FINAL REPORT

Long-term SUCCESS:
SUCCession and Ecosystem dynamics
in the Sagebrush Steppe following wildfires

JFSP PROJECT ID: 15-1-07-2

January 2020

Jonathan D. Bakker
School of Environmental and Forest Sciences, University of Washington

G. Matt Davies
School of Environment and Natural Resources, Ohio State University

Claire E. Wainwright
School of Environmental and Forest Sciences, University of Washington

Simon C. Power
School of Environment and Natural Resources, Ohio State University

Long-term SUCCESS:
SUCCession and Ecosystem dynamics
in the Sagebrush Steppe following wildfires

Table of Contents

Contents

List of Tables

List of Figures

List of Abbreviations & Acronyms

ALE	Arid Lands Ecology Reserve
BIC	Bayesian Information Criterion
BLM	Bureau of Land Management
BRMaP	Biological Resource Management Plan plots
DW	Wilderman plots
ESD	Ecological site description
FEIS	Fire Effects Information System
GDD	Growing Degree Days
GIS	Geographic information system
HLI	Heat Load Index
HRNM	Hanford Reach National Monument
Ii	Herbaceous 'invadedness' index
LCTA	Land Cover Trend Analysis plots
NMDS	Non-metric multi-dimensional scaling
S-I space	Shrub-Invadedness space (bivariate)
Si	Shrub index
SIT	Steppe-In-Time plots
USDA	US Department of Agriculture
UW	University of Washington
YTC	Yakima Training Center

Keywords

Sagebrush steppe, wildfire, restoration, vegetation dynamics, multivariate statistics, grassland, long-term studies, composition, species richness

Acknowledgements

Abstract

This project examined the effects of wildfires and other factors on succession and ecosystem dynamics in sagebrush steppe ecosystems of the mid-Columbia basin in Washington state. This proposal was directly relevant to the JFSP Task 15-1-07 research questions. Our objectives were to A) quantify and model controls on post-fire vegetation composition, B) characterize vegetation dynamics, and C) evaluate and refine quantitative state-and-transition models. We leveraged new field data collection by combining data collected in 2017 with extensive historical vegetation data (1989-2010). Extant plot-level descriptors (fire and restoration histories, soils, climate) were verified, updated, and expanded. Overall, our results highlight the power of quantitative analyses to understand vegetation dynamics. We organized our findings into four key issues.

First, we developed two quantitative indices, a shrub index and an invadedness index, that form a bivariate 'S-I space' in which to track vegetation dynamics in the sagebrush steppe. We illustrate these indices using historical plot data (1994-2010). Plots represented four distinct community groups in 1994, and these community groups exhibited distinct movement patterns within S-I space. This approach provides managers with a straightforward way to track ecosystem change as evidenced by changes in dominant plant functional types. Furthermore, S-I space is numerically simple to use and to update with new data.

Second, we proposed two quantitative measures of ecosystem resilience. Using our S-I space, we calculated resistance as the net change over an interval, and stability as the average distance moved across consecutive monitoring periods. Resistance was best explained by the initial community group to which each plot belonged, and stability was best explained by community group and elevation. Temporal patterns in these measures differed among community groups.

Third, we examined the relative importance of fire and restoration in driving long-term successional trajectories. The vegetation was classified into five community groups at the initial measurement. Successional trajectories (1992-2017) differed among groups in terms of both the amount of change and the directionality of the changes. Successional trajectories were more strongly related to fire history and restoration activities than to recent seasonal weather patterns.

Fourth, we assessed how the drivers of vegetation dynamics vary with temporal scale. Re-measurements of permanent plots produce an extensive set of temporal intervals. We analyzed more than 3000 unique intervals between measurements of the same plot in different years, ranging from 1 to 26 years. The drivers of changes in species richness varied with temporal scale. Abiotic variables such as growing degree days and water-year precipitation were important at short intervals. Heat load index (HLI) and water-year precipitation were important at intermediate intervals, along with some disturbances (military training usage, grazing) in some places. At long intervals, change in richness was related to HLI, elevation, and distance to the nearest road.

Objectives

This project stemmed from a 2015 Request for Proposals that included the following research questions (JFSP Task 15-1-07):

1) How do successional patterns vary temporally and spatially?
2) How has climate change affected successional patterns?
3) How have fires affected achievement of ecosystem restoration objectives?

In response to these questions, we proposed a research project assessing long-term vegetation dynamics, by analyzing how dynamics are affected by disturbance (fire, grazing and military training) and post-disturbance restoration activities (herbicide, seeding and planting of native species) along with abiotic and biotic factors. We focused on the sagebrush steppe of south-central Washington state. Our project leveraged a unique series of long-term fire, restoration and vegetation datasets collected on and around two key sites - the Arid Lands Ecology Reserve (ALE; part of the Hanford Reach National Monument) and the Yakima Training Center (YTC).

Our project had three objectives:

A. Quantify and model controls on post-fire vegetation composition
B. Characterize vegetation dynamics
C. Evaluate and refine quantitative state-and-transition models

We addressed aspects of all objectives, although we modified and expanded some of the analyses originally proposed. Our research to date has provided insight into four key issues:

1. Developing quantitative indices to track states and transitions
2. Quantifying and evaluating controls on ecosystem resilience
3. Assessing the relative importance of fire and restoration in driving differences in long-term successional trajectories
4. Quantifying how drivers of vegetation dynamics vary with temporal scale

After providing background information and summarizing the study sites and data collection, we highlight each of these topics in turn. For each topic, we summarize the analytical methods used, results, and discussion. A concluding section summarizes the key findings from this study.

Background

Sagebrush steppe ecosystems are among the most imperilled in the western United States (Noss et al. 1995). Their degradation includes increased dominance by flammable invasive annual grasses (e.g. cheatgrass, *Bromus tectorum*) which create a positive feedback with fire frequency and extent, resulting in the loss of native shrub and herbaceous species. Increased fire frequency and extent can be associated with compounded disturbances followed by both ecological "surprises" and incremental changes in ecosystem structure. An example of the former case is provided by Davies et al. (2012), who documented the emergence of novel communities

dominated by *Phlox longifolia*, a resprouting hemi-shrub. An example of the latter case is provided by Bagchi et al. (2013), who demonstrated gradual ecosystem changes until tipping-points were reached and systems changed to a new state dominated by weedy and invasive species. Thus, whilst an understanding of long-term post-fire dynamics is urgently needed for the sagebrush steppe, this can only be developed within the context of changes to overall fire regimes, rather than the impact of individual burns, and on the basis of multi-year studies of vegetation dynamics rather than snapshots widely separated in time.

Plant communities vary in their resistance and resilience to wildfires as a function of their pre-fire species composition, level of invasion, and the life-history traits of dominant species (Davies et al. 2012). Generalized descriptions of community state have been proposed as a key indicator of ecosystems' susceptibility to long-term change as a result of fire. State and Transition Models have been developed (e.g. Bestelmeyer et al. 2009, Kachergis et al. 2012) to describe the effects of fire, and post-fire succession, in sagebrush ecosystems. However, most of these models are based on the effects of individual fires in a limited range of conditions, and they may also confound temporary changes in composition/community type ("phases" *sensu* Bagchi et al. 2013) with fundamental changes in state and ecological function. This led Briske et al. (2008) to argue that new models to quantify post-fire changes in sagebrush steppe communities are urgently needed. Davies et al. (2012) proposed that community state could be tracked in a model defined by two axes, with one axis related to the relative abundance of shrubs versus herbs, and the other axis to the relative abundance of native versus invasive species. Such a model would provide simple metrics by which managers could track ecosystem dynamics. However, this model was qualitative and required validation and refinement in a wider range of conditions.

Wildfires have important consequences for many activities undertaken by land managers, including restoration actions (Dettweiler-Robinson et al. 2013; Knutson et al. 2014). An improved understanding of succession and ecosystem dynamics would enable managers to make informed decisions about the likely ecological consequences of fire management and restoration strategies. For example, heavily degraded areas that are unlikely to develop into desirable communities might be identified as preferred locations for fire lines, thereby protecting more intact habitats, while restoration actions could be targeted to those communities where they are likely to be most effective.

In this project, we re-measured permanent plots that burned one or more times between 1 and 30 years prior to our monitoring. The plots span a diverse range of edaphic conditions, and some received post-fire restoration treatments. We combined new and historical data to examine fire effects on succession and ecosystem dynamics. To provide a necessary context within which to understand these changes, we also re-measured plots which have not burnt during this period.

Study Sites and Data Collection

Study Sites

Our focus was the mid-Columbia basin within Washington State. The area is near the northern edge of the sagebrush steppe biome and contains a number of endangered species and ecosystems. The remaining sagebrush steppe habitat is concentrated in public lands such as Hanford Reach National Monument (HRNM, owned by Department of Energy and managed by US Fish and Wildlife Service), Yakima Training Center (YTC, owned by the Department of Defense) and areas owned by the Bureau of Land Management (BLM). Data were collected in landscapes in and around HRNM, and within YTC. Both regions include sites with a range of elevations, aspects, soil types, climatic conditions and vegetation communities. These regions provide an excellent setting in which to develop an understanding of factors that drive long-term ecosystem responses to wildfire, and the analytical methods we propose will be relevant for other regions.

Historical Data

This study capitalized on four sets of permanent vegetation plots:
- Biological Resource Management Plan (BRMaP; Evans & Lih 2005; Bakker et al. 2011; n = 25): plots span the range of vegetation communities found on HRNM in 1996. A total of 173 plot × year observations are available from 1996 to 2010.
- Land Cover Trend Analysis (LCTA; Tazik et al. 1992; Jones & Kunze 2003; n = 262): plots span the range of abiotic conditions, disturbance histories, and vegetation communities on YTC. A total of 1949 historical plot × year observations are available from 1989 to 2002.
- Steppe-In-Time (SIT; Evans & Lih 2005; Bakker et al. 2011; n = 36): plots span private and public lands (including ALE) throughout Benton and Yakima counties, covering a wide range of abiotic conditions, disturbance histories, and vegetation communities. A total of 375 plot × year observations are available from 1992 to 2010.
- Wilderman plots (DW; Wilderman 1994; n = 32): plots span the range of vegetation communities on ALE in 1994. A total of 224 plot × year observations are available from 1994 to 2010.

New Plot-level Explanatory Data

Several plot-level explanatory variables had previously been collected for most BRMaP, SIT, and DW plots. We verified and updated these data, obtained comparable information for the LCTA plots, and obtained new explanatory variables for all plots.

Ecological Site Description (ESD) – Ecological Site Descriptions (ESDs) are a means of identifying areas with similar abiotic conditions. For example, the 'Dry Stony 10-16 PZ" ESD has dry stony soils and average annual precipitation of 10-16". GIS overlays were used to

identify the ESD of each plot. These data were obtained for all plots in all four historical datasets (https://esis.sc.egov.usda.gov/).

Fire history – We analyzed fire perimeters provided by MTBS (http://mtbs.gov; 1984-present) and GeoMAC (http://www.geomac.gov); smaller fires (< 1000 acres) not covered by either source were identified by analyzing aerial photographs and maps provided by natural resource managers. Fire data were summarized by time since last fire and fire frequency (number of fires in the decade prior to data collection) for each plot × year combination.

Restoration activities – Restoration activities were calculated for every year of interest for each plot. They were tallied by type of activity (herbicide, planting, etc.).

Edaphic conditions – Key variables are the elevation, aspect, slope, soil type, and soil depth of each plot. These variables are assumed to be constant over the time period of interest. Elevation, slope, and aspect are derived from ASTER digital elevation models (http://asterweb.jpl.nasa.gov/data_products.asp) and the UW Geomorphological Research Group (http://gis.ess.washington.edu/data/index.html). Soil type is from the USDA (http://websoilsurvey.nrcs.usda.gov/app) for the mid-Columbia Basin, and Hajek (1966) for ALE. Soil depth was obtained 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; larger values indicate warmer and drier conditions (McCune & Keon 2002).

Climate/weather – Precipitation and temperature data were obtained from the PRISM database (PRISM Climate Group, http://prism.oregonstate.edu). We used the precipitation data to calculate water-year precipitation and winter precipitation for each plot in each year. The water year is from October 1 of the previous year to September 30 of the focal year, while winter is defined here as October 1 through March 31. We used the temperature data to calculate cumulative growing degree days (GDDs) for each plot between January 1 and July 1 of each year. We used a base temperature of 10°C for GDD calculations. We only used the first half of the year as most plant growth occurs during this period in this ecosystem.

New Field Data Collection

New data were collected in 2017 on a subset of the permanent vegetation plots. Our datasets contain more plots than we could possibly measure during a study of this magnitude. We therefore selected a stratified sample that spanned the range of fire history, restoration, and edaphic conditions of our plots. We also focused on the most common ecological site descriptions (ESDs). Our original target was to re-measure 200 plots, but wildfires, weather conditions, and logistic constraints prevented us from meeting this goal. Nonetheless, we are pleased to have been able to gather as much data as we did. A summary of the characteristics of the plots that were re-monitored is shown in Table 1.

We re-monitored 116 plots, distributed as follows:

- Biological Resource Management Plan (BRMaP; n = 25): We re-monitored all 25 plots, increasing the size of this dataset to 198 plot × year observations from 1996 to 2017.
- Land Cover Trend Analysis (LCTA; n = 262): We re-monitored 63 plots, increasing the size of this dataset to 2012 plot × year observations from 1989 to 2017.
- Steppe-In-Time (SIT): We re-monitored 28 plots (15 on ALE, 13 off ALE), increasing the size of this dataset to 403 plot × year observations from 1992 to 2017.

Table 1. Characteristics of plots re-monitored in 2017.

Years Since Fire	# of Plots
1	36
5	5
10	18
14-17	5
21	4
27	2
30+ (Unburned)	44
Number of Times Burned (1987-2016)	
0	44
1	16
2	20
3	34
Years Since Restoration	
Unrestored	60
1-4	16
5-9	27
10-20	8
20+	3

Each plot consisted of a transect either 100 m (BRMaP and LCTA) or 200 m (SIT) in length. Historical procedures varied among datasets, but we followed a consistent and simplified methodology in 2017. Each plot was monitored by recording the presence of vascular plant species in 20 quadrats (20 x 50 cm) evenly spaced along the transect. Abundance was expressed as the frequency of occurrence in the quadrats of a plot. This sampling strategy enables direct comparisons of vegetation on the BRMaP, SIT, and LCTA plots in 2017. Historical LCTA data were obtained from a slightly larger area, so we sampled two additional quadrats in these plots. When frequency of occurrence is calculated using all 22 quadrats, the total area sampled is similar to that used historically, permitting analyses of vegetation dynamics on the LCTA plots over time.

Characterizing Plant Functional Traits

Insights into fire effects and succession can be gained by considering plants not just in terms of their taxonomy but also in terms of their functional traits. We focused on traits related to resource acquisition, growth, reproduction, and response to disturbance (Table 2; Moretti & Legg 2009). We compiled much of this information from the USDA Plants database (http://plants.usda.gov/), floras (e.g., Hitchcock et al. 1955-1969), herbaria (e.g., http://www.burkemuseum.org/herbarium), the Fire Effects Information System (FEIS; https://www.feis-crs.org/feis/), the TR8 package (https://cran.r-project.org/package=TR8), and other sources.

We gathered information about as many of the taxa recorded at YTC as possible. Some taxa were recorded to genus level during field data collection; in these cases, we identified all species of that genus that occur in the area, obtained information for those species, and calculated the genus-level value as the average of the values for the species.

These data continue to be gathered and verified, and will be used in subsequent analyses.

Table 2. Plant functional traits. Data type is ordinal (O), nominal (N), or quantitative (Q).

Trait	Data Type	Description	Relevance
Maximum height	O	Range / Average (5 classes)	Growth
Native status	N	Yes / No	
Life history	O	Annual / Biennial / Perennial	Growth, Resource Acquisition, Response to Disturbance
Raunkiaer growth form	O	Hemicryptophyte / Therophyte / Phanerophyte / Geophyte / Chamaephyte	Growth, Resource Acquisition, Response to Disturbance
Seed mass	O	Range / Average (7 classes)	Reproduction
Nitrogen fixing ability	N	Yes / No	Resource Acquisition
Pollination strategy	O	Animal / Wind / Self	Reproduction
Dispersal mechanism	O	Animal / Wind / Gravity	Reproduction
Phenology	Q	Month of start of flowering	Reproduction
Flowering duration	Q	Number of months	Reproduction

Developing Quantitative Indices to Track States and Transitions

Note: this section draws extensively on Wainwright et al. (2020).

Analytical Methods

Davies et al. (2012) proposed that vegetation dynamics within the sagebrush steppe could be qualitatively related to two axes, one related to the balance between shrubs and grasses and the other to the balance between native and exotic species. We developed quantitative versions of these axes.

- *Shrub index* (*Si*): We calculated a shrub index as the abundance of shrubs divided by the total abundance of all live plants (i.e., shrubs and herbaceous species). $Si = 0$ if a plot contains no shrubs and $Si = 1$ if it only contains shrubs.
- *Invadedness index* (*Ii*): We calculated an herbaceous "invadedness" index as the abundance of non-native herbaceous species divided by the total abundance of all herbaceous species. $Ii = 0$ if a plot contains no non-native species and $Ii = 1$ if it only contains non-native species. We focused on herbaceous species for this calculation because all shrubs in our system are native species.

Together, these two indices form a bivariate 'S-I space' that describes community structure and enables the movement of plots and communities to be tracked over time.

We applied these indices to historical data from the 32 Wilderman (DW) plots. These plots were established in 1994 (Soll et al. 1999), resurveyed annually from 2001 to 2004 (Evans & Lih 2005), and resurveyed in 2009 and 2010 (Bakker et al. 2011). In total, therefore, each plot was monitored 7 times, for a total of 224 plot-years.

The taxa identified during monitoring were classified into functional groups on the basis of five attributes:

- Plant life-form (graminoid, shrub, forb [including sub-shrubs])
- Longevity (annual, perennial)
- Origin (native, non-native)
- Post-fire regeneration strategy (resprouter, obligate seeder) – shrubs only
- Plant size (large, small) – bunchgrasses only

This classification scheme corresponds to that used by Davies et al. (2012). Not all combinations of attributes were present in our flora. For this analysis, we focused on 9 plant functional types that capture most species and >99% of the cover. The covers of all taxa within each plant functional type were summed in each plot-year.

Using data from the first measurement in 1994, we classified the plots into community groups based on their plant functional types. Data were Wisconsin standardized and expressed as a Bray-Curtis dissimilarity matrix, and groups were identified through a hierarchical cluster analysis with Ward's clustering criterion.

Finally, we calculated Si and Ii for each plot-year, and plotted the plot-years in S-I space. By focusing on particular community groups, plots, and/or years, we were able to visualize vegetation dynamics. We assessed evidence for changes in state by examining the position and separation of "basins of attraction" (*sensu* Briske et al. 2017) in S-I space using 2-dimensional kernel density estimates.

Results

In 1994, these plots represented four distinct community groups, which we characterized based on the dominant plant functional type: obligate seeder, grass-forb, pristine sprouter, and invaded sprouter.

These community groups occupied distinct areas of the S-I space in 1994 (Figure 1). Trajectories were generally consistent among plots within each community group.

Plots in the obligate seeder group displayed the largest movement in S-I space, and there were two clear basins of attraction: a basin with high Si and low Ii, and a larger basin with low Si but large variation in Ii (Figure 2,
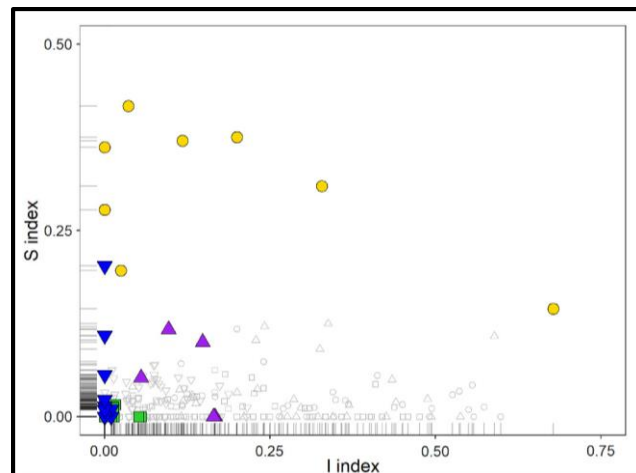
Figure 1. Plot positions in S-I space, defined by a shrub index (S index) and an invadedness index (I index). Each symbol is a plot-year combination. Bands on the x- and y-axes indicate the density of observations for each index. Plot positions in 1994 (large, colored points) are distinguished from other monitoring years (small, gray points). Color and shape differentiate the four community groups: gold circle = obligate seeder; green square = grass-forb; purple triangle = invaded sprouter; blue inverted triangle = pristine sprouter. Modified from Wainwright et al. (2020; Figure 1A).

upper left panel). Plots moved between these basins during the first monitoring interval, which included the 2000 wildfire. A second fire in 2007 was followed by an increase in shrub relative abundance (*Si*), due to a combination of shrub recovery and a decline in herbaceous cover.

The grass-forb group showed no clear separation in S-I space between pre- and post-fire periods (Figure 2, upper right panel). Observations were instead organized along a gradient of invasion. This group was relatively uninvaded before the fires but became more invaded over time. The 2000 fire provided an opportunity for invasive species to gain a foothold, though the 2007 fire did not lead to further invasion (perhaps due to extensive efforts to control invasives). The relative cover of several shrub species increased in some plots in this group.

Figure 2. Plot positions in S-I space for each community group in all years (note differences in axis ranges for each group). Fill colors demarcate the year of monitoring: white = initial positions in 1994; gray = years immediately following the 2000 wildfire (2001–2004); black = years following the 2007 wildfire (2009 and 2010). Contour lines indicate plot × year density within the S-I space, as obtained through 2D kernel density estimation. Modified from Wainwright et al. (2020; Figure 2).

In the pristine sprouter group, shrub dominance remained relatively stable or was slightly reduced during the first period (1994-2001) though invasive dominance increased markedly (Figure 2, lower right panel). There was no clear separation into basins.

The invaded sprouter group changed the least from initial to final monitoring but experienced substantial interim changes in invasive dominance (Figure 2, lower left panel). Two separate basins of attraction emerged that differed in *Si*, though patterns with respect to *Ii* were consistent between the two basins.

Discussion

The approach demonstrated here provides managers with methods to track community change and identify communities at risk of sustained state transitions. The methodologies developed here provide a straightforward way to track ecosystem change as evidenced by changes in dominant plant functional types. Defining plant communities based on plant functional types facilitates the search for patterns across sites and could help us identify broad principles to guide

ecological restoration. S-I space provides a simple bivariate image that can illustrate differences among communities and changes over time.

Locating plot-years within S-I space is numerically much simpler than the commonly used ordination approaches. Ordinations are computationally intensive and can be difficult to interpret. Furthermore, ordinations cannot be easily updated – incorporating new data into an ordination can alter the positions of previous observations relative to one another. In contrast, the location of a plot-year in S-I space is unaffected by the locations of other plot-years. Plot-years can be compared to one another, but managers could also identify other reference conditions depending on monitoring program goals. For example, they could identify those plots with $Ii > 0.5$ if they wanted to prioritize invasive control in areas where invasive species account for more than half of the herbaceous cover.

If adopted, our approach could increase efficiency of field data collection because it would not be necessary to identify all plant species. To calculate Si, observers would simply have to estimate the covers of shrubs and of herbaceous species. To calculate Ii, observers could estimate the combined cover of key non-native species and that of all other species.

Finally, we note that these approaches are flexible and could be adapted to other ecosystems. Managers could draw on their knowledge of other ecosystems to identify the key plant functional traits with which to characterize communities. They could also replace our Si and Ii indices with indices that reflect the key functional attributes of those systems, while retaining the ability to graphically depict community changes in a bivariate space.

Evaluating Controls on Ecosystem Resilience

Note: this section draws extensively on Wainwright et al. (2020).

Analytical Methods

A key aspect of vegetation dynamics is understanding how the vegetation responds to disturbances. If a community is resilient, it can maintain its structure and function following changes in the disturbance regime (SER 2004). Resilience can be assessed using two indicators, resistance and stability. Resistance is the extent to which a community retains its structure and function, while stability is the ability of a community to maintain its successional trajectory. We quantified resistance and stability as follows:

- *Resistance*: A more resistant community will change less over time than a less resistant community. Specifically, we expressed resistance as the distance between the position of a community at the start and end of a time interval. This distance diminishes as resistance increases. We multiplied these values by -1 so that less negative values indicate higher resistance.

- *Stability*: A more stable community will have less fluctuation over time. We expressed this as the average distance a community moves across consecutive monitoring periods. We multiplied average distances by -1 so that less negative values indicate higher stability.

If a community has only been monitored twice, its resistance and stability are equivalent.

We tested these concepts using the Wilderman (DW) plots, with vegetation data categorized by plant functional types and expressed in S-I space (see previous section). We calculated resistance and stability based on the Euclidean distances among plot-years, using data from the entire monitoring period (1994-2010).

We tested whether resistance and stability varied among community groups and whether they were affected by elevation, fire history, and/or post-fire restoration. Elevation is highly correlated with soil type, temperature and precipitation at our site. Fire history was the number of times a plot was within a fire perimeter between 1994 and 2010, and ranged from one to three. Post-fire restoration was expressed as a binary variable indicating whether a plot had been subject to one or more restoration treatments. We fit general linear models of these terms and their interactions, and then used stepwise regression with the Bayesian information criterion to select final models that balanced complexity with explanatory power.

Finally, we examined whether temporal patterns in resistance and stability differed among community groups. To do so, we calculated resistance and stability values between 1994 and each subsequent monitoring date (1994-2001, 1994-2002, etc.). We used linear mixed models to test the effect of time interval (number of years since 1994), community group, and their interaction. Plot identity was included as a random effect.

Results

Resistance and stability over the entire monitoring period (1994-2010) were positively correlated (Figure 3A). Resistance was best explained by community group (Figure 3B). The obligate seeder group was significantly less resistant than all other groups. Stability was best explained by both community group and elevation (Figure 3C). The obligate seeder group was significantly less stable than all other groups, and stability also increased with elevation.

Patterns of resistance varied among community groups and with length of the temporal interval (Figure 4). Resistance was much lower in the obligate-seeder group than in the other groups, and changed minimally over time. In comparison, resistance was strongly increasing in the invaded sprouter group and high but declining in the pristine sprouter group. The pristine sprouter group also had noticeably less inter-plot variation in resistance than was evident for other groups.

Patterns of stability also varied among community groups and over time (Figure 4). Stability increased over time in the obligate seeder group, though it appeared to level off after the first few intervals. Other groups showed little variation in stability over time.
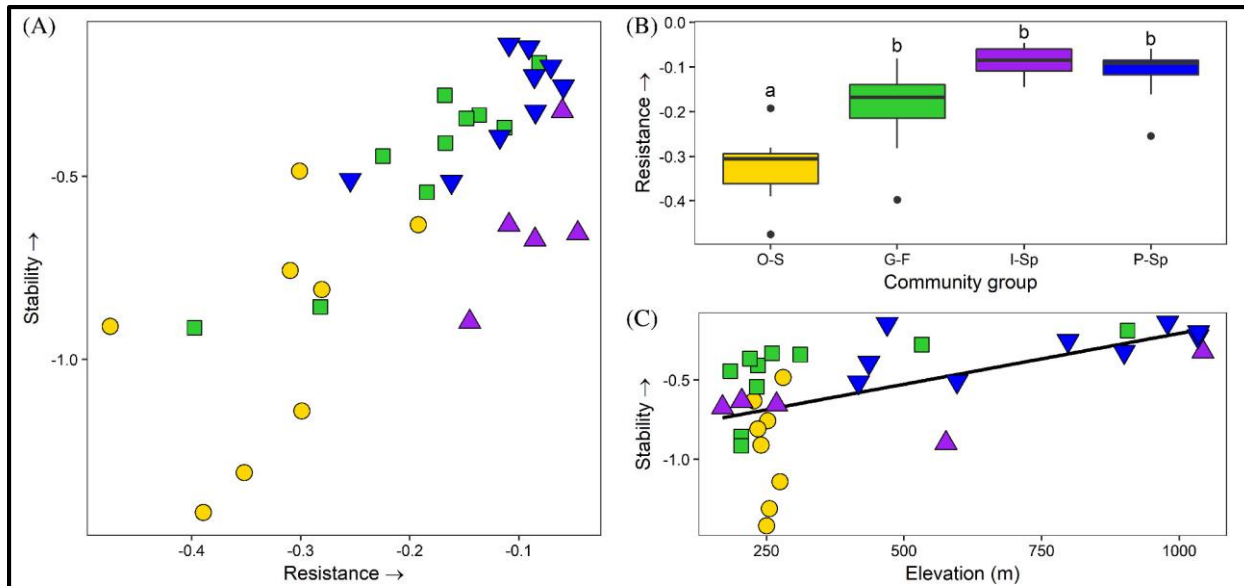
Figure 3. Relationship between stability and resistance from 1994 to 2010, and key variables explaining how they differ among plots. (A) Relationship between stability and resistance for each plot (n = 32). See text for definitions of resistance and stability. (B) Resistance differed significantly among community groups. Lowercase letters denote significant differences between groups. (C) Stability varied among community groups and with elevation. Colors and shapes differentiate the four community groups: gold circle = obligate seeder (O-S); green square = grass-forb (G-F); purple triangle = invaded sprouter (I-Sp); blue inverted triangle = pristine sprouter (P-Sp). Modified from Wainwright et al. (2020; Figure 3).
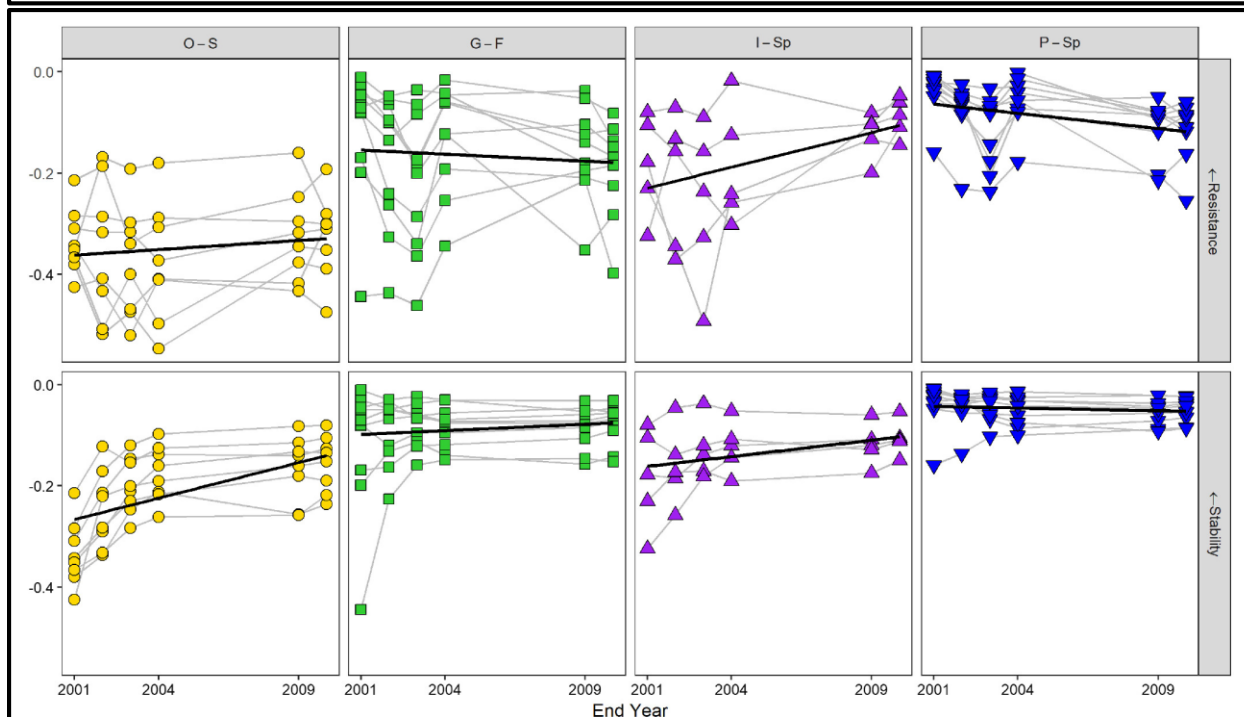
Figure 4. Plot resistance and stability for each community group over time relative to 1994 (x-axis: end year of the interval). See text for definitions of resistance and stability. Note that resistance and stability are equivalent in 2001, at the end of the first monitoring interval. Temporal patterns differed among community groups for both resistance and stability. Symbol color and shape as in Figure 3. O-S = obligate seeder; G-F = grass-forb; I-Sp = invaded sprouter; P-Sp = pristine sprouter. Modified from Wainwright et al. (2020; Figure 4).

Discussion

The approach demonstrated here provides managers with methods to quantify resilience in relation to disturbance, and to begin distinguishing aspects of resilience.

Community groups were identified based on plant functional types at the start of the monitoring period (1994), and these identities continued to determine responses to disturbance over the next 16 years (until 2010). In particular, we highlight the importance of shrub regenerative traits (obligate seeder vs. resprouter) and origin (native vs. invasive). For example, the obligate seeder group had lower resistance than all other groups because the shrubs that dominated in 1994 were unable to re-establish after fire, whereas the invaded sprouter group had high resistance because the shrubs could resprout and invasive species were already present in 1994.

Resilience can be characterized as 'helpful' or 'unhelpful' depending on whether communities return to a desired state or are trapped in an undesired state (Standish et al. 2014). The pristine sprouter group provides an example of helpful resilience, as plots in this group rapidly recovered after fire. In contrast, the obligate seeder group provides an example of unhelpful resilience, as its community composition changed dramatically following the 2000 fire but changed less so in subsequent years. Despite restoration efforts, the plots in this group have transitioned to a degraded state from which they will not easily recover.

Stability increased with elevation, suggesting that low-elevation areas are more vulnerable to disturbance. Fire history and restoration were not identified as predictors of resistance or stability. We think this likely relates to the fact that these factors are somewhat correlated with community group and elevation. In addition, assessments of these factors would be more powerful if the sampled plots spanned a wider range of fire histories and restoration practices.

As quantified here, resistance and stability can be calculated over any time interval of interest, and thus can provide insight into the rate at which ecosystems recover from disturbance. Communities do not have to be monitored every year, though comparisons of stability among communities will only be equitable if the communities were monitored in the same years. Finally, we calculated resistance and stability within the S-I space, but the method described here could be applied to any distance-based representation of community dynamics. For example, in the Supplementary Material of Wainwright et al. (2020), we calculated resistance and stability from the locations of plot-years in a non-metric multidimensional scaling (NMDS) ordination.

Long-term Successional Trajectories in Relation to Fire and Restoration

Note: this section draws extensively on unpublished work by Power et al.

Analytical Methods

We remeasured many of the permanent plots in 2017. Our objective here was to update and build upon previous work (Davies et al. 2012) which had investigated changes through 2009. Specifically, we sought to understand how the long-term trajectories of plant communities were affected by repeated fires and by restoration efforts. We drew on a recent exploration of trajectory analysis (De Cáceres et al. 2019) that proposed measures of trajectory length and directionality. These measures are helpful in determining the extent to which change is directional. For example, they can help identify whether repeated fires have a gradual or idiosyncratic effect on a community's trajectory (*sensu* Matthews et al. 2013). We also used the concepts of resistance and stability as explained in the previous section.

We focused on BRMaP and SIT plots measured in 1992 (SIT only), 1996 (BRMaP only), 2002, 2009, and 2017. The two datasets have different starting points because they began in different years, but for analytical purposes we treated these as a single time point (i.e., 1992/1996). In total, 37 plots met the criteria of having been measured in these four years.

Using data from the first measurement (1992/1996), we classified the plots into community groups based on their relative species abundances. Data were Wisconsin standardized and expressed as a Bray-Curtis dissimilarity matrix, and groups were identified through a hierarchical cluster analysis with Ward's clustering criterion.

Data were compiled in a plot-year × species matrix, received the same adjustments as for cluster analysis above, and were then subject to non-metric multidimensional scaling (NMDS). We used a 3-dimensional solution (stress = 17.54). This provided a low-dimension representation of the patterns among plot-years: compositional dissimilarity increases with distance in this ordination space.

For each plot, the NMDS ordination includes coordinates representing its position at each of the four monitoring events. Considering these events in temporal order, there are therefore three consecutive segments (1992/1996 to 2002, 2002 to 2009, and 2009 to 2017). Each segment's length was calculated as the distance between the coordinates of the beginning and ending monitoring events, and these lengths were summed to yield the plot's trajectory. Trajectory lengths were divided by interval length so that they are reported on an annual basis; this accounts for the different starting dates of the BRMaP and SIT plots. To understand whether the trajectory represented directional change over time, we determined each plot's directionality as the sum of the angles between consecutive monitoring events. Directionality was scaled so that it could range from 0 (no directionality) to 1 (a straight line). In addition, we calculated resistance and stability as described in the previous section. We used one-way ANOVA to test for differences

among community groups with respect to each response variable (annualized trajectory length, directionality, resistance, stability).

One of our objectives was to understand the effects of fire and restoration efforts on successional trajectories. The effect of any action is a function of its intensity (more intensity = stronger effect) and how long ago it occurred (an event that occurred longer = weaker). We defined intensity as the number of events, and combined these two elements into indices defined as:

$$\text{Fire Index} = \frac{\text{cumulative number of fires to date}}{\text{years since last fire}}$$

$$\text{Restoration Index} = \frac{\text{cumulative number of restoration efforts to date}}{\text{years since last restoration effort}}$$

These indices were calculated for each plot at each monitoring event. Values were normalized to range between 0 and 1, with higher values indicating a potentially greater impact by fire or restoration.

Weather patterns could also influence successional trajectories. Since most plant growth begins in early spring in this system, we focused on winter precipitation patterns. We used winter (October to March) precipitation data to calculate the winter precipitation anomaly:

$$\text{Winter Precipitation Anomaly} = \frac{\text{mean winter precipitation in last three years}}{\text{normal winter precipitation (1987-2017)}} - 1$$

Positive anomaly values indicate above-average precipitation, and negative values indicate below-average precipitation.

Each potential explanatory variable (fire index, restoration index, winter precipitation anomaly) was fitted as a non-linear surface to the full time series NMDS ordination using general additive models with thinplate splines. The mean position of each community group at each monitoring event was then overlaid onto these surfaces.

Results

In 1992/1996, the plots were classified into five different community groups: Big Sage Shrubland, Leguminous Shrubland, Sandberg Grassland, Invaded Grassland, and Invaded Shrubland. As suggested by their names, these community groups largely reflect differences in the relative abundance of shrubs and grasses, and in the extent of invasion by *B. tectorum*. Dynamics of these functional groups changed substantially over time in some community groups (Figure 6).

Trajectory length differed among community groups and was significantly larger for the Big Sage Shrubland and Invaded Shrubland than for other community groups (Figure 5a). Both communities experienced a dramatic decline in shrubs, particularly the obligate seeder *A. tridentata*, between 1992/1996 and 2002 (Figure 6c). Space left by shrubs was initially colonized by forbs as evidenced by their *ca.* 3-fold increase in abundance. By 2017, however, forb abundance had declined to 1992/1996 levels and *B. tectorum* had surged to > 25% cover (Figure 6b).

Directionality also differed among community groups (Figure 5b). The Leguminous Shrubland exhibited the most directionality; its trajectory followed a consistent

Figure 5. Differences in community trajectory and resilience properties among communities. Community trajectories were expressed as (a) annualized trajectory length and (b) directionality (0 = undirected; 1 = straight). Resilience was expressed as (c) resistance and (d) stability. See text for details of how each metric was calculated. Boxes correspond to the interquartile range (IQR; 25th to 75th percentile), whiskers extend out 1.5x IQR, and values beyond the whiskers are shown as points. Within the boxes, thick horizontal lines indicate medians and diamonds indicate means. Within each panel, lowercase letters identify significant differences among communities (P < 0.05). BSS = Big Sage Shrubland; LS = Leguminous Shrubland; SG = Sandberg Grassland; IG = Invaded Grassland; IS = Invaded Shrubland.

direction within the NMDS space. Comparisons of functional types indicated that this community group showed little variation in grass/forb abundance but rather a gradual decline in the abundance of resprouting shrubs (Fig. 6c). In contrast, the Big Sage Shrubland and Invaded Shrubland showed the least directionality. Comparisons of functional types indicated much more variation over time in these community groups.

Resilience metrics indicated different patterns among community groups. Resistance did not differ among community groups (Figure 5c), but stability was significantly lower in the Big Sage Shrubland and the Invaded Shrubland than in the others (Figure 5d).

Fire index was significantly related to the NMDS axes (Figure 7, left column); locations of plot-years in the 3-dimensional ordination space explained 47% of the variation in fire index. While all communities were affected by fire, the Big Sage Shrubland and Invaded Shrubland
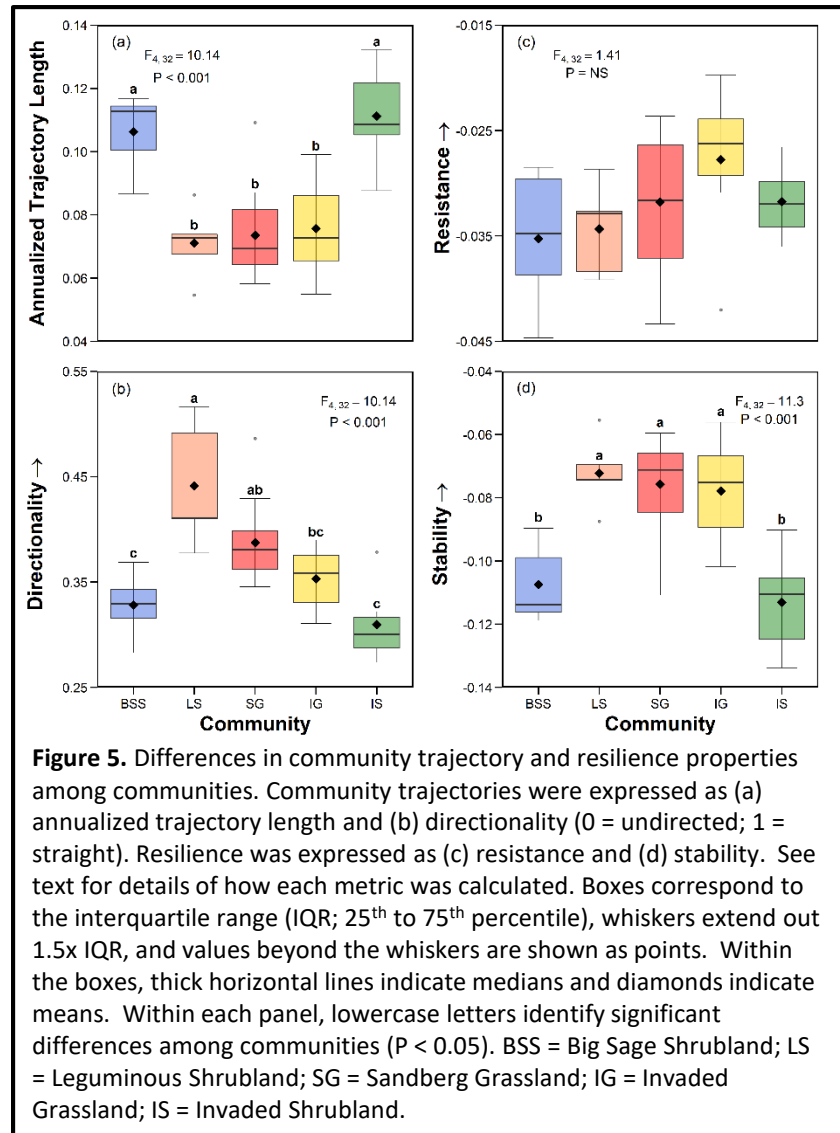
communities were associated with the lowest fire indices and their trajectories did not show a strong relationship with fire index. In contrast, the trajectory of the Leguminous Shrubland was positively related to fire index. The Sandberg Grassland did not vary with fire index until the last interval. The trajectory of the Invaded Grassland did not directly relate to fire index.

The locations of plot-years in the 3-dimensional ordination space explained 39% of the variation in restoration index (Figure 7, center column). Trajectories of the Big Sage Shrubland and Invaded Shrubland followed changes in the restoration index, increasing before 2009 and decreasing dramatically between 2009 and 2017. The Leguminous Shrubland and Sandberg Grassland were not affected by restoration; their trajectories largely followed isoclines of the restoration index. The trajectory of the Invaded Grassland did not directly relate to restoration index.

Although not statistically significant, the locations of plot-years in the 3-dimensional ordination space explained 32% of the variation in winter precipitation anomaly (Figure 7, right column). The anomaly varied among monitoring events, shifting from slightly above average (0.01) in 1992/1996 to below average (-0.09) in 2002. The trajectory of the Invaded Shrubland reflected this decline; those of other communities did not.

Discussion

Community groups exhibited very different successional trajectories. The trajectory of the Leguminous Shrubland was linear, reflecting a gradual rise in the prevalence of forbs and a decline in resprouting shrubs. The trajectory of the Sandberg Grassland was somewhat linear but exhibited little change until the last interval. The Invaded Grassland did not have an apparent pattern to its trajectory.

The Big Sage Shrubland and the Invaded Shrubland both changed substantially during the study period, but by 2017 were near where they began in 1992/1996. While this might appear to indicate stability, these communities had much lower stability than all others. The 2000 fire removed *A. tridentata*, a fire-sensitive obligate seeder shrub. Forbs dominated the vegetation in 2002 and 2009. *B. tectorum* had particularly low abundance in 2009 but in 2017 had about the same levels as in 1992/1996. Although the nearly U-shaped trajectories of these community groups suggest a degree of resilience to frequent fires (up to 4 fires in 21 years), the ability of *B. tectorum* to remain present through restoration efforts (herbicide treatments) and to proliferate following their discontinuation (2009) implies that this resilience may be unhelpful (*sensu* Standish et al. 2014).

In contrast, the Leguminous Shrubland appears to have helpful resilience with respect to frequent fires, as evidenced by its relatively short trajectory and high stability. This is likely because the community contains resprouting shrubs which can recover more rapidly and consistently following fire. Worryingly, however, the repeated fires have gradually reduced resprouting shrub abundances, suggesting that their resilience may change if the current fire regime continues.

One limitation of trajectory analysis is that it treats all taxa equivalently. *A. tridentata*, the key obligate seeder shrub in this system, is a critical habitat component and its loss from the Big Sage Shrubland and Invaded Shrubland following the 2000 fire has necessarily altered the utility of this landscape for sage grouse and other organisms. Moreover, the failure of *A. tridentata* to re-establish afterwards indicates that both communities have shifted to an alternative state in which the dominant physiognomy is invasive annual grasses and forbs, and not perennial obligate seeder shrubs.

Compared to the shrubland communities, the grassland community groups appear much more stable and resilient. These communities are dominated by resprouting perennial grasses such as *Poa secunda* and shrubs such as *Grayia spinosa*, and showed little change over the monitoring period, implying a degree of resilience to repeated fires.

The future of the sagebrush steppe includes frequent fire and increasing prevalence of invasive species. This analysis indicates that the fate of plant communities depends on their functional composition (obligate seeder versus resprouter shrubs; shrubs versus grass/forb). Maintenance of obligate seeder shrub communities, for example, will require long-term restoration initiatives that exclude or greatly limit the occurrence of fire.
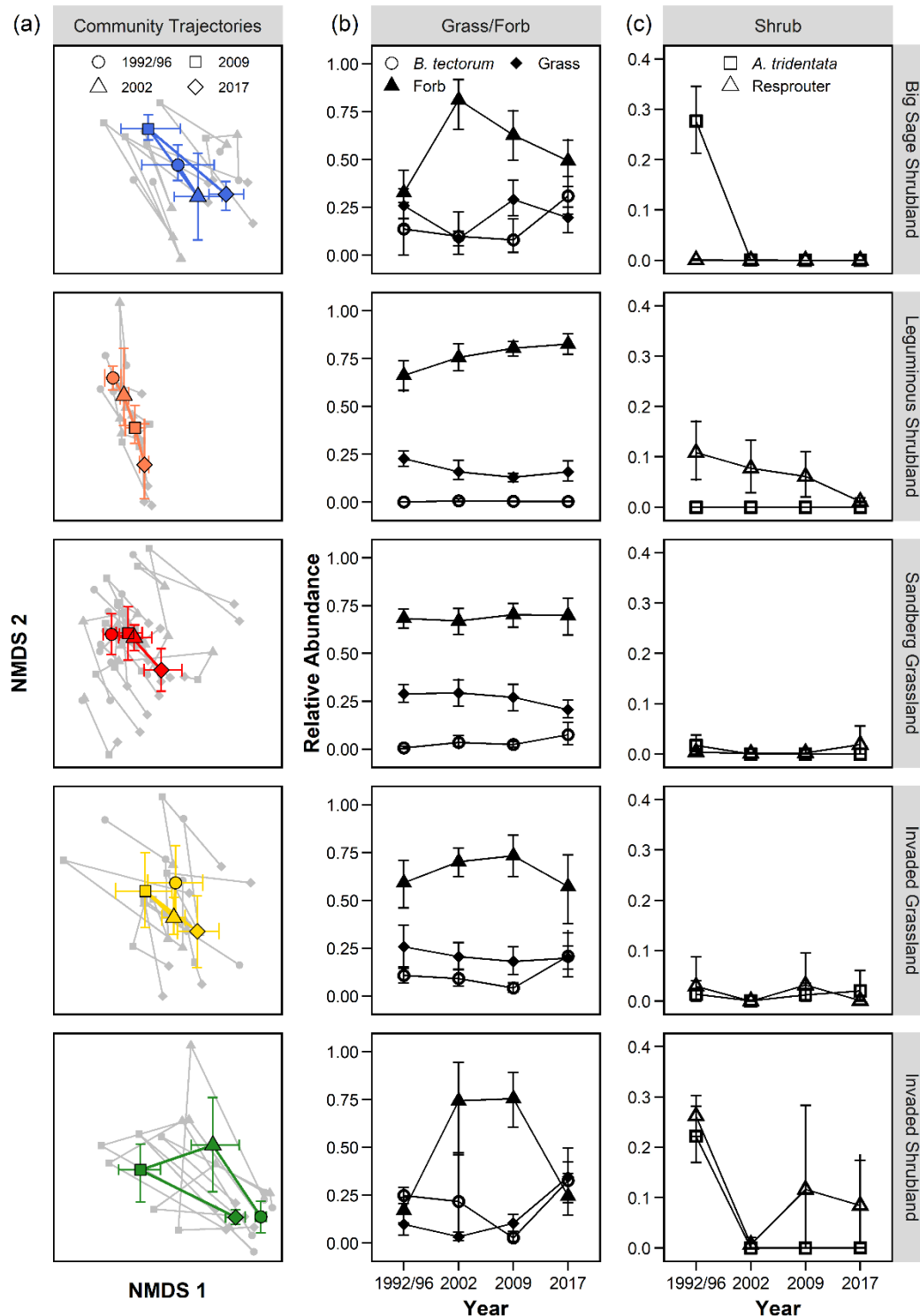
Figure 6. (a) Community trajectory pathways spanning 25 years (1992/1996 to 2002 to 2009 to 2017) for five plant communities. Grey points represent a plot's position in a year, and lines connect years in chronological order. Colored points indicate the average across all plots for each year. Plots are drawn in the 2-dimensional space defined by a NMDS ordination of all plot-years, and span the same space in all 5 panels. (b,c) Changes in mean relative abundance of functional groups and specific species over time. Whiskers represent bootstrapped 95% confidence intervals.

Figure 7. Relationships between community trajectories and fire, restoration, and winter precipitation from 1992/1996 to 2017. Points indicate the mean position of each community group in each year, and are connected in chronological order. Mapped across the ordination are surfaces (isoclines) of predicted values of the fire index (left), restoration index (center), and winter precipitation anomaly (right). See text for details of how the indices and anomaly are calculated. Numbers on the isoclines indicate index values (range 0-1) and winter precipitation anomalies (negative = below average; positive = above average).

Quantifying How Drivers of Vegetation Dynamics Vary with Temporal Scale

Note: this section draws extensively on unpublished work by Wainwright et al.

Analytical Methods

Ecological communities respond to drivers that act over widely varying temporal scales. For example, seasonal weather patterns can alter community structure from one year to the next, whereas soils, long-term climate trends, and chronic disturbances can alter communities over long time scales. We sought to gauge the relative importance of disturbance, restoration, abiotic, and biotic drivers of change across multiple temporal scales in the sagebrush steppe.

We examined data from the LCTA plots on the Yakima Training Center (YTC). These plots were established in 1989, monitored through 2004, and re-monitored in 2017 as part of this project. We focused on plots classified within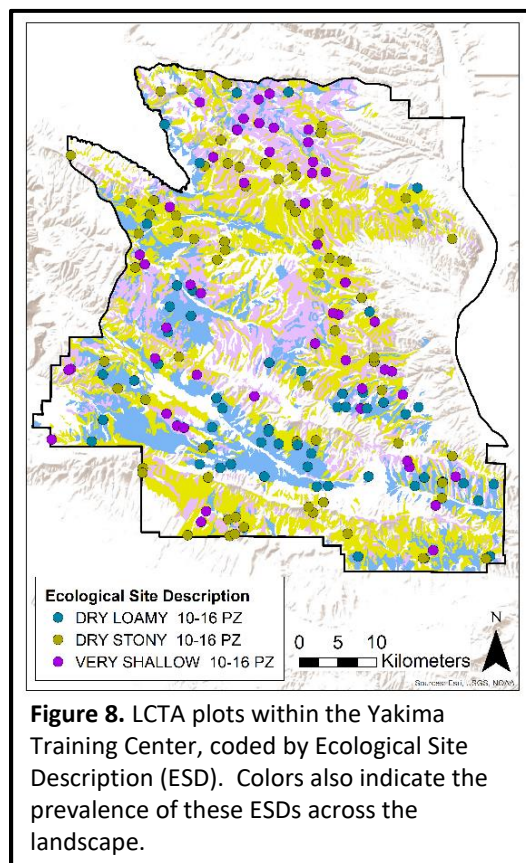 three ESDs with widespread spatial distributions across YTC: "Dry Stony 10-16 PZ" (hereafter "Dry Stony"; 71 plots), "Dry Loamy 10-16 PZ" ("Dry Loamy"; 53 plots), and "Very Shallow 10-16 PZ" ("Very Shallow"; 51 plots). Plot locations are shown in Figure 8.

Each plot was monitored in multiple years between 1991 and 2017, for a total of 1128 unique plot-year combinations (476 Dry Stony, 328 Dry Loamy, 324 Very Shallow). We expressed our response and explanatory variables for each plot across time intervals ranging from one to 26 years, excluding intervals with low replication ($n < 10$). Our final dataset included 3006 of the possible 3121 plot-year-interval combinations. For clarity, we tracked separately those intervals where the final measurement was historical (2004 or earlier) or in 2017.

Figure 8. LCTA plots within the Yakima Training Center, coded by Ecological Site Description (ESD). Colors also indicate the prevalence of these ESDs across the landscape.

We gathered 12 explanatory variables (potential drivers) spanning three categories (biotic, abiotic, disturbance). Some drivers are constant over time whereas others vary among intervals. The explanatory variables are defined in Table 3. Community groups were determined by applying hierarchical cluster analysis to the plant community data within each ESD. Each ESD contained several broad but distinct plant community groups. The Dry Stony ESD contained four community groups: dwarf shrub-exotic, big sagebrush-bunchgrass, big sagebrush-exotic, and big sagebrush-exotic-forb. The Dry Loamy ESD contained three community groups:

bunchgrass-forb, bunchgrass-exotic, and exotic. The Very Shallow ESD contained two community groups: dwarf shrub, and big sagebrush-exotic.

Table 3. Explanatory variables (potential drivers).

Name	Category	Description	Note
Community Group	Biotic	Community group within ESD.	At start of focal interval
B. tectorum	Biotic		Relative cover at start of focal interval
HLI	Abiotic	Heat Load Index; Calculated using aspect, slope, and latitude	Constant over time
Elevation	Abiotic		Constant over time
Soil depth	Abiotic		Constant over time
Precipitation	Abiotic	Water year precipitation	Averaged over all years in focal interval
GDD	Abiotic	Growing Degree Days	Averaged over all years in focal interval
TA usage	Disturbance	Military Training Area usage level: Low, Low-Moderate, Moderate, Moderate-High, High	Constant
Road	Disturbance	Distance to nearest road	Constant
Grazing	Disturbance	Number of years in which grazing was recorded at plot	Summed over all years in focal interval
Fire	Disturbance	Number of years in which fire was recorded at plot	Summed over all years in focal interval
Restoration	Disturbance	Whether maintenance activities were documented during interval	Binary (Yes/No)

We selected four response variables that reflect aspects of vegetation dynamics:
- Multivariate compositional change (Bray-Curtis dissimilarity)
- Change in species richness
- Change in *B. tectorum* cover
- Change in native shrub cover

Before calculating these variables, necessary taxonomic adjustments were made so that data were comparable among years and field crews. Each response variable was calculated between the initial and final year of the interval.

Analysis was conducted in three phases. We began by assessing whether interval length affected the response, and whether this effect varied among ESDs. To do so, we ran a linear model fitting a response variable as a function of ESD, interval length, and their interaction. Second, we fit each potential explanatory variable to each response variable, analysing each interval within each ESD separately. Third, we applied stepwise regression to the full set of explanatory variables and two-way interactions, again analysing each interval within each ESD separately. For these regressions, we used Bayesian Information Criterion (BIC) to select models that balanced complexity with explanatory power.

Results

Note: For clarity and conciseness we focus here only on change in species richness, and describe a subset of the relationships that we modelled. Change in richness tended to increase with

interval length. Here, we distinguish among short (1-5 years), intermediate (6-12 years), and long (>12 years) intervals.

When tested individually, most explanatory variables were significantly associated with change in richness in some intervals (Figure 9, Figure 10). However, a number of these variables were not retained in the parsimonious models identified through stepwise regressions. Parsimonious models often included abiotic variables and disturbance variables, but rarely included biotic variables (Figure 11).

At short intervals, change in richness was positively related to water-year precipitation and GDD, and these effects were consistent across the three ESDs. Fire had a negative effect on change in richness, but only in the Dry Loamy ESD.

At intermediate intervals, HLI was often negatively related to change in richness in the Dry Loamy and Dry Stony ESDs. In the Very Shallow ESD, HLI was not retained but water-year precipitation continued to be positively related to change in richness. TA usage was significantly related to change in richness in the Dry Loamy ESD, while grazing was related to it in the Dry Stony ESD. The effect of grazing was generally positive, though it was strongly negative at seven-year intervals. Maintenance was positively related to richness in the Dry Stony ESD at nine-year intervals. Fire and TA usage were negatively related to richness in the Very Shallow ESD at six-year intervals.

At long intervals (Dry Stony ESD only), change in richness was negatively related to HLI and positively related to elevation, and positively related to distance to road.

Discussion

The model selection process identified several explanatory variables that are consistently related to change in richness, and also demonstrated that these patterns change with interval length. For example, water-year precipitation had a positive effect in most short intervals but few intermediate intervals, and was not significant in any long intervals.

ESDs identify regions with similar climate and soils, yet our results indicate strong abiotic controls on change in richness within ESDs. All abiotic variables were retained in at least one model. Dynamic variables such as water-year precipitation and GDD were strong at short intervals, likely because of how they are calculated – averaging across all years within the interval; another approach, not explored here, would be to weight recent years more strongly than previous years. HLI and elevation are temporally constant, so it is unclear why they would be more important at intermediate or long intervals than at short intervals. Even when assessed individually via simple linear regression (Figure 9), these variables have no relationship with change in richness at short intervals. Soil depth was the weakest of the abiotic variables tested – it was only retained in one model and was not statistically significant in that model. This is somewhat surprising as soil depth is one of the factors that distinguish ESDs, but might indicate

that soil depth is more important at larger spatial scales, and/or that there is little variation in soil depth within ESDs.

The biotic variables – initial community group and initial *B. tectorum* abundance – were not significant drivers of change 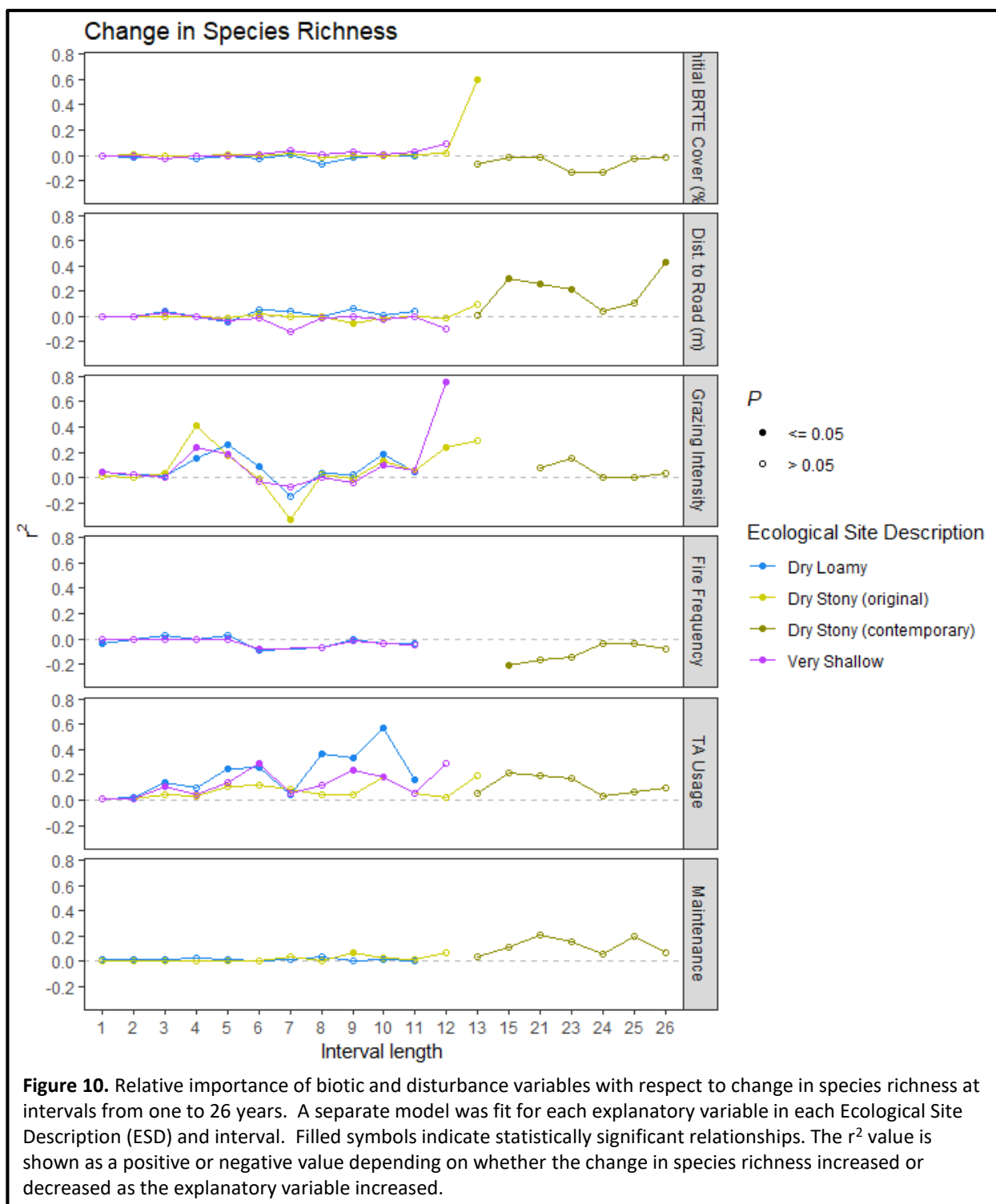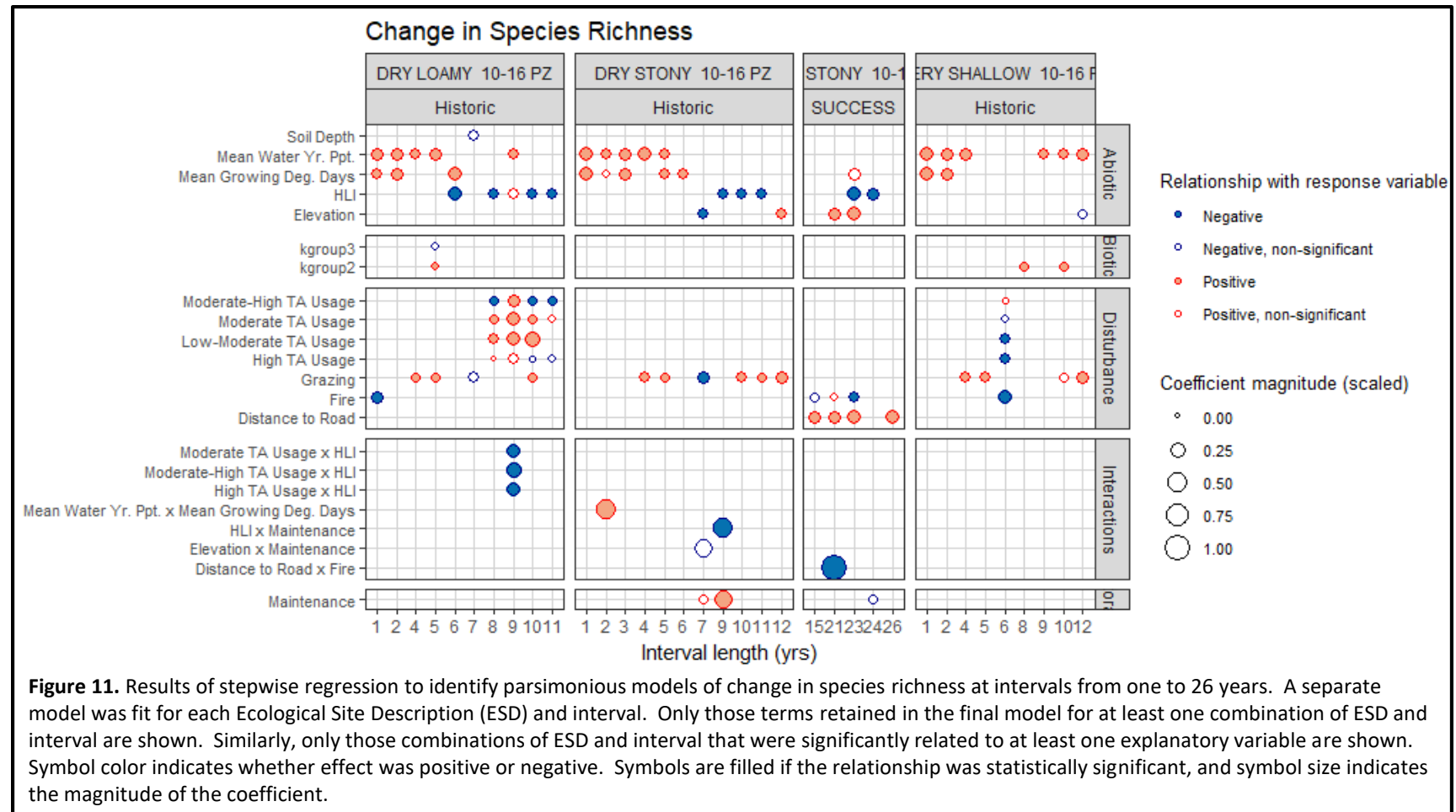in richness. Initial community group was only retained in a few models, and initial *B. tectorum* abundance was not retained in any models.

Overall, disturbance-related variables were less important than expected based on previous research (e.g., Mitchell et al. 2017). These variables also had some surprising relationships with change in richness. Grazing was retained in various models from 4- to 12-year intervals; it was likely not retained in models for long intervals because livestock grazing ceased in 1995 and so over these intervals enough time has passed that the vegetation no longer shows its influence. TA usage was particularly important in the Dry Loamy ESD, suggesting that perhaps these areas bear the brunt of more training activities, although this doesn't explain why effects were pronounced only over intermediate intervals. Fire was retained in few models but not in the same intervals for different ESDs, perhaps reflecting the fact that there has been relatively little fire on YTC in recent years. Distance to road was not retained in models at short or intermediate intervals but was retained with a positive effect in most models at long intervals. The reasons for this pattern are not clear. Finally, maintenance or restoration activities were only retained as a significant term in one interval in one ESD. This could indicate that there was relatively little variation in the extent to which maintenance activities were implemented or recorded.

This analysis highlights the importance of considering multiple factors that can affect vegetation responses, and considering these factors over multiple timescales. Our results demonstrate how the relative importance of these factors can vary depending on the temporal scale examined. Recent weather conditions are helpful for understanding short-term vegetation dynamics in sagebrush steppe ecosystems at YTC. Over longer timescales, however, edaphic variation and disturbances also need to be taken into account.

Figure 9. Relative importance of abiotic variables with respect to change in species richness at intervals from one to 26 years. A separate model was fit for each explanatory variable in each Ecological Site Description (ESD) and interval. Filled symbols indicate statistically significant relationships. The r^2 value is shown as a positive or negative value depending on whether the change in species richness increased or decreased as the explanatory variable increased.

Figure 10. Relative importance of biotic and disturbance variables with respect to change in species richness at intervals from one to 26 years. A separate model was fit for each explanatory variable in each Ecological Site Description (ESD) and interval. Filled symbols indicate statistically significant relationships. The r^2 value is shown as a positive or negative value depending on whether the change in species richness increased or decreased as the explanatory variable increased.

Figure 11. Results of stepwise regression to identify parsimonious models of change in species richness at intervals from one to 26 years. A separate model was fit for each Ecological Site Description (ESD) and interval. Only those terms retained in the final model for at least one combination of ESD and interval are shown. Similarly, only those combinations of ESD and interval that were significantly related to at least one explanatory variable are shown. Symbol color indicates whether effect was positive or negative. Symbols are filled if the relationship was statistically significant, and symbol size indicates the magnitude of the coefficient.

Conclusions

This project examined the effects of wildfires and other factors on succession and ecosystem dynamics in sagebrush steppe ecosystems. It supports previous work demonstrating that long-term monitoring is necessary to distinguish temporary changes in species composition from permanent changes in ecosystem state (Bakker et al. 2011). By re-measuring permanent plots, we were able to examine much longer time scales – up to 28 years – than would have been feasible in a study of this duration. Extant plot-level descriptors (fire and restoration histories, soils, climate) were verified, updated, and expanded.

Our results highlight the power of quantitative analyses to understand vegetation dynamics. Quantitative indices provide a means to track vegetation dynamics. For example, our shrub index (Si) and invadedness index (Ii) together form a bivariate 'S-I space' that enables changes in community structure to be tracked over time. This approach provides managers with a straightforward way to track ecosystem change as evidenced by changes in dominant plant functional types. Furthermore, S-I space is numerically simple to use, and to update with new data. Ecosystem resilience is an important attribute, and one that is best evaluated through long-term studies. We distinguish two aspects of resilience, resistance and stability. We calculated resistance as the distance between a plot's locations at the start and end of an interval, and stability as the average distance moved across consecutive monitoring periods. These aspects could be calculated based on compositional data or positions in an ordination or, as demonstrated here, locations in S-I space. Trajectory analysis permits consideration of the among and direction of change in plant communities. A unique aspect of permanent plots is that each re-measurement produces a unique set of temporal intervals – responses in the re-measurement year can be compared not just to that in the previous measurement but to those in all prior measurements. Change can be calculated for each interval, and those changes can then be related to explanatory variables to identify those factors that drive changes at different time scales.

Finally, the dataset that was compiled during this study could support valuable future research. These plots continue to experience fire. For example, some of the plots that we re-measured in 2017 had burned in the 2016 Range 12 Fire, but the Arid Lands Ecology Reserve has also experienced fires in 2017 (Silver Dollar Fire), 2018 (Wagon Wheel Fire), and 2019 (Cold Creek Fire). Some plots have burned up to 3 times in the last four years. Fire is a common occurrence in these ecosystems now, and they need to be managed in light of this reality. Understanding the historical vegetation dynamics of these plots would provide context for such management decisions.

Literature Cited

Bagchi et al. 2013. Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe. *J. Appl. Ecol.* 50:1131-1141.

Bakker et al. 2011. *Vegetation impacts of recurring fires on sagebrush ecosystems in Washington: implications for conservation and rehabilitation*. Final report for project 08-1-5-20, JFSP, Boise, ID.

Bestelmeyer et al. 2009. State and transition models for heterogeneous landscapes: a strategy for development and application. *Range. Ecol. Manage.* 62:1-15.

Briske et al. 2008. Recommendations for development of resilience-based state-and-transition models. *Range. Ecol. Manage.* 61:359-367.

Briske et al. 2017. Nonequilibrium ecology and resilience theory. Pages 197-227 in Briske (editor) *Rangeland Systems: Processes, Management and Challenges*. Springer, Cham, Switzerland.

Davies et al. 2012. Trajectories of change in sagebrush-steppe vegetation communities in relation to multiple wildfires. *Ecol. Appl.* 22:1562-1577.

De Cáceres et al. 2019. Trajectory analysis in community ecology. *Ecol. Mon.* 89:e01350.

Dettweiler-Robinson et al. 2013. Outplanting Wyoming big sagebrush following wildfire: stock performance and economics. *Range. Ecol. Manage.* 66:657-666.

Evans & Lih. 2005. *Recovery and rehabilitation of vegetation on the Fitzner-Eberhardt Arid Lands Ecology Reserve, Hanford Reach National Monument, following the 24 Command Fire - Final report: 2001-2004*. The Nature Conservancy, Seattle, WA.

Hajek. 1966. *Soil survey – Hanford project in Benton County Washington*. BNWL-243. Battelle Northwest, Pacific Northwest Laboratory, Richland, WA.

Hitchcock et al. 1955-1969. *Vascular plants of the Pacific Northwest*. Parts 1-5. University of Washington Press, Seattle, WA.

Jones & Kunze. 2003. *Land Condition-Trend Analysis (LCTA) technical report 1989-2002 Yakima Training Center, WA*. CEMML, Colorado State University, Fort Collins, CO.

Kachergis et al. 2012. Differences in plant species composition as evidence of alternate states in the sagebrush steppe. *Range. Ecol. Manage.* 65:486-497.

Knutson et al. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *J. Appl. Ecol.* 51:1414-1424.

Matthews et al. 2013. Disturbance and trajectory of change in a stream fish community over four decades. *Oecologia* **173**:955–969.

McCune & Keon. 2002. Equations for potential annual direct incident radiation and heat load. *J. Veg. Sci.* 13:603–606.

Mitchell et al. 2017. Relative importance of abiotic, biotic, and disturbance drivers of plant community structure in the sagebrush steppe. *Ecol. Appl.* 27:756-768.

Moretti & Legg. 2009. Combining plant and animal traits to assess community functional response to disturbance. *Ecography* 32:299-309.

Noss et al. 1995. *Endangered ecosystems of the United States: a preliminary assessment of loss and degradation*. Biological Report 28. National Biological Service, USDI, Washington, D.C.

Society for Ecological Restoration International Science & Policy Working Group [SER]. 2004. *The SER International primer on ecological restoration*. Society for Ecological Restoration International, Washington, D.C.

Soll et al. 1999. *Biodiversity inventory and analysis of the Hanford site. Final report: 1994–1999*. The Nature Conservancy, Seattle, WA.

Standish et al. 2014. Resilience in ecology: abstraction, distraction, or where the action is? *Biol. Cons.* 177:43–51.

Tazik et al. 1992. U.S. *Army land condition-trend analysis (LCTA) plot inventory field methods*. Technical Report N-92/03. U.S. Army Corps of Engineers Research Laboratory, Champaign, IL.

Wainwright et al. 2020. Methods for tracking sagebrush-steppe community trajectories and quantifying resilience in relation to disturbance and restoration. *Rest. Ecol.* 28:115-126.

Wilderman. 1994. *Plant communities of the Fitzner/Eberhardt arid lands ecology reserve and the north slope of the Hanford site: findings of the 1994 inventory*. The Nature Conservancy of Washington, Seattle, WA.

Appendix A: Contact Information for Key Project Personnel

Principal Investigators
Dr. Jonathan D. Bakker
School of Environmental and Forest Sciences, University of Washington,
Seattle, WA, 98195
E-mail: jbakker@uw.edu, Phone: 206.221.3864

Dr. G. Matt Davies
School of Environment and Natural Resources, Ohio State University,
Columbus, OH, 43210
E-mail: davies.411@osu.edu; Phone: 614-292-3567

Other Key Personnel
Dr. Claire Wainwright
School of Environmental and Forest Sciences, University of Washington,
Seattle, WA, 98195
E-mail: cewain@uw.edu

Dr. Simon Power
School of Environment and Natural Resources, Ohio State University,
Columbus, OH, 43210
E-mail: power.778@osu.edu

Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

Articles in Peer-Reviewed Journals

Published or in press

Wainwright, C.E., G.M. Davies, E. Dettweiler-Robinson, P.W. Dunwiddie, D. Wilderman, and J.D. Bakker. 2020. Methods for tracking sagebrush-steppe community trajectories and quantifying resilience in relation to disturbance and restoration. *Restoration Ecology* 28:115-126. doi:10.1111/rec.13060. [JFSP ID No. 3978]

In preparation

Power, S.C., J.D. Bakker, and G.M. Davies. Long-term successional trajectories in relation to fire and restoration.

Wainwright, C.E., J.D. Bakker, S.C. Power, and G.M. Davies. Divergent short- and long-term successional patterns following repeated wildfire in a sagebrush-steppe ecosystem.

Wainwright, C.E., R.M. Mitchell, and J.D. Bakker. Disturbance, abiotic, and biotic contexts for vegetation dynamics over different temporal scales.

Technical Reports

Two research briefs were planned with the Northwest Fire Science Consortium, but they do not have capacity to do more this fiscal year. They posted our published article (Wainwright et al. 2020) on their website and linked to it in their newsletter.

Conference and Symposium Abstracts

Bakker, J.D. 2018. New approaches for quantifying vegetation dynamics. Netherlands Institute of Ecology, Wageningen, The Netherlands. [JFSP ID No. 8300]

Wainwright, C.E., and J.D. Bakker. 2018. Succession in Columbia Basin sagebrush steppe following wildfire: insights from long-term vegetation monitoring. Fire Continuum conference, Missoula, MT. [JFSP ID No. 8295]

Wainwright, C.E. 2018. Succession and ecosystem dynamics in the sagebrush-steppe. Washington Botanical Symposium, Seattle WA. [JFSP ID No. 8302]

Wainwright, C.E., and J.D. Bakker. 2017. Responses of sagebrush communities to multiple drivers of change. Society for Range Management conference, St. George, UT. [JFSP ID No. 8298]

Wainwright, C.E., and J.D. Bakker. 2017. Monitoring vegetation dynamics: you get what you sample for. Ecological Society of America conference, Portland, OR. [JFSP ID No. 8299]

Poster

Wainwright, C.E., G.M. Davies, and J.D. Bakker. 2017. Succession and ecosystem dynamics in the sagebrush steppe following wildfires. Washington Botanical Symposium, Seattle, WA. [JFSP ID No. 8297]

Other Outreach

Data
Field data collected in 2017 were sent directly to land managers at the Yakima Training Center and the Hanford Reach National Monument. In addition, some of the re-measured plots are located on lands that are not managed by government agencies. Reports about vegetation dynamics (1992-2017) on their property were sent to four landowners.

Website
Wainwright, C.E. 2017. Long-term SUCCESS: Succession and ecosystem dynamics in the
    sagebrush steppe. https://blogs.uw.edu/ecolsage/ [JFSP ID No. 8296]
Project description on Northwest Fire Science Consortium website:
http://www.nwfirescience.org/long-term-success-succession-and-ecosystem-dynamics-
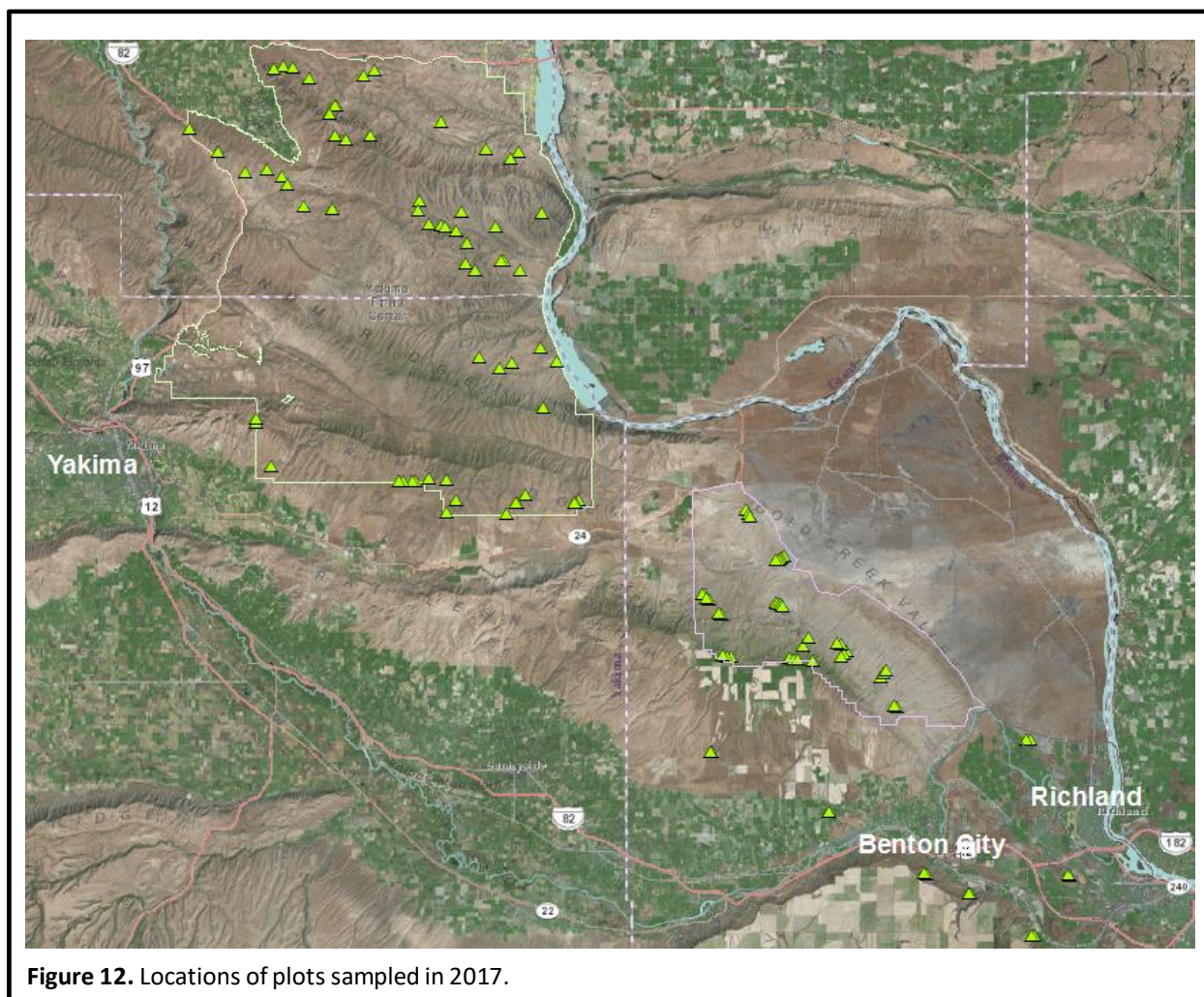   sagebrush-steppe [JFSP ID No. 8301]
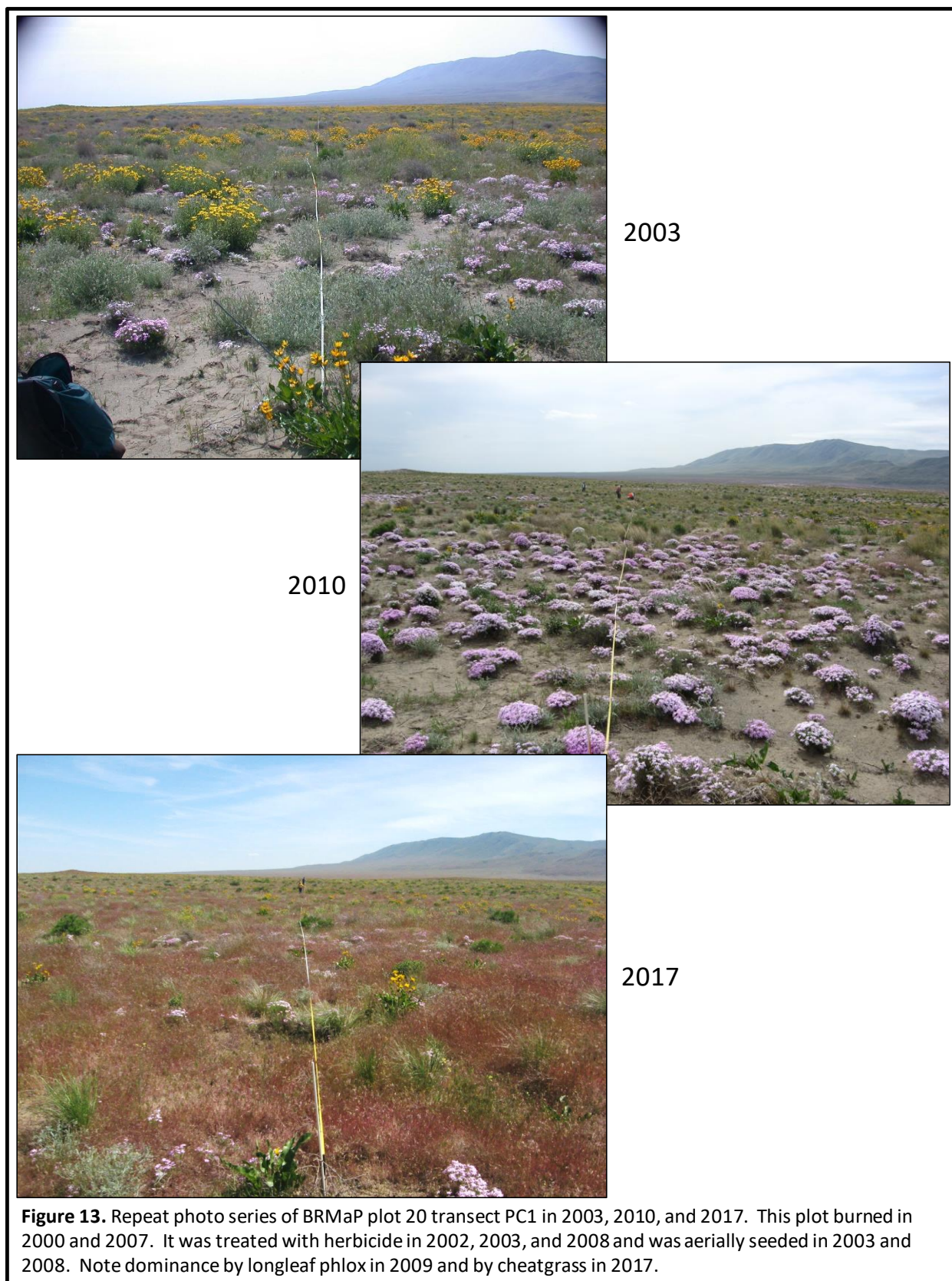
Annual Reports (2016-2018)
Bakker, J.D., G.M. Davies, and C.E. Wainwright. Long-term SUCCESS: SUCCession and
    Ecosystem dynamics in the Sagebrush Steppe following wildfires. Annual report to the
    Joint Fire Science Program for Project 15-1-07-2.

Final Report
Bakker, J.D., G.M. Davies, C.E. Wainwright, and S.C. Power. 2020. Long-term SUCCESS:
    SUCCession and Ecosystem dynamics in the Sagebrush Steppe following wildfires. Final
    report to the Joint Fire Science Program for Project 15-1-07-2.

Appendix C: Additional Images

Figure 12. Locations of plots sampled in 2017.

Figure 13. Repeat photo series of BRMaP plot 20 transect PC1 in 2003, 2010, and 2017. This plot burned in 2000 and 2007. It was treated with herbicide in 2002, 2003, and 2008 and was aerially seeded in 2003 and 2008. Note dominance by longleaf phlox in 2009 and by cheatgrass in 2017.
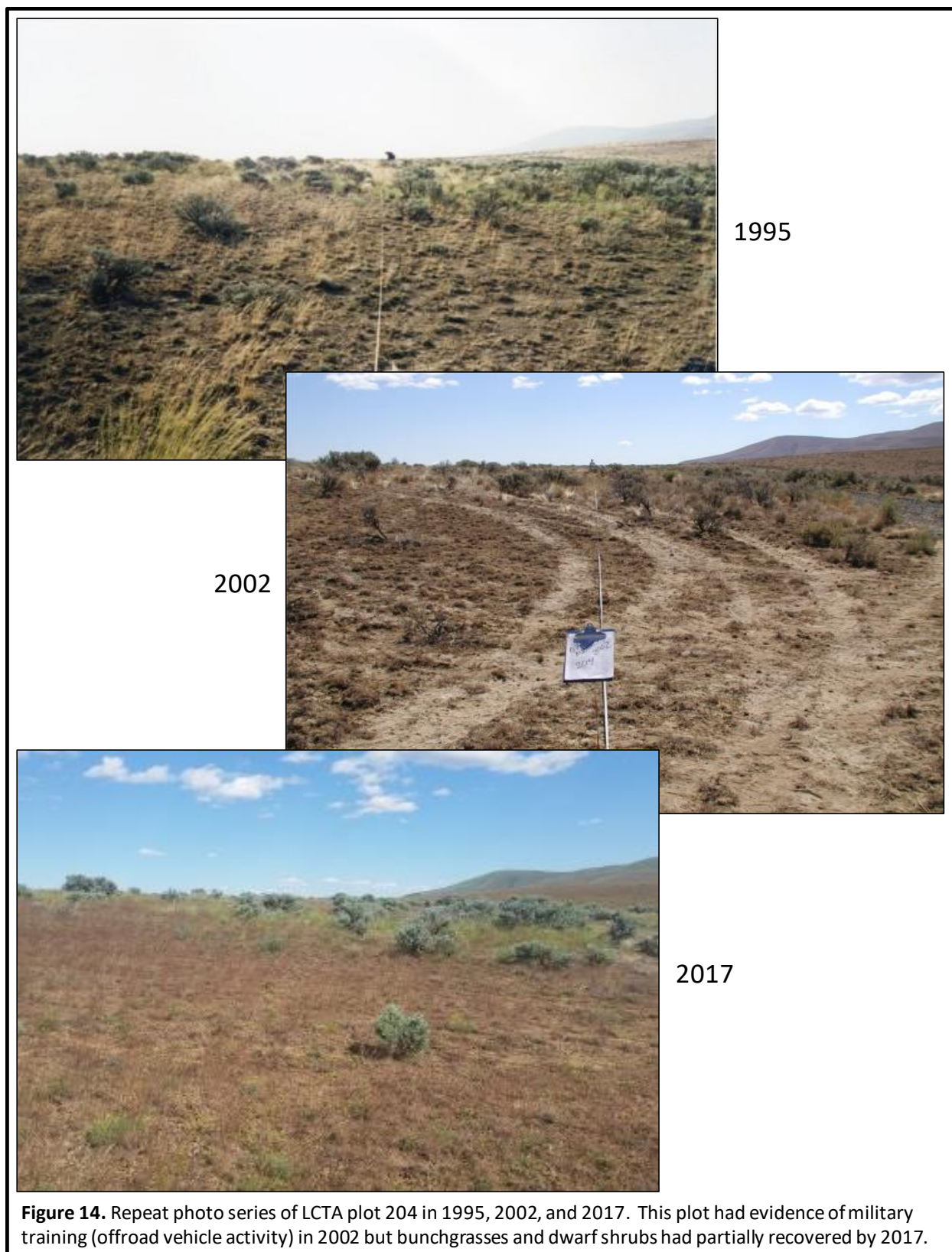
Figure 14. Repeat photo series of LCTA plot 204 in 1995, 2002, and 2017. This plot had evidence of military training (offroad vehicle activity) in 2002 but bunchgrasses and dwarf shrubs had partially recovered by 2017.