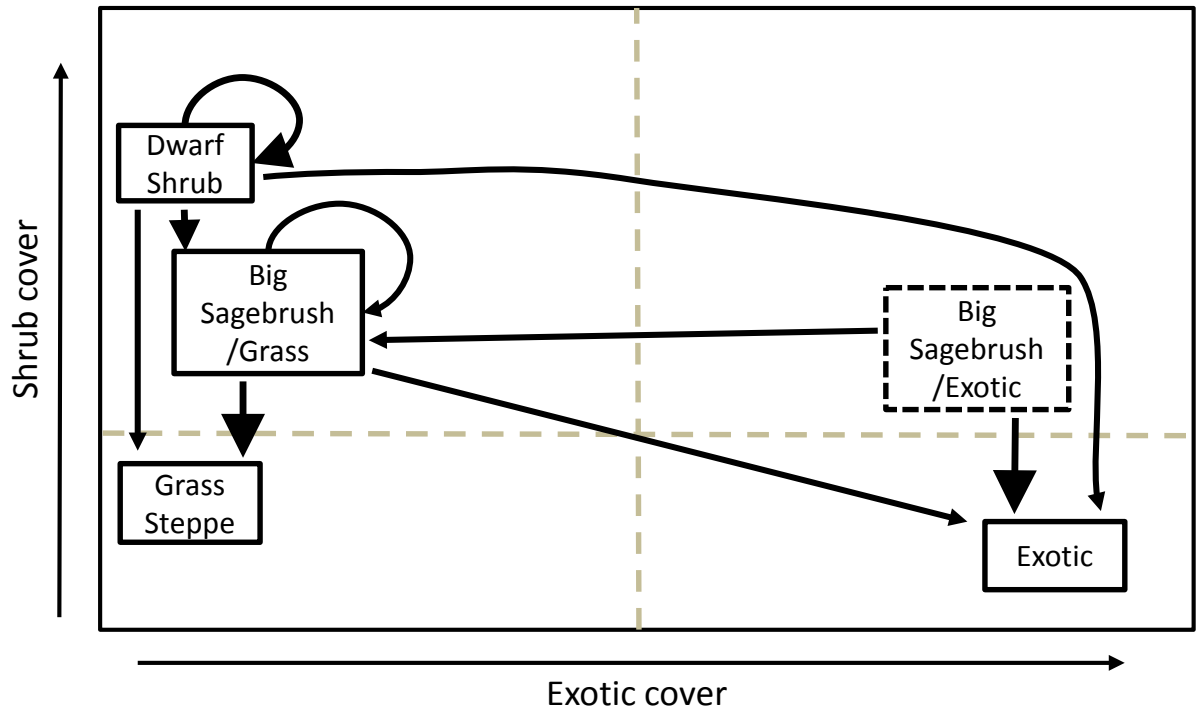


Figure 10. State and transition model with one dimension explained by the relative cover of exotics and the other by the relative cover of shrubs, *sensu* Davies *et al*. (2012). Boxes represent communities (solid = stable, dashed = transient), and observed transitions are shown as arrows, with arrow width roughly proportional to the transition probability. The horizontal and vertical grey dashed lines indicate proposed thresholds between stable states.

Discussion

Sagebrush steppe ecosystems are a valuable asset both from a military-training perspective and from a conservation standpoint. Military training activities at YTC are threatened when critical habitat is seriously degraded and must be restored or closed to training. Identifying common plant community types across YTC, and determining how fire, disturbance, and maintenance alter these communities, are of critical importance for supporting the mission of YTC. The implications of military training for conservation of endangered taxa are reflected in the dynamics of the plant communities on YTC.

Vegetation Communities and Transitions at YTC

Overall, vegetation transitioned from three communities in 1989 into four communities in 2002. These communities differed in stability.

The Big Sagebrush/Grass community was stable at the scale of the landscape but not at the plot scale. At the landscape scale, this community was identified in both years, but at the plot scale, only 16% of the plots classified in this community in 1989 were also classified in it in 2002 (Table 11). Other plots transitioned to it in 2002 from the Big Sagebrush/Exotic and the Dwarf Shrub communities in 1989. Plots that transitioned from the Big Sagebrush/Exotic community lost much of their exotic cover and gained cover of native forbs and grasses. The strong reduction in exotic cover in these plots is surprising and warrants further investigation.

The Dwarf Shrub community was stable at both the landscape scale and at the plot scale. Half of the plots that were classified in this community in 1989 were also classified in it in 2002. However, only one plot transitioned to this community from any of the other 1989 communities.

The Big Sagebrush/Exotic community was a transient community, only present in 1989. Most of these plots transitioned to the Exotic community in 2002.

The Exotic and Grass Steppe communities were new communities, identified in 2002 but not in 1989. Plots transitioned to the Exotic community from all of the 1989 communities, and to the Grass Steppe community from two of the three 1989 communities.

Disturbances as Drivers of Vegetation Dynamics

Disturbances were not clearly identified with any of the transitions among communities, though some disturbance metrics were correlated with changes in particular response variables (Table 12). The fact that disturbances were not more strongly associated with vegetation change may reflect the fact that we analyzed vegetation dynamics from 1989 to 2002 and thus significant disturbances had to cause pronounced and long-term changes. Analyses at a finer temporal resolution of one to a few years may clarify the short-term effects of disturbances.

Military activities can profoundly impact vegetation by, for example, causing soil compaction, erosion and loss of vegetation cover (Thurow et al. 1993; Belnap & Warren 2002). Military vehicle impacts on plant communities have been shown to decrease woody plant and native bunchgrass cover, increase the presence of exotic species, and decrease diversity (Haugen et al. 2003). In addition, disturbance by tracked-vehicles has been found to convert long-lived perennial communities to communities dominated by short-lived perennial species. We explored two metrics of military training, intensity of training activities and training area (TA) usage. Military training activities were noted during re-measurements of each plot and thus the intensity of these activities reflects the actual history of each plot. The relative intensities assigned to the various military training activities are arbitrary (Table 1), though it is not clear how to avoid these subjective assessments of intensity. Nonetheless, we expected training intensity to be more insightful than TA usage, and this expectation was supported: military training intensity was significantly related to several vegetation metrics while training area usage was not (Table 12). In particular, higher intensities of military training were associated with reduced plant cover and richness, and greater changes in composition. Interestingly, military training intensity was not related to the relative abundance of any functional groups.

Roads can serve as vectors for non-native species, but distance to the nearest road was not retained in any of the final models in our analyses. A few species were indicators of areas far from roads, but this does not mean that their abundance or distribution has been caused by roads, particularly because roads are not built randomly across the landscape.

Instead, we suspect that the fact that these patterns may reflect a tendency for roads to be built in some communities (e.g., Grass Steppe) rather than others (e.g., Dwarf Shrub).

Although livestock grazing at YTC ceased around 1995, grazing history still impacted several aspects of vegetation change between 1989 and 2002. Plots where grazing was recorded in more years changed more in vegetation composition but also had higher total cover and species richness than those grazed in fewer years. Also, grazing reduced the relative cover of native grasses but increased that of shrubs; this effect has also been observed in many other grazing studies. Increased abundance of shrubs affects habitat quality and susceptibility to future wildfire.

The impacts of fire on sagebrush steppe communities are well understood. Generally fires reduce the cover of non-sprouting shrubs like *Artemisia tridentata* and of fire-sensitive forbs, driving communities towards a state dominated by perennial herbs and grasses (D'Antonio and Vitousek 1992, Cook et al. 1994, Bates et al. 2009, Davies et al. 2012). Vegetation patterns at YTC support this finding: fire reduced the prevalence of shrubs and increased the prevalence of native grasses and of the legume *Lupinus sericeus* in particular. Other work has also shown that the invasive grass *Bromus tectorum* can result in a positive feedback loop with fire, though this species was not identified as an indicator of burned plots in our analysis.

Maintenance activities were conducted on a small number of plots used in this study. Generally, small-scale maintenance activities have low success in restoring or preventing invasion in the shrub-steppe, and aggressive restoration activities have been suggested as the primary way to slow loss of shrub habitat (Hemstrom et al. 2002). Maintained plots experienced seeding, prescribed burns, chemical applications, or a combination of treatments. Maintenance activities could occur multiple times within a single plot over the study period. Unfortunately, information about seeding mixes used, or the target of chemical applications were not available, and previous research in the sage-steppe has indicated that restoration success through seeding depends on interactions between the species seeded and the recipient community (Eiswerth et al. 2009). Although this metric was not retained in any of the final models, it is possible that the effects of these actions

would be evident over shorter time scales. For example, prescribed fire effects can be highly transient (Seefeldt et al. 2007).

Relation to other Vegetation Classifications

Jones & Kunze (2003) used the 1989 data to classify plots into four wildlife-habitat types: big sagebrush shrub-steppe, grassland-steppe, dwarf-shrub-steppe, and weedy annual. The weedy annual habitat type was not common enough to warrant further investigation. Their classification was somewhat subjective, focusing primarily on shrub cover but also incorporating information such as soil depth. Our classifications, based on a quantitative analysis of the relative abundances of all species, differs in some interesting ways from their classification.

Almost half of their plots (n = 93) were classified as grassland-steppe wildlife habitat (Table 14). In 1989, this group mostly corresponded with our Big Sagebrush / Grass community, though plots from this wildlife habitat type were also common in the other communities. Their next most common wildlife habitat type, big sagebrush shrub-steppe, was also dominated by plots from our Big Sagebrush / Grass community along with plots from the other communities. Their dwarf-shrub-steppe wildlife habitat type closely corresponded with our Dwarf Shrub community: all but one of the plots in this wildlife habitat type were in this community.

Table 14. Number (percentage) of plots within each 1989 community (row) that were classified by Jones & Kunze (2003) into each of four wildlife habitat types.

		Wildlife Habitat Types				
		Big Sagebrush Shrub-Steppe	Grassland-Steppe	Dwarf-Shrub-Steppe	Weedy Annuals	Total
1989 Comm.	Big Sagebrush / Grass	39 (44%)	48 (55%)	0	1 (1%)	88
	Big Sagebrush / Exotic	17 (44%)	19 (49%)	1 (3%)	2 (5%)	39
	Dwarf Shrub	9 (12%)	26 (35%)	39 (53%)	0	74
	Total	65	93	40	3	201

A comparison of their classification with our 2002 communities suggests somewhat closer agreement (Table 15). Our Grass Steppe and Exotic communities are both part of their

grassland-steppe wildlife habitat type, though plots from the other two communities are also part of it. Similarly, their big sagebrush shrub-steppe wildlife habitat type is comprised of about equal proportions of plots from our Grass Steppe, Exotic, and Big Sagebrush / Grass communities. The agreement between our Dwarf Shrub community and their dwarf-shrub-steppe wildlife habitat type is not quite as strong as in 1989 (34 vs. 39 of 40 plots), though our classification of the Dwarf Shrub community appeared to be more precise in 2002 as 89% of the plots in it were part of this wildlife habitat type in 2002, compared to only 53% in 1989.

Table 15. Number (percentage) of plots within each 2002 community (row) that were classified by Jones & Kunze (2003) into each of four wildlife habitat types.

		Wildlife Habitat Types				
		Big Sagebrush Shrub-Steppe	Grassland-Steppe	Dwarf-Shrub-Steppe	Weedy Annuals	Total
2002 Comm.	Grass Steppe	26 (39%)	40 (61%)	0	0	66
	Exotic	18 (33%)	31 (57%)	3 (6%)	2 (4%)	54
	Big Sagebrush / Grass	21 (49%)	19 (44%)	3 (7%)	0	43
	Dwarf Shrub	0	3 (8%)	34 (89%)	1 (3%)	38
	Total	65	93	40	3	201

Strengthening Current State and Transition Models

This analysis verifies and generalizes the STM proposed by Davies et al. (2012). Data from YTC was collected on a far larger geographic and environmental scale, and from more transects, than those used by Davies et al., allowing our model to provide a more general test of the states, transitions, and drivers proposed.

Our model includes some additions to the previously proposed model, primarily through the inclusion of the Dwarf Shrub community. As noted earlier, this community contains several unique species (*Artemisia rigida*, *Stenotus stenophyllus, Eriogonum thymoides, Phlox hoodii*), has low cover of invasive species, and is highly stable. *Artemisia rigida* is often associated with lithosols and basalt scablands (Rosentreter 2005), suggesting that this community is edaphically constrained. Jones & Kunze (2003) also noted that it was present on shallow soils, though the soil depth data that we used here did not support this –

perhaps because the USDA data integrate over larger spatial scales than the data they used. Future research should be devoted to understanding the environmental controls on this community and how fire, disturbance and maintenance impact it.

Our model also extends the work of Davies et al. (2012) by including a wider range of disturbances. Fewer of these plots experienced fire, but they experienced differing amounts of livestock grazing and military training activities. However, while these disturbances affected the dynamics of individual plots, they were not clearly associated with particular transitions.

Davies et al. (2012) noted that *Poa secunda* is functionally distinct from other native perennial bunchgrasses due to its shallow rooting depth, and identified a community dominated by this species. We did not find evidence of this community at YTC as *P. secunda* was ubiquitous, occurring in almost every plot. This may relate to the differences in fire history, as *P. secunda* increased particularly in abundance following repeat fires (Davies et al. 2012).

Implications for Military Training and Management

These analyses indicate that the Dwarf Shrub community is relatively stable while the other communities were more dynamic. Disturbances were not strongly associated with any particular transition, but altered the dynamics of individual plots. In particular, more intense military training activities reduced total cover and species richness, and resulted in greater compositional changes between 1989 and 2002.

Several species were associated with high training intensities, suggesting that these species would increase in abundance as training intensity increases. This includes desirable species such as *Artemisia tridentata* but worrisomely also includes *Bromus tectorum*. Further investigation of these relationships is warranted.

Several species were associated with low training intensities, suggesting that these species would decrease in abundance as training intensity increases. Included in this group were *Festuca idahoensis* and *Poa fendleriana*, both of which were also indicators of the Grass Steppe community (Table 9).

Further investigation of the relationships between training intensity, as noted by activities recorded on each plot, and TA usage, as characterized by Jones & Kunze (2003) would be helpful to understand differences in response to these factors. We will explore this in the future.

Future Research Directions

The findings of this initial report could be strengthened in a number of ways, particularly by analyzing interim data, incorporating plant functional traits, remeasuring plots to examine changes since 2002, and using simulation modeling to project changes in vegetation over time across YTC.

First, this analysis considered vegetation change between two time points: at the establishment of the plots in 1989 and at the final census 14 years later in 2002. Analyses of data collected during interim re-measurements will further strengthen and refine the STMs by clarifying whether transitions occur rapidly (e.g., immediately after a disturbance) or gradually, and will strengthen the applicability of these models to military training needs. Analyzing interim dates would also allow us to include plots from the northern expansion of YTC, thus expanding the spatial scope of the analysis. Analyses of interim data should provide more nuanced understandings of vegetation responses to disturbance. For example, livestock grazing largely ceased around 1995 so we would expect the effects of grazing to be stronger in the early 1990s and to diminish over time. Similarly, several pulses in military training occurred during this period in response to mission goals and needs (Jones & Kunze 2003). More detailed analyses should seek to clarify the short- and long-term effects of military training on vegetation communities, and could also focus on particular types of training such as tracked vehicles (Althoff & Thien 2005, Althoff et al. 2009). These analyses should incorporate additional information about military training that was noted by Jones & Kunze (2003) but not incorporated into this analysis. This expanded analysis has been funded by the Department of Defense Legacy program (projects 14-623 and 15-623).

Second, this analysis was species-based, but a major finding of Davies et al. (2012) was the importance of plant functional traits in determining response to repeat disturbance.

Kachergis et al. (2013) found that while trait-based approaches were not as sensitive as species-based approaches to range management, they provided complementary insights. We are compiling trait information for the key species on YTC and will incorporate these data into future analyses.

Third, it would be valuable to re-measure the LCTA plots and quantify how the vegetation has changed since 2002. If combined with recent disturbance histories, this would permit an examination of vegetation changes at YTC over more than a quarter century – since 1989 – strengthening our understanding of vegetation dynamics within the sagebrush steppe and the effects of military training on these dynamics. It is possible that the communities identified in this analysis are "transitional" when examined over longer time frames that include new or compound disturbances. Since YTC has conducted considerable maintenance activities since 2002, this analysis would also strengthen our understanding of how restoration and management drive community change, a question that we were unable to answer definitively with the historical data. We have secured funding from the Joint Fire Science Program to remeasure a subset of the LCTA plots along with plots on the Arid Lands Ecology Reserve and other sites in central Washington. These measurements are tentatively scheduled to occur Spring 2017.

Finally, it could be insightful to apply simulation modeling to the resulting state-and-transition models to project changes in vegetation over time across YTC. State-and-transition simulation models are stochastic and can predict transitions in response to interactions between vegetation succession, disturbances, and management (Daniel & Frid 2012). Several software tools exist for this purpose, including a free one called ST-Sim. We hope to explore this approach in the future.

Acknowledgements

This report is part of Department of Defense Legacy Project 13-623. We thank the staff at the Yakima Training Center for access to GIS and other data, and for their comments on an earlier version of this work. GIS analyses were conducted by, and maps were prepared by,

Jean Caldwell (Caldwell and Associates, Olympia, WA). G. Matt Davies and Eva Dettweiler-Robinson provided helpful reviews of an early draft of this work.

Bibliography

Allen-Diaz, B., and J. W. Bartolome. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. *Ecological Applications* 8:795-804.

Althoff, P. S., and S. J. Thien. 2005. Impact of M1A1 main battle tank disturbance on soil quality, invertebrates, and vegetation characteristics. *Journal of Terramechanics* 42:159-176. doi: 10.1016/j.jterra.2004.10.014.

Althoff, P. S., T. C. Todd, S. J. Thien, and M. A. Callaham. 2009. Response of soil microbial and invertebrate communities to tracked vehicle disturbance in tallgrass prairie. *Applied Soil Ecology* 43:122-130. doi: 10.1016/j.apsoil.2009.06.011.

Baker, M. E. and R. S. King. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods in Ecology and Evolution* 1:25-37.

Bakker, J. D. 2008. Increasing the utility of indicator species analysis. *Journal of Applied Ecology* 45:1829-1835. doi: 10.1111/j.1365-2664.2007.0.

Bates, J. D., E. C. Rhodes, K. W. Davies, and R. Sharp. 2009. Postfire succession in big sagebrush steppe with livestock grazing. *Rangeland Ecology & Management* 62:98-110. doi: 10.2111/08-096.

Belnap, J., and S. D. Warren. 2002. Patton's tracks in the Mojave Desert, USA: an ecological legacy. *Arid Land Research and Management* 16:245-258.

Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114-126.

Bestelmeyer, B. T., K. Moseley, P. L. Shaver, H. Sanchez, D. D. Briske, and M. E. Fernandez-Gimenez. 2010. Practical guidance for developing state-and-transition models. *Rangelands* 32:23-30.

Blindow, I., G. Andersson, A. Hargeby, and S. Johansson. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshwater Biology* 30:159-167.

Boyd, C. S., J. L. Beck, and J. A. Tanaka. 2014. Livestock grazing and sage-grouse habitat: impacts and opportunities. *Journal of Rangeland Applications* 1:58-77.

Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems* 17:360-375. doi: 10.1007/s10021-013-9725-5.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77:117-145.

Clements, F. E. 1916. *Plant Succession: An analysis of the development of vegetation*. Carnegie Institute of Washington, Washington, DC.

Cook, J. G., T. J. Hershey, and L. L. Irwin. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. *Journal of Range Management* 47:296-302.

Daniel, C. J., and L. Frid. 2012. Predicting landscape vegetation dynamics using state-and-transition simulation models. Pg. 5-22 in B. K. Kerns, A. J. Shlisky, and C. J. Daniel (tech. eds.). Proceedings of the First Landscape State-and-Transition Simulation Modeling Conference; June 14-16, 2011; Portland, OR. Gen. Tech. Rep. PNW-GTR-869. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.

Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs, and J. Evans. 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications* 22:1562-1577.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573-2584. doi: 10.1016/j.biocon.2011.07.016.

De Cáceres, M., P. Legendre, and M. Moretti. 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119:1674-1684.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.

Dyksterhuis, E. J. 1958. Ecological principles in range evaluation. *The Botanical Review* 24:253-272.

Eiswerth, M. E., K. Krauter, S. R. Swanson, and M. Zielinski. 2009. Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. *Journal of Environmental Management* 90:1320-1325. doi: 10.1016/j.jenvman.2008.07.009.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207-231.

Gunderson, L. H. 2000. Ecological resilience--in theory and application. *Annual Review of Ecology and Systematics* 31:425-439.

Haugen, L. B., P. D. Ayers, and A. B. Anderson. 2003. Vehicle movement patterns and vegetative impacts during military training exercises. *Journal of Terramechanics* 40:83-95. doi: 10.1016/j.jterra.2003.09.004.

Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, USA. *Conservation Biology* 16:1243-1255.

Jones, D. S., and M. Kunze. 2003. *Land Condition-Trend Analysis (LCTA) Technical Report: 1989-2002, Yakima Training Center, WA*. CEMML TPS 03-10. Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO. 291 p.

Kachergis, E., M. E. Fernandez-Gimenez, and M. E. Rocca. 2012. Differences in plant species composition as evidence of alternative states in the sagebrush steppe. *Rangeland Ecology and Management* 65:486-497. doi: 10.2111/REM-D-11-00137.1.

Kachergis, E., M. E. Rocca, and M. E. Fernandez-Gimenez. 2013. Comparison of species and trait-based approaches for describing sagebrush steppe response to range management. *Applied Vegetation Science* 16:355-364. doi: 10.1111/avsc.12004.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environmental Change* 6:37-52.

Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology* 51:1414-1421. doi: 10.1111/1365-2664.12309.

Lavin, M., T. J. Brummer, R. Quire, B. D. Maxwell, and L. J. Rew. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern Idaho, U.S.A. Ecology and Evolution 3:1626-1641. doi: 10.1002/ece3.574.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603-606.

Prevéy, J. S., M. J. Germino, and N. J. Huntly. 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. *Ecological Applications* 20:1890-1902.

Prevéy, J. S., M. J. Germino, N. J. Huntly, and R. S. Inouye. 2009. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology* 207:39-51. doi: 10.1007/s11258-009-9652-x.

Rosentreter, R. 2005. Sagebrush identification, ecology, and palatability relative to sage-grouse. Pg. 3-16 in N. L. Shaw, M. Pellant, and S. B. Monsen (compilers). Sage-grouse habitat restoration symposium proceedings; 2001 June 4-7; Boise, ID. Proceedings RMRS-P-38. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Seefeldt, S. S., M. J. Germino, and K. DiCristina. 2007. Prescribed fires in *Artemisia tridentata* ssp. *vaseyana* steppe have minor and transient effects on vegetation cover and composition. *Applied Vegetation Science* 10:249-256.

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106-113.

Thurow, T. L., S. D. Warren, and D. H. Carlson. 1993. Tracked vehicle traffic effects on the hydrologic characteristics of central Texas rangeland. *Transactions of the ASAE [American Society of Agricultural Engineers]* 36:1645-1650.

Trakhtenbrot, A., and R. Kadmon. 2005. Environmental cluster analysis as a tool for selecting complementary networks of conservation sites. *Ecological Applications* 15:335-345.

Watts, S. E. 1998. Short-term influence of tank tracks on vegetation and microphytic crusts in shrubsteppe habitat. *Environmental Management* 22:611-616.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266-274.

Wisdom, M. J., M. M. Rowland, M. A. Hemstrom, and B. C. Wales. 2005. Landscape restoration for greater sage-grouse: implications for multiscale planning and monitoring. Pg. 62-69 in N. L. Shaw, M. Pellant, and S. B. Monsen (compilers). Sage-grouse habitat restoration symposium proceedings; 2001 June 4-7; Boise, ID. Proceedings RMRS-P-38. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Wright, H. A., and J. O. Klemmedson. 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. *Ecology* 46:680-688.

Appendix 1: Species retained for compositional analyses.

Table A1.1. The following species occurred on ≥ 5% of the 402 plot-year combinations (201 plots x 2 years (1989, 2002)). Species are listed alphabetically by their USDA Plants code.

Code	Scientific Name	Common Name	Longevity	Life Form	Nativity
ACMI2	*Achillea millefolium*	yarrow	Perennial	Forb	Native
ACTH7	*Achnatherum thurberianum*	Thurber's needlegrass	Perennial	Grass	Native
ARRI2	*Artemisia rigida*	stiff sagebrush	Perennial	Shrub	Native
ARTR2	*Artemisia tridentata*	big sagebrush	Perennial	Shrub	Native
ARTR4	*Artemisia tripartita*	threetip sagebrush	Perennial	Shrub	Native
ASCA12	*Astragalus caricinus*	buckwheat milkvetch	Perennial	Forb	Native
ASPU9	*Astragalus purshii*	woolypod milkvetch	Perennial	Forb	Native
BAHO	*Balsamorhiza hookeri*	Hooker's balsamroot	Perennial	Forb	Native
BRTE	*Bromus tectorum*	cheatgrass	Annual	Grass	Exotic
CHVI8	*Chrysothamnus viscidiflorus*	yellow rabbitbrush	Perennial	Shrub	Native
CRAT	*Crepis atribarba*	slender hawksbeard	Perennial	Forb	Native
ELELH	*Elymus elymoides*	squirreltail	Perennial	Grass	Native
ERLI	*Erigeron linearis*	desert yellow daisy	Perennial	Forb	Native
ERNAS2	*Ericameria nauseosa*	gray rabbitbrush	Perennial	Shrub	Native
ERPO2	*Erigeron poliospermus*	cushion fleabane	Perennial	Forb	Native
ERSP7	*Eriogonum sphaerocephalum*	rock buckwheat	Perennial	Forb	Native
ERTH4	*Eriogonum thymoides*	thymeleaf buckwheat	Perennial	Forb	Native
FEID	*Festuca idahoensis*	Idaho fescue	Perennial	Grass	Native
LOTR2	*Lomatium triternatum*	nineleaf biscuitroot	Perennial	Forb	Native
LUSE4	*Lupinus sericeus*	silky lupine	Perennial	Forb	Native
LUSU5	*Lupinus sulphureus*	sulphur lupin	Perennial	Forb	Native
PHHO	*Phlox hoodii*	spiny phlox	Perennial	Forb	Native
PHLO2	*Phlox longifolia*	longleaf phlox	Perennial	Forb	Native
POFEF	*Poa fendleriana*	muttongrass	Perennial	Grass	Native
POSE	*Poa secunda*	Sandberg bluegrass	Perennial	Grass	Native
PSSPS	*Pseudoroegneria spicata*	bluebunch wheatgrass	Perennial	Grass	Native
SAKA	*Salsola kali*	Russian thistle	Annual	Forb	Exotic
SIAL2	*Sisymbrium altissimum*	tall tumblemustard	Annual	Forb	Exotic
STST5	*Stenotus stenophyllus*	narrowleaf goldenweed	Perennial	Forb	Native
VUMI	*Vulpia microstachys*	small fescue	Annual	Grass	Native

Appendix 2: Environmental cluster analysis.

We focused on four abiotic variables (elevation, soil depth, Heat Load Index, and percent sand) and two climatic variables (mean annual temperature, mean annual precipitation) as described in the text. All variables were scaled so that differences in units did not affect the classification. We used hierarchical agglomerative clustering with Euclidean distances and Ward's linkage method (the 'ward.D2' method) in the "hclust" function of the *vegan* package (v.2.2-0) in R (v.3.1.2).

The scree plot suggested the presence of 2, 5, or 7 communities (Figure A2.1). However, while these communities differ environmentally (Figure A2.2), preliminary analyses suggest minimal differences in vegetation (Figure A2.3). Environmental cluster analysis will continue to be explored in future aspects of this project.

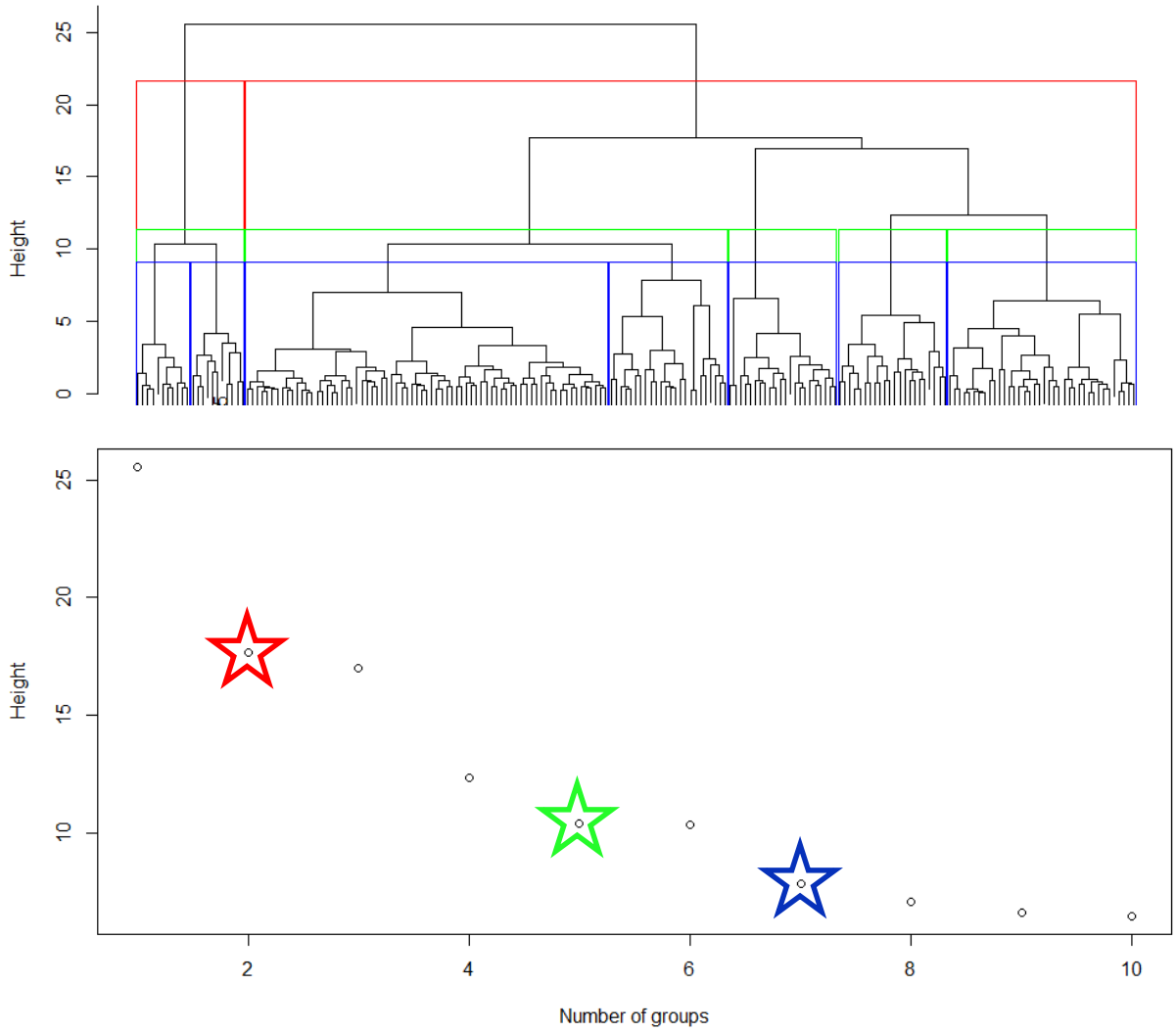


Figure A2.1. Dendrogram and scree plot from hierarchical cluster analysis of environmental data. Boxes in the dendrogram indicate the groups identified at different locations in the scree plot (red = 2 groups, green = 5 groups, blue = 7 groups).

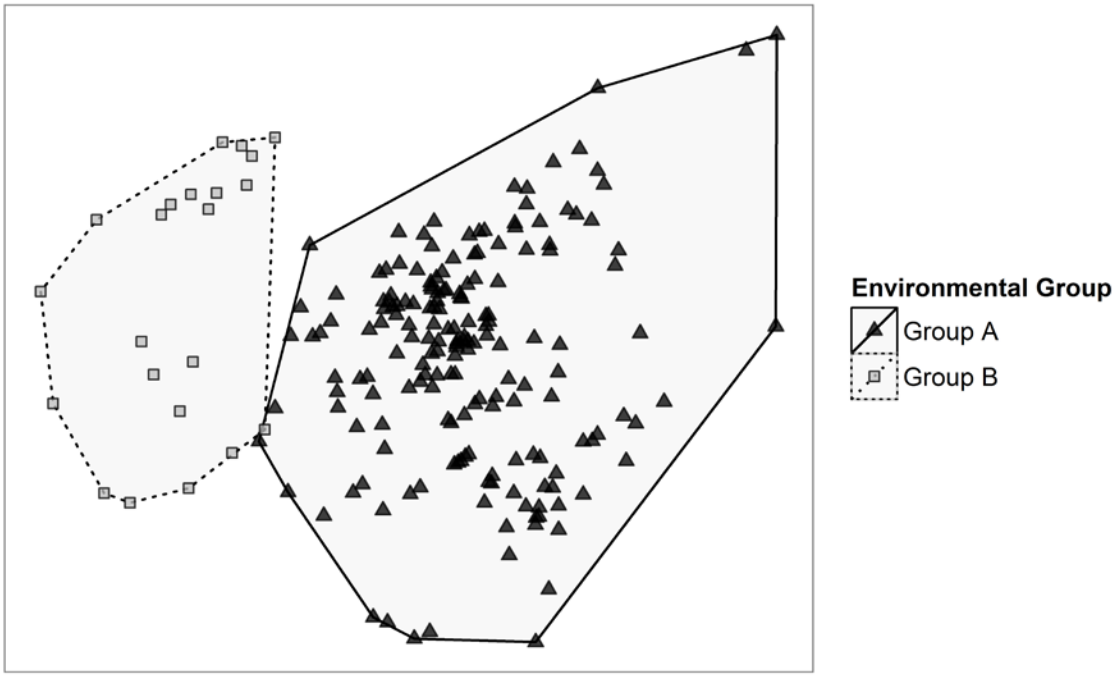


Figure A2.2. NMDS ordination of two groups of plots identified by a hierarchical cluster analysis of their environmental variables. This solution had a stress of 0.138.

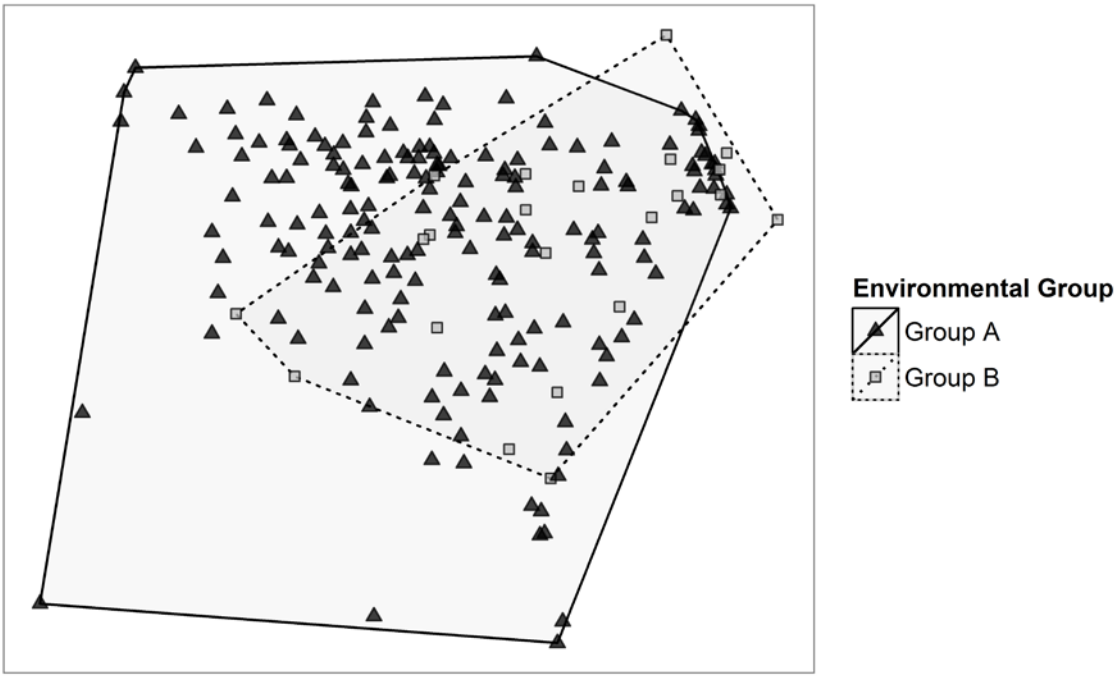


Figure A2.3. NMDS ordination of 1989 vegetation, with plots coded by their group identity as identified by a hierarchical cluster analysis of their environmental variables. This solution had a stress of 0.149.

Appendix 3: Dendrograms and scree plots for plant communities in 1989 and 2002.

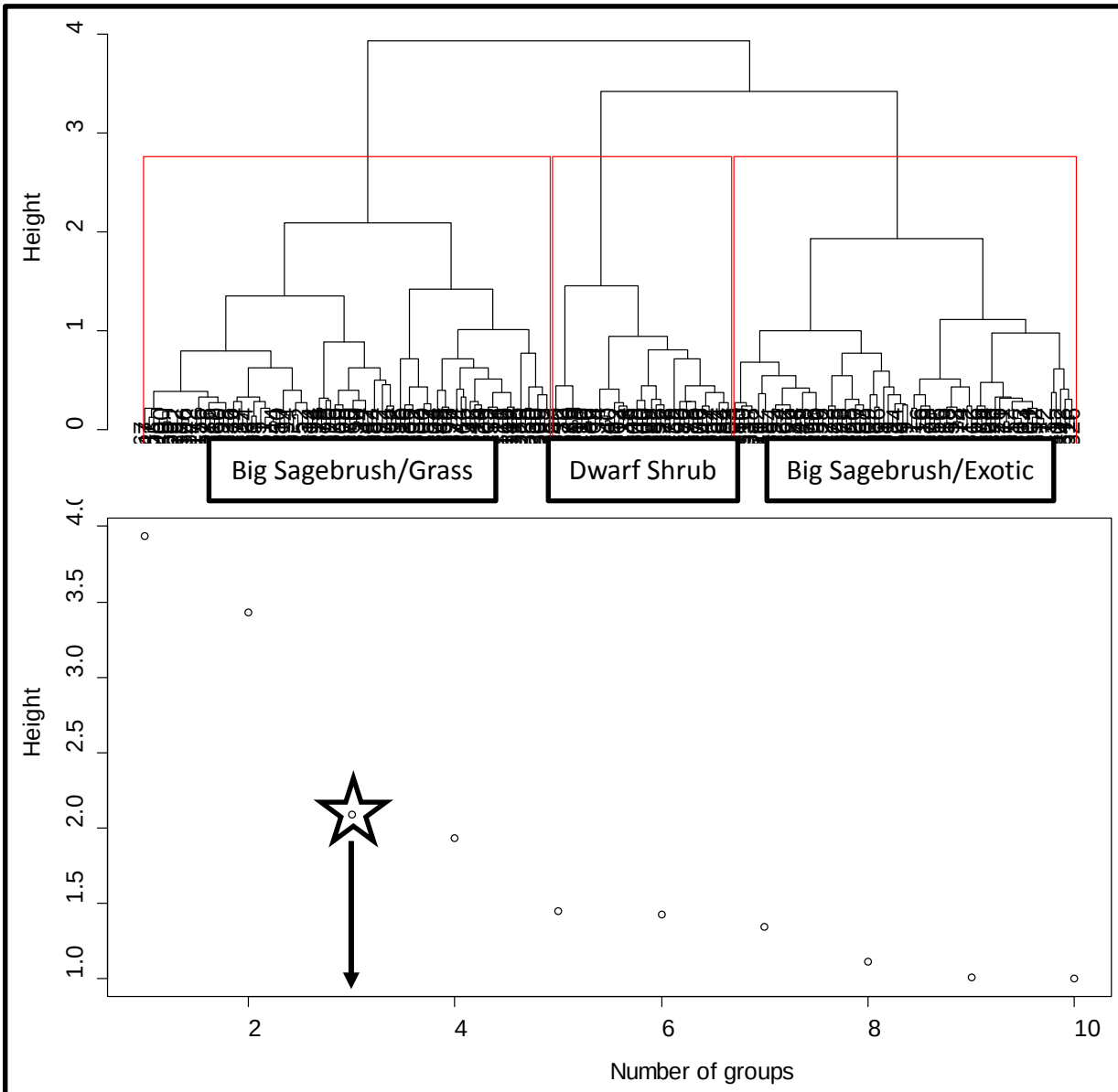


Figure A3.1. Dendrogram and scree plot from hierarchical cluster analysis of 1989 compositional data. Red boxes in the dendrogram indicate the final groups. The optimal number of groups is indicated by the star and arrow in the scree plot.

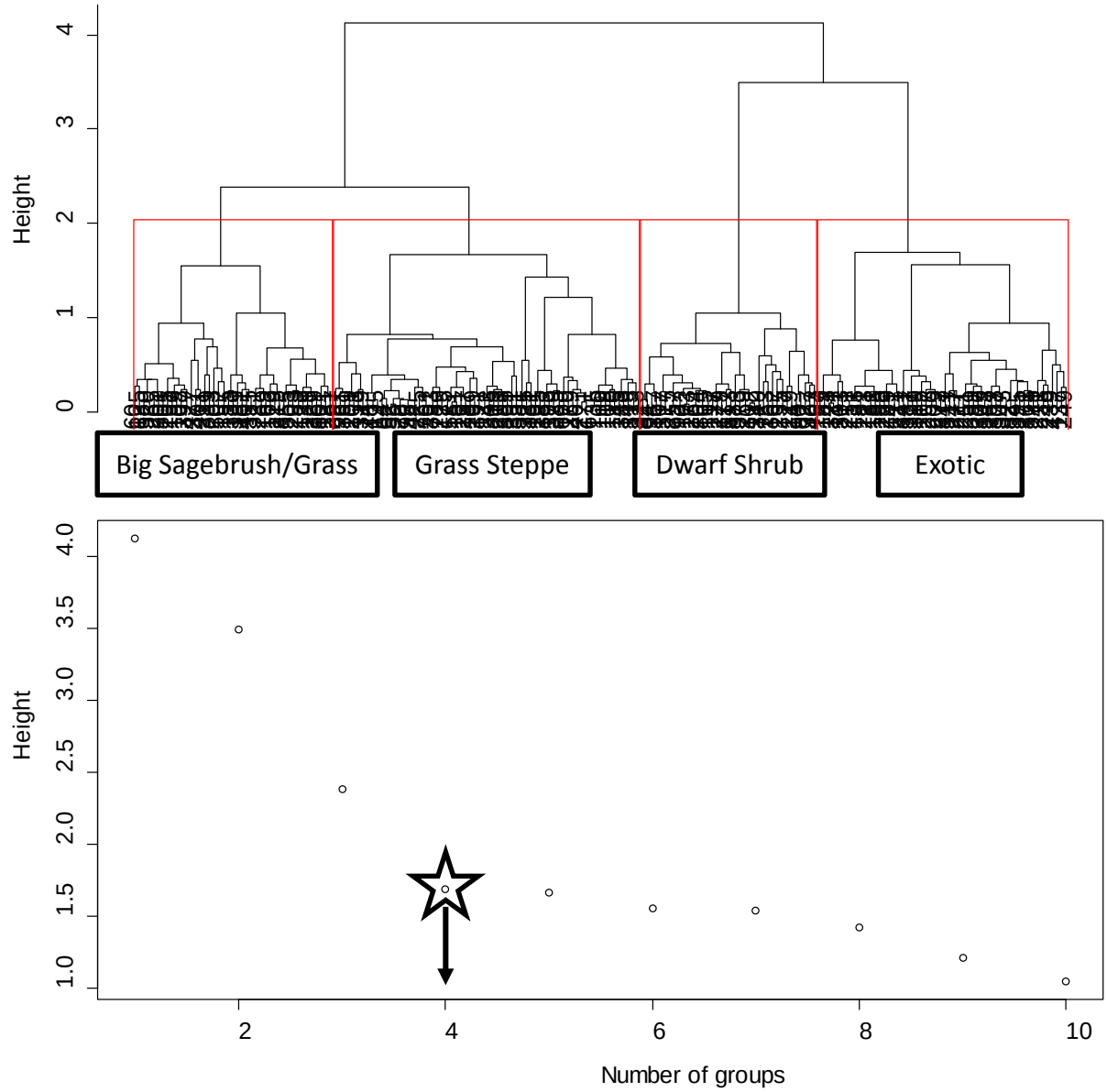


Figure A3.2. Dendrogram and scree plot from hierarchical cluster analysis of 2002 compositional data. Red boxes in the dendrogram indicate the final groups. The optimal number of groups is indicated by the star and arrow in the scree plot.

Appendix 4: Analysis results.

Table A4.1. Summary of ANOVA analyses examining differences in environmental conditions between community groups identified via hierarchical cluster analysis of compositional data from 1989 and 2002. Each variable was tested separately for each year. Significant *P*-values are in bold.

	1989 Communities			2002 Communities		
Environmental Characteristic	df	*F*	*P*	df	*F*	*P*
Elevation	2, 198	18.0	**<0.0001**	3, 197	7.2	**0.0001**
Heat Load Index (HLI)	2, 198	7.5	**0.0008**	3, 197	7.2	**0.0001**
Sand (%)	2, 198	19.4	**<0.0001**	3, 197	12.8	**<0.0001**
Soil Depth	2, 198	0.9	0.4010	3, 197	1.3	0.2810

Table A4.2. Summary of ANOVA analyses examining differences in total cover and species richness between communities in 1989 and 2002. Each variable was tested separately for each year. Significant *P*-values are in bold.

	1989 Communities			2002 Communities		
Response Variable	df	*F*	*P*	df	*F*	*P*
Total Cover	2, 198	23.0	**<0.0001**	3, 197	24.4	**<0.0001**
Species Richness	2, 198	7.9	**0.0005**	3, 197	5.2	**0.0019**

Table A4.3. Summary of ANOVA analyses examining differences in the relative abundance of functional groups between communities in 1989 and 2002. Each variable was tested separately for each year. Significant *P*-values are in bold.

	1989 Communities			2002 Communities		
Functional Group	df	*F*	*P*	df	*F*	*P*
Exotic	2, 198	231.3	**<0.0001**	3, 197	140.7	**<0.0001**
Native Forb	2, 198	20.8	**<0.0001**	3, 197	21.1	**<0.0001**
Native Grass	2, 198	67.7	**<0.0001**	3, 197	42.1	**<0.0001**
Shrub	2, 198	0.3	0.7100	3, 197	14.7	**<0.0001**

Table A4.4. Summary of ANOVA analyses examining changes among plots from the 1989 "Big Sagebrush/Grass" community that transitioned to various other communities in 2002. Plot ID is not shown but was included as a blocking term to account for temporal autocorrelation among re-measurements (this also served as the error for the '2002 community' term). Significant Community x Year interaction terms were followed by pairwise tests to determine whether variables were different among years within each 2002 community. There is only one Bray-Curtis distance between the composition of a plot in 1989 and 2002, so the Year and Community x Year terms were not included in the analysis of that variable.

	2002 Community (df = 2, 85)		Year (df = 1, 85)		2002 Community x Year (df = 2, 85)	
Response Variable	*F*	*P*	*F*	*P*	*F*	*P*
Bray-Curtis distance	2.5	0.0916	-	**-**	-	-
Total Cover	3.0	0.0561	24.6	**<0.0001**	1.7	0.1810
Species Richness	1.4	0.2450	6.6	**0.0121**	1.2	0.3156
Exotic Cover	67.1	**<0.0001**	5.9	**0.0174**	32.6	**<0.0001**
Native Forb Cover	3.9	**0.0240**	4.1	**0.0452**	1.1	0.3516
Native Grass Cover	10.0	**0.0001**	0.2	0.6328	6.7	**0.0020**
Shrub Cover	4.2	**0.0178**	6.1	**0.0159**	3.6	**0.0309**

Table A4.5. Summary of ANOVA analyses examining changes among plots from the 1989 "Big Sagebrush/Exotic" community that transitioned to various other communities in 2002. Plot ID is not shown but was included as a blocking term in all analyses to account for temporal autocorrelation among re-measurements. The transitions to the "Dwarf Shrub" community is not included in the analysis as only one plot experienced this change, and no plots transitioned to the "Grass Steppe" community. Significant Community x Year interaction terms were followed by pairwise tests to determine whether variables were different among years within each 2002 community. There is only one Bray-Curtis distance between the composition of a plot in 1989 and 2002, so the Year and Community x Year terms were not included in the analysis of that variable.

	2002 Community (df = 1, 36)		Year (df = 1, 36)		2002 Community x Year (df = 1, 36)	
Response Variable	*F*	*P*	*F*	*P*	*F*	*P*
Bray-Curtis distance	3.5	0.0710	-	**-**	-	-
Total Cover	1.0	0.3150	8.6	**0.0059**	0.2	0.6474
Species Richness	2.6	0.1170	2.9	0.0980	3.0	0.0894
Exotic Cover	19.2	**<0.0001**	10.1	**0.0031**	11.0	**0.0021**
Native Forb Cover	0.1	0.7220	1.9	0.1760	2.4	0.1310
Native Grass Cover	4.5	**0.0419**	7.3	**0.0104**	4.2	**0.0483**
Shrub Cover	15.7	**0.0003**	0.1	0.7555	3.4	0.0743

Table A4.6. Summary of ANOVA analyses examining changes among plots from the 1989 "Dwarf Shrub" community that transitioned to various other communities in 2002. Plot ID is not shown but was included as a blocking term in all analyses to account for temporal autocorrelation among re-measurements. Significant Community x Year interaction terms were followed by pairwise tests to determine whether variables were different among years within each 2002 community. There is only one Bray-Curtis distance between the composition of a plot in 1989 and 2002, so the Year and Community x Year terms were not included in the analysis of that variable.

	2002 Community (df = 3, 70)		Year (df = 1, 70)		2002 Community x Year (df = 3, 70)	
Response Variable	*F*	*P*	*F*	*P*	*F*	*P*
Bray-Curtis distance	6.0	**0.0011**	-	**-**	-	-
Total Cover	20.0	**<0.0001**	16.1	**0.0001**	2.4	0.0766
Species Richness	6.6	**0.0005**	1.4	0.2480	1.2	0.3040
Exotic Cover	43.9	**<0.0001**	15.7	**0.0002**	23.7	**<0.0001**
Native Forb Cover	5.0	**0.0033**	2.9	0.0935	0.9	0.4597
Native Grass Cover	9.7	**<0.0001**	23.2	**<0.0001**	6.1	**0.0009**
Shrub Cover	6.0	**0.0011**	2.1	0.1470	1.8	0.1560

Additional Materials

Other materials produced as part of this Legacy project include:

- **GIS layers** associated with these data and analyses.
- **Maps** of JBLM YTC showing analysis results.
- A **Fact Sheet** summarizing the project.
- A **Transfer Plan** explaining how this approach could be applied to other datasets, both from the LCTA program and other sources, and from other military installations and ecosystems.
- A **draft manuscript** for submission to a peer-reviewed scholarly publication.