



Analysis adapted from text mining quantitatively reveals abrupt and gradual plant-community transitions after fire in sagebrush steppe

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Abstract

Context Plant communities vary both abruptly and gradually over time but differentiating between types of change can be difficult with existing classification and ordination methods. Structural topic modeling (STRUTMO), a text mining analysis, offers a flexible methodology for analyzing both types of temporal trends.

Objectives Our objectives were to (1) identify post-fire dominant sagebrush steppe plant association types and ask how they vary with time at a landscape (multi-fire) scale and (2) ask how often major association changes are apparent at the plot-level scale.

Methods We used STRUTMO and plant species cover collected between 2002–2022 across six large burn areas (1941 plots) in the Great Basin, USA to characterize landscape change in dominant plant association up to 14 years post-fire. In a case study, we assessed frequency of large annual changes ($\geq 10\%$ increase in one association and decrease in another) between associations at the plot-level scale.

Results STRUTMO revealed 10 association types dominated by either perennial bunchgrasses, mixed

perennial or annual grasses and forbs, or exotic annual grasses. Across all study fires, associations dominated by large-statured perennial bunchgrasses increased then stabilized, replacing the Sandberg bluegrass (*Poa secunda*)-dominated association. The cheatgrass (*Bromus tectorum*)-dominant association decreased and then increased. At the plot-level, bidirectional changes among associations occurred in $\sim 75\%$ of observations, and transitions from annual invaded to perennial associations were more common than the reverse.

Conclusions The analysis revealed that associations dominated by some species (i.e. crested wheatgrass, *Agropyron cristatum*, Siberian wheatgrass, *Agropyron frigidum*, or medusahead, *Taeniatherum caput-medusae*) were more stable than associations dominated by others (i.e. Sandberg bluegrass or cheatgrass). Strong threshold-like transitions were not observed at the multi-fire scale, despite frequent ephemeral plot-level changes.

Keywords Post-fire community change · Structural topic modeling · State and transition · Sagebrush steppe

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Introduction

Whether plant communities organize in distinct deterministic states or interspecifically along landscape or temporal gradients has been a central question in

ecology (Gleason 1926; Clements 1936; Shipley and Keddy 1985; Austin 1985, 1986, 2013). To account for these two different conceptual models of vegetation organization, ecologists may utilize either classification or ordination to quantitatively identify unique species assemblages (Kent and Ballard 1988; Kent 2011; Causton 1988). Classification involves binning plant communities into discrete states that are described by dominant species or functional group types, while ordination involves reduction of multi-dimensional community data into lower dimensional space and allowing the gradients to be characterized (Prentice 1977, Kent 2011, e.g. Wainwright et al. 2020). Both approaches have limitations. Classification methods cannot adequately represent gradual spatial or temporal change, but ordination methods may lack interpretability because their output test statistics are dimensionless and not relatable to any measurable unit (Kent and Ballard 1988). Ordination methods can represent how communities vary across abiotic gradients, but they have limitations in quantifying how individual species abundances vary within these communities. Because species composition and relative abundances can affect community stability and propensity towards change (e.g. Tanaka et al. 1994; Collins 2000), developing methods for delineating distinct species assemblages is an important research need for predicting future vegetation outcomes.

In Western North America, there are many potential community types of the widespread sagebrush steppe biome that are created by environmental gradients in space, such as across climates and soils, and in time, such as following disturbance. Sagebrush steppe communities are undergoing pressure or rapid change from their native, diverse perennial condition towards wildfire-prone, exotic annual grasslands, referred to as the exotic annual grass-fire cycle (e.g. Germino et al. 2022). Directing the recovering plant communities towards establishment of native perennials and away from exotic annuals is considered pivotal for avoiding loss of sagebrush steppe (Chambers et al. 2014). The vast areas occupied by sagebrush steppe are thus heavily treated wildlands, with 3.76 million or 7.4% treated at least once since 1940 (Pilliod et al. 2007).

Many of the conceptual models used to understand community change in sagebrush steppe are based on classification methods, including state and transition

models (STMs) that describe discrete plant community types and are used to generalize predictions of community changes in relation to press (e.g. grazing) or pulse (e.g. fire) disturbances (e.g., Hemstrom et al. 2002; Stringham et al. 2003; Ellsworth et al. 2020). Often, transitions from one vegetative state to another are depicted by changes between dominant functional groups (i.e., sagebrush to annual or perennial grassland). STMs may be site-specific based on ecological site descriptions of potential vegetation given soil types (e.g. Ellsworth et al. 2020) or generalized across the biome (e.g. Chambers et al. 2014).

The STM concept relies on the a priori identification of thresholds or discrete “tipping points” that cause plant-community state transitions (Bestelmeyer et al. 2017). Specifically, STMs posit that transitions among vegetation phases are predicted by light and moderate internal and external drivers, such as weather and appropriate grazing practices (Stringham et al. 2003; Chambers et al. 2014). Transitions between two vegetative states occur when the severity and/or frequency of internal or external forces cause a shift in dominant functional group abundances (Bestelmeyer et al. 2003, 2004). Transition rates and states are often derived from expert opinion (Provencher et al. 2016). We suggest that there is a need for additional empirical evidence to support expert-derived states and thresholds, as well as analytical methods which can differentiate between abrupt thresholds and gradual change. Long-term (10 years+) field studies that track whole vegetation community by species over time in the Great Basin sagebrush ecosystem, especially those on managed burned areas, are rare (but see Anderson and Inouye 2001; Bates et al. 2020; Pyke et al. 2022). Of the few long-term community datasets available, reversible and gradual community change was observed in a mostly uninvaded, undisturbed 50,000 Ha region (Anderson and Inouye 2001; Bagchi et al. 2013), while persistent and abrupt change towards exotic annual grasses was observed after fuels treatments if a reduction below 20% perennial bunchgrass threshold was reached (Chambers et al. 2014; Pyke et al. 2022). Neither of these studies are representative of the vast complex, post-fire sagebrush steppe landscapes (megafires) that receive heavy treatment for restoration or rehabilitation across the western United States and thus objective analyses of whether sagebrush-steppe community organization displays discrete or gradual

variation over time and space and evidence for potential thresholds are needed, especially within the context of disturbance (like fire) or management.

To assess the data for evidence of discrete thresholds in post-fire sagebrush-steppe community change, we propose an alternate approach to commonly used classification and ordination methods. Text-mining analyses such as Latent Dirichlet allocation (LDA), have recently emerged as alternative methods for decomposing complex species data into plant community types in a way that preserves interpretability of results and allows for flexibility in analyzing plant community gradients (Valle et al. 2014, 2021; Albuquerque et al. 2019; Hudon et al. 2021). The general concept underlying LDA is that there are a pre-specified number of latent (not directly measurable) community types that exist in different proportions across the landscape (Valle et al. 2014). A key aspect of LDA is use of a multivariate extension of the beta-probability distribution, known as the Dirichlet distribution, to determine the proportion of each species within each latent community and then the proportion of each latent community type at each site (Valle et al. 2014). By allowing multiple community types per site rather than assigning each site to single community type (as with other ordination methods), LDA is superior in accounting for both gradual or abrupt changes over time and space. Thus, the net advantage of LDA is it allows flexibility in identifying whether plant-community dynamics tend towards more distinct structured community states or exist across a more stochastic gradient, without superimposing a prior assumption towards either.

While at least one method of combining regression with LDA in ecological community analyses has been developed (Valle et al. 2021), hybrid LDA-regression methods are rare and are needed to enable LDA as a predictive rather than descriptive method only. “Structural Topic Modeling” (here referred to as “STRUTMO”) is widely used in social science and text analysis to incorporate predictive covariates into LDA (Roberts et al. 2013). In STRUTMO, a “content covariate”, which is a variable that is somewhat analogous to a random effect within mixed effect regression models, allows the species compositions of specific community types to vary based on a grouping factor or continuous variable (Roberts et al. 2013). This resulting flexibility makes STRUTMO suitable for data with repeated measures or studies with

experimental blocking, both common contexts in ecological research. To our knowledge, STRUTMO has never been used for ecological analysis but is a potentially powerful tool for identifying vegetative community structure variation over space and time.

In this paper, we utilize structural topic modeling to describe sagebrush-steppe plant community trajectories after fire in six wildfires that occurred between 2001 and 2015 in the Great Basin, USA. These burn areas were chosen because each had detailed management records available and significant monitoring effort after the first three post-wildfire years (not standard for many agency-managed wildfires) and collectively, they span a wide range of elevations, topographies, and ecotypes. We combine data from different plots monitored in different years across each burn area to analyze generalized landscape-scale (multi-fire) community trends. We then assess micro-scale community trends with data from one fire, the 2015 Soda megafire, where the available monitoring data was substantially more temporally and spatially intensive than the other burned areas (annual repeated monitoring of > 1000 plots for five years).

Our questions included:

1. What are the plant associations in the first 14 years of post-fire community recovery?
2. After fire, do plant associations vary abruptly or gradually over time at a landscape scale (across multiple widespread large burn areas)?
3. In a case study of the Soda wildfire, how often are major abrupt interannual association changes apparent at the plot-level scale and between which associations do changes occur?

Methods

Sites

We utilized post-fire species data collected from six fires spread across the Great Basin (four of them megafires, > 100,000 ha), including the Murphy fire in southern Idaho that burned in 2007, the Rush fire in northeastern California and western Nevada that burned in 2012, the Holloway fire in northern Nevada/southern Oregon that burned in 2012, the Soda wildfire in southern Idaho/Oregon that burned in 2015, and two fire complexes that burned on

the Orchard Combat Training Center, one in 2001 (referred to as OCTC 2001 from here on out), and one in 2012 (referred to as OCTC 2012 from here on out) (Fig. 1). The burn regions are dispersed across the Great Basin and collectively span a large elevational and topographic gradient. Our sites primarily represent historic Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities. The major land resource areas (areas that are geographically related in soils, water, climate, vegetation and land use) for each wildfire are described by the Natural Resources Conservation Service (NRCS) as follows (US Department of Agriculture 2022). The Murphy and Soda fires are located in the Owyhee High Plateau, for which dominant soil orders are aridisols and mollisols (Fig. 1). The OCTC is located in the Snake River Plains, where the dominant soil order is aridisols (Fig. 1). The Holloway fire is located in the Humboldt Basin and Range area, where the dominant soil orders are aridisols and entisols (Fig. 1). The Rush Fire is located in the Malheur High Plateau, where the dominant soil orders are aridisols and mollisols (Fig. 1). Additional site characteristics are presented

in Table 1. Seeded species for each site is given in Appendix 1, Table 1.

Data collection and spatial filtering

There was some variation in collection method, species identification, and number of sampling events for each of the wildfires. A summary of the variations and analytical solutions used to address them are provided in Appendix 2, Table 1. Species cover field data was collated from point-intercept data collected by state and federal agencies including the Bureau of Land Management (BLM), U.S. Geological Survey, Idaho State Guard, and Idaho Fish and Wildlife. Portions of the data are available through the BLM's TerraDat hub, other data was provided directly by agency personnel. Some plots were repeatedly monitored between two to five times and some plots were only monitored once. Some plots were located in areas that were untreated, while others were treated once or multiple times. Monitoring data was collected starting the year after fire and

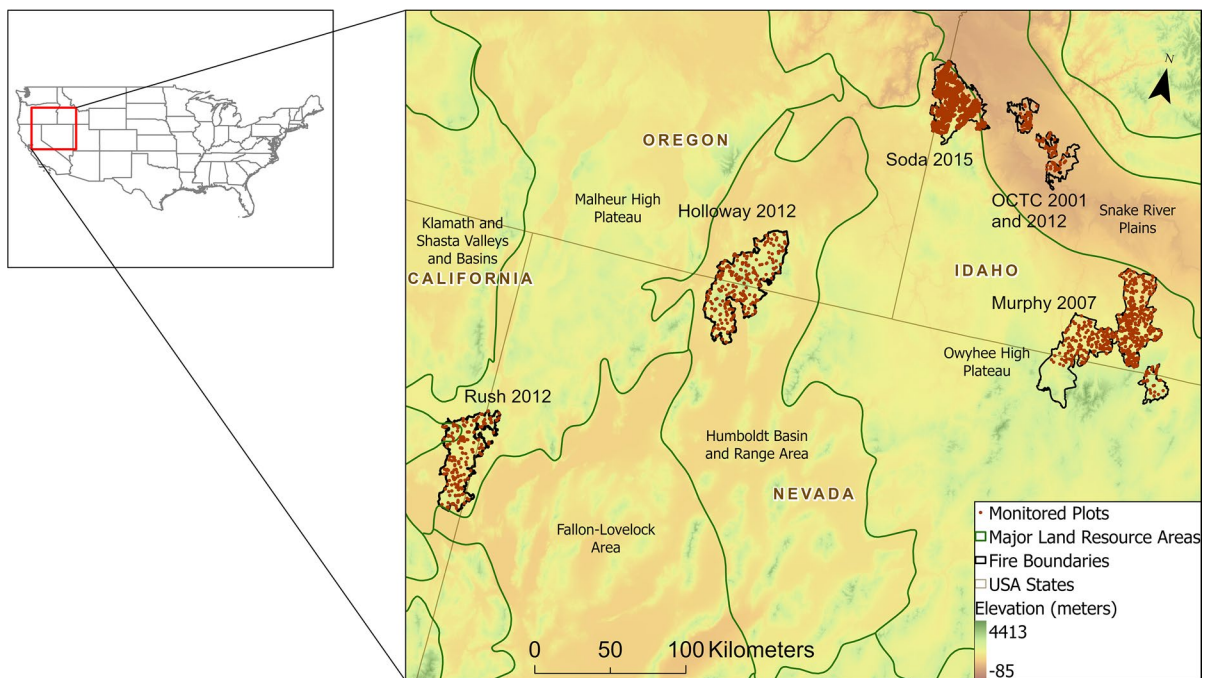


Fig. 1 Map of the study area location in the United States (red box, upper lefthand corner), and fire boundaries, locations of monitored plots, and major land resource areas (left box).

Major land resource areas are areas that are geographically related in soils, water, climate, vegetation and land use

Table 1 Site characteristics and management information for each wildfire included in the study

Fire	Year	Area (ha)	BLM district, state	Prior or post fire history	Elevation range (m)	Treatments	Dominant ecological site type
Murphy	2007	273,000	Twin Falls and Boise, Idaho; Elko, Nevada	Post: Kinyon Road Fire (2012), Bruneau fire (2018)	1144–2735	Drill seeding (bitterbrush and perennial bunchgrasses), aerial seeding (sagebrush and winterfat), seedling planting of sagebrush	Low sagebrush (<i>Artemisia arbuscula</i>), Wyoming sagebrush (<i>A. tridentata</i> ssp. <i>wyomingensis</i>), basin sagebrush (<i>A. tridentata</i> ssp. <i>tridentata</i>), mountain sagebrush (<i>A. tridentata</i> ssp. <i>vaseyana</i>)
Holloway	2012	186,000	Burns and Vale, Oregon; Winnemucca, Nevada	None relevant for plots monitored	1287–2590	Drill seeding (perennial bunchgrasses), aerial seeding (perennial bunchgrasses, sagebrush), herbicide, seedling planting of sagebrush	Low sagebrush (<i>Artemisia arbuscula</i>), Wyoming sagebrush (<i>A. tridentata</i> ssp. <i>wyomingensis</i>), mountain sagebrush (<i>A. tridentata</i> ssp. <i>vaseyana</i>)
Rush	2012	128,000	Susanville, California	Prior: Rush Fire (2002), Smoke Fire (2002), Stoney fire (2004) burned over 5 plots, No relevant post fire history	1224–2431	Drill seeding (sagebrush), aerial seeding (sagebrush), seedling planting of sagebrush	Wyoming sagebrush (<i>A. tridentata</i> ssp. <i>wyomingensis</i>), mountain sagebrush (<i>A. tridentata</i> ssp. <i>vaseyana</i>)
Soda	2015	113,000	Boise, Idaho; Vale, Oregon	Prior: Trimby (2002)	750–2055	Drill seeding (perennial bunchgrasses), aerial seeding (perennial bunchgrasses, sagebrush, forb), herbicide, seedling planting of sagebrush	Wyoming sagebrush (<i>A. tridentata</i> ssp. <i>wyomingensis</i>), low sagebrush (<i>A. arbuscula</i>), salt desert with saltbrush (<i>Atriplex</i> ssp.) mixed with greasewood (<i>Sarcobatus vermiculatus</i>) and spiny hopsage (<i>Grayia spinosa</i>)
OCTC	2001 2012	9000 49,000	Boise, Idaho	Prior: Extensive, Post: None	862–1066	None	Wyoming sagebrush (<i>A. tridentata</i> ssp. <i>wyomingensis</i>), winterfat (<i>Krascheninnikovia lanata</i>)

continued to five (Soda), eight (Rush), nine (OCTC 2012), ten (Holloway, OCTC 2001), or fourteen years (Murphy) post-fire.

Many plots on Murphy, Holloway, and some of Rush were not repeatedly monitored in the exact same location but were located near plots that were monitored in different years. We therefore identified contiguous sub-regional spatial clusters of plots with similar landscape positioning, characteristics, and management/disturbance history that we expected to follow similar vegetative trajectories to form a chronosequence. Our goal was to eliminate data points where the plot was (1) measured only once and (2) spatially distinct from surrounding areas.

We used the spatially constrained multivariate clustering tool in ArcPro (ESRI, Redlands, CA) to form clusters with a minimum of 3 and a maximum of 25 plots. The tool uses an algorithm called SKATER (Spatial “K”luster Analysis by Tree Edge Removal) that spatially partitions contiguous data that share similar covariates (Assuncao 2006). Covariates for clustering included treatment history, fire history (times burned in the 10 years prior to focal fire), and elevation. The SKATER algorithm does not place bounds on the maximum distance between plots, but the average distance between plots in a cluster was 2.9 km.

Once plots were assigned to a spatial cluster, we extracted annual herbaceous, perennial herbaceous, bareground, and shrub fractional cover data for each plot location from the Rangeland Analysis Platform (RAP) remote-sensing data (Allred et al. 2021) for one year pre-fire, and one, three, and ten (or most recent year for Soda Wildfire) years post-fire. We screened the plots within each spatial cluster to ensure that in any given year, the standard error in RAP cover among plots assigned to the same cluster was not more than 10%, and if it was then the plot cluster was discarded. Although RAP cover data can vary in accuracy, it varies consistently with elevation and other landscape characteristics (Applestein and Germino 2022a), making it a reliable metric of coarse similarity between closely located plots in similar elevational zones. RAP data was only used for the spatial filtering process to identify spatially similar areas; the subsequent community analysis utilizes field-data only.

Data organization

The total number of plot-year data points utilized for analysis after spatial filtering (see above) was 7803 (from 1941 unique plot locations). Cover data from most of Murphy ($n=438$), Holloway ($n=335$), Rush ($n=288$), OCTC 2001 ($n=277$), and OCTC 2012 ($n=537$) were collected via line-point intercept methods on transects ranging from 25 to 100 m. Each plot contained one to three transects. A small number of the plot-year data points on Murphy ($n=70$) had species cover collected utilizing Daubenmire frames. Cover data from Soda ($n=5858$) was collected via grid-point intercept on overhead 3×2 m aerial photos (see Germino et al. 2022).

Datasets tended to vary in the coding of how individual species were recorded, and the differences were corrected to ensure uniformity. Occasional entries were labeled with genus instead of species; if a large proportion of entries of a genus were not identified to species, we aggregated all species in this genus. We maintained separate records for unidentified species entries that only occurred one or two times in the data (full species list and aggregations are shown in Appendix 2, Table 2). Rare species that never had more than 5% relative cover in any plot during any year were removed from the data for further analysis. Our focus was on relative differences in species cover calculated as the number times a species was recorded via point intercept divided by the total number of times any type of vegetation, including biological soil crust, was recorded via point intercept. We included biological soil crusts as a component of the whole plant community because it has been shown that they affect vascular community composition (Bowker et al. 2022) and are affected by fire (Condon and Pyke 2018). Due to differing classifications for biocrusts across datasets, we lumped them all into a single “biocrust” category.

Structural Topic Modeling

Our application of STRUTMO followed a process similar to the LDA application of Valle et al. (2014). We have changed some of the commonly used model parameter terms from STRUTMO application in social science to make these terms more applicable to ecology. In ecological applications, latent components of LDA are typically

referred to as “communities”, but we will refer to them from this point forward as “associations” so not to confuse the reader with the concept of community types from ecological site descriptions. LDA assumes that there are different proportions of distinct plant associations across the landscape and that each of these associations is composed of different proportions of species. The number of associations is set a priori but the species composition of each association is determined probabilistically by the data (see below) based on collections of species that tend to occur together. The matrix describing the proportion of each association at each plot is called the prevalence matrix, θ and the matrix describing the species composition of each association by proportion is called the composition matrix, Φ (examples are given in Appendix 3).

$$\theta * \phi = D(\text{measured data})$$

θ and Φ are latent (not directly measured) and the values within them are random variables derived from Dirichlet distributions. The shape of the Dirichlet distributions (spread and skew) determine how similar or distinct the different associations are (i.e. how much overlap there is between species compositions of different associations and how much overlap there is in different association composition at a plot). The LDA model can therefore identify either indistinct associations (ambiguous/random species mixing) or distinct associations (strong covariation between specific sets of species).

There are limitations to LDA, including that 1) there is no way to account for correlation between associations, 2) the composition matrix is the same everywhere (i.e. no allowance for the species compositions of each association to vary across the landscape), and 3) there is no way to incorporate covariates or to utilize the model for prediction. LDACov (Valle et al. 2021) has been developed as an extension of LDA to incorporate covariates via a two-stage process of fitting a LDA model to estimate the composition matrix and then a negative binomial regression to get estimates of association abundance. However, this approach still does not allow for variation in the species composition of each association and is currently limited to count data that can be fit to a negative binomial distribution. Structural topic modeling (STRUTMO)

overcomes these limitations with incorporation of covariates and correlation between associations in a single-stage process with input data modeled as a binomial random variable (Roberts et al. 2013, 2019). Rather than determining the values in the prevalence matrix by fitting Dirichlet distributions with no predictors (as in LDA), the model is fed additional information about environmental covariates to determine how prevalent each association is at a given plot. Like LDA, STRUTMO allows for the existence of multiple associations within a single plot (consider a 25 m-radius circular spoke plot with different patches of vegetation). For a single plot, p , there is vector, X_p , which contains the values of the covariates of that plot. The model fits a matrix of weights, τ , which are the coefficients for the covariate predictors and are derived from a half-Cauchy distribution. Multiplying X_p (covariate values) by τ (coefficient matrix) gives the vector θ_p , the proportion of each association at plot p . Collectively, these vectors compose the prevalence matrix, θ . τ is estimated via Bayesian inference using non-conjugate variational expectation–maximization, as is the correlation between topics (Roberts et al. 2013).

Although plant associations can be generalizable across landscapes, the exact species composition at different locations is likely to vary. Within STRUTMO, the species composition of each association can be varied by a grouping variable (in social science, this is referred to as a “content” variable). The grouping variable is analogous to a random effect within regression analysis and can account for repeated measures or blocking designs. The baseline (or global) species proportions are given by the vector m . To delineate each association, the model fits a vector κ_a , the species-level deviations away from baseline for association a . To include variation by plot, the model fits a vector, κ_p , species-level deviations specific to plot p . Both κ_a and κ_p are added to m . There is the option to include interactions between κ_a and κ_p , but we did not incorporate this into the following analysis due to computational constraints. Once both κ_a and κ_p are both added to m , a logistic transformation is applied to convert values to proportions and obtain $B_{p,a,s}$, the proportion of species s within association a at plot p . Collectively, each of these values compose the matrix Φ . m , κ_a , and κ_p are estimated via Bayesian

inference using nonconjugate variational expectation–maximization (Roberts et al. 2013).

In our STRUTMO application, we asked how the proportion of each plant association changed with time since fire. We utilized the R package, *stm* (Roberts et al. 2019, R 4.1, R Core Team 2021), which does not automatically determine the best number of associations, K , for the analysis. To determine K , a preliminary analysis with the *searchK* function was used to compare models with no covariates with stepwise K ranging from 3 to 20. Only marginal improvements in model likelihood and residuals were observed for $K > 10$, so $K = 10$ was selected for the full model with covariates to balance model fit and interpretability. We expected to see changes in the proportion of each association as time-since-fire increased and differences between sites, and so time-since-fire and site were included in the full model as covariates affecting the prevalence matrix, θ . We did not expect the relationship between time-since-fire and the abundance of each association to be linear, so we fit this term as non-linear (using a spline, which is a piecewise polynomial function with different coefficients for each subinterval). We also included a unique plot identifier as the grouping variable affecting the composition matrix, Φ , because we expected the individual species composition of each association to vary from baseline at each individual plot. The deviation from baseline by plot level as a composition covariate accounted for repeated monitoring of plots over time.

STRUTMO provides plot-level estimates of the proportion of each association. To generalize and quantify exactly how each association varied across time-since-fire and sites (i.e. the conditional expectation of prevalence), we conducted regressions where the proportions of each different association were the outcome variables via the “estimateEffects” function in the *stm* package. One limitation of this methodology is that the regression is based on a normally distributed response and can therefore predict association proportions less than 0 or greater than 1. We therefore truncated any predictions outside of this range.

Year-to-year community change: Soda Case Study

In order to assess frequency of large interannual fluctuations in plant-community composition within the

first 5 years after fire, we selected only data from the Soda wildfire, where plots were repeatedly monitored every year for five years ($n = 5805$). We calculated the proportion of plot-year records between 2016–2020 where any association changed by a magnitude of 10% or greater. For these selected community fluctuations, we counted the number of times specific associations negatively covaried (one increased by at least 10% while the other decreased by the same amount). We created heatmaps to depict the frequency of negative covariations between associations.

Results

What are the plant associations in the first 14 years of post-fire community recovery and how do they vary over time at a landscape scale?

Below, we distinguish species from associations in the STRUTMO outputs. Specifically, “composition” refers to the relative cover of each species within an association and “prevalence” refers to the relative cover of each association within an area (at either the “plot” or “landscape”, i.e. multi-fire, scale).

Mean cover of sagebrush was $< 1\%$ of the aggregate total community cover and $< 15\%$ of any individual site cover, at any site or year. None of the communities observed up to 14 years post-fire were characterized as being dominated by sagebrush. STRUTMO identified 10 association types that could be classified into three groups; perennial-dominant, mixed annual and perennial, and annual-dominant. The five perennial-dominant associations were (1) “Sandberg bluegrass (*Poa secunda*)-dominant” (composition $> 90\%$ Sandberg bluegrass), (2) “Bluebunch wheatgrass (*Psuedoroegneria spicata*)-dominant” (composition $> 90\%$ bluebunch wheatgrass), (3) “Squirreltail (*Elymus elymoides*) and native perennial forbs”, (4) “Siberian wheatgrass (*Agropyron fragile*)-dominant” (composition $> 75\%$ Siberian wheatgrass) and (5) “Crested wheatgrass (*Agropyron cristatum*)-dominant” (composition $> 75\%$ crested wheatgrass) (Fig. 2). The three mixed associations were (1) “Biocrust and annual forbs w/sparse shrubs”, Fig. 2), “Partially invaded early seral grasses and forbs”, and (3) “Invasive biennial forbs” (Fig. 2). The two annual-dominant associations were (1) “Medusa-head (*Taeniatherum caput-medusae*)-dominant”

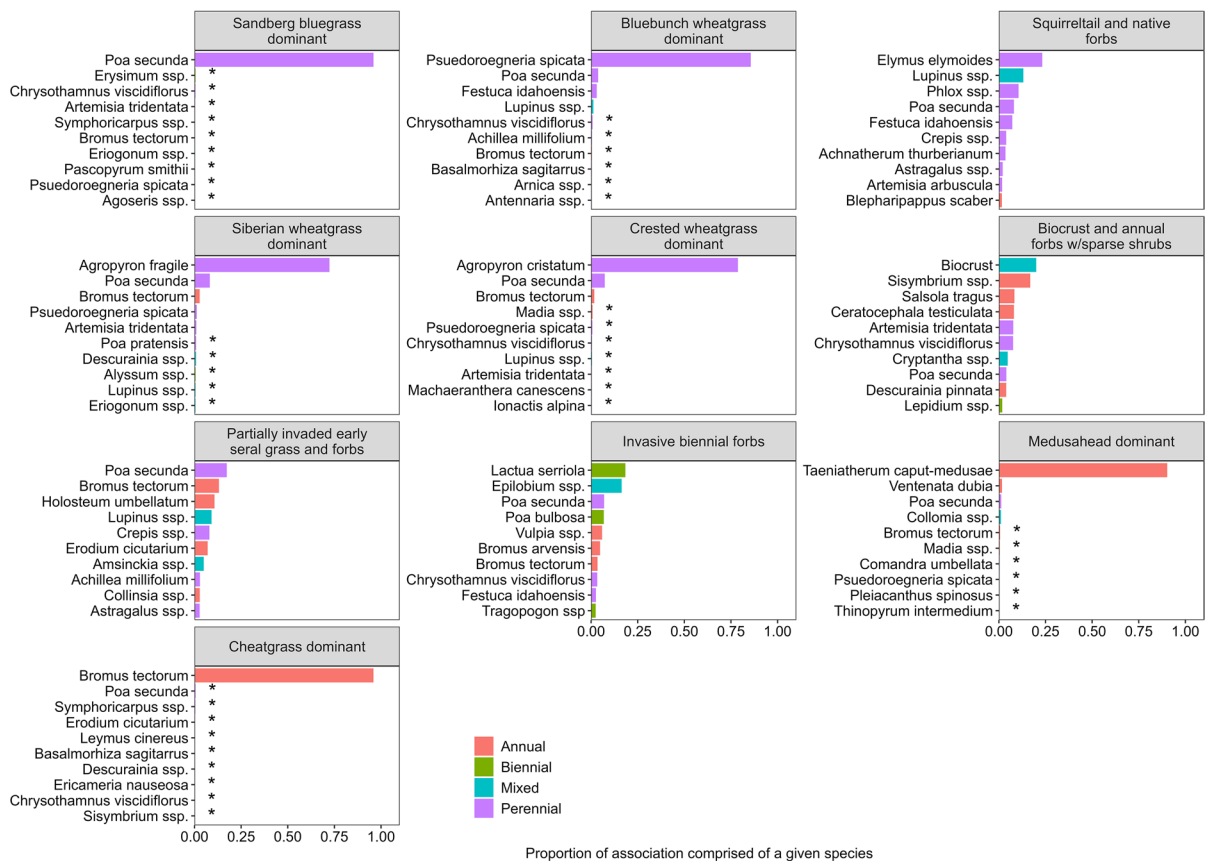


Fig. 2 Rank abundance of species within each association (labeled at the top of each graph), as the proportion (relative cover) of each species in each association. Only the top ten most abundant species in each association are shown. The

life cycle duration of each species is displayed by color. Species the comprise less than 0.009 (0.9%) of an association are denoted with a star

(composition > 90% medusahead) and (2) “Cheatgrass (*Bromus tectorum*)-dominant” (composition > 90% cheatgrass) (Fig. 2). The only species observed within the top ten most abundant species for all association types was Sandberg bluegrass (Fig. 2). Cheatgrass was present in various abundances in seven out of ten of the association types (Fig. 2). Overall, the dominance of single, different species in each association indicated strong distinction between associations (Fig. 2).

The most prevalent associations across all fires and all years were “Sandberg bluegrass-dominant” (landscape prevalence ~24%), “Cheatgrass-dominant” (landscape prevalence ~23%), and “Bluebunch wheatgrass-dominant” (landscape prevalence ~18%). “Crested wheatgrass-dominant” and “Siberian wheatgrass-dominant” were the least common association

types, with a landscape prevalence of ~3% and 2%, respectively. We found no strong correlation between these association types (Pearson’s $R < 0.4$ for all).

Across all burned areas, the fitted proportion of each association changed gradually with time-since-fire, rather than abruptly (Fig. 3). The largest, single-association changes occurred within the first 2 years after fire, and they included a reduction in the “Partially invaded early seral grass and forb” association from a landscape prevalence of ~12% to ~4% and a corresponding increase in the “Bluebunch wheatgrass-dominant” from a landscape prevalence of ~5% to ~8% and “Squirreltail and native forb” from a landscape prevalence of ~12% to ~17% between years one and two (Fig. 3). After the second year, the “Partially invaded early seral grass and forb” association decreased until seven years post-fire as the “Invasive

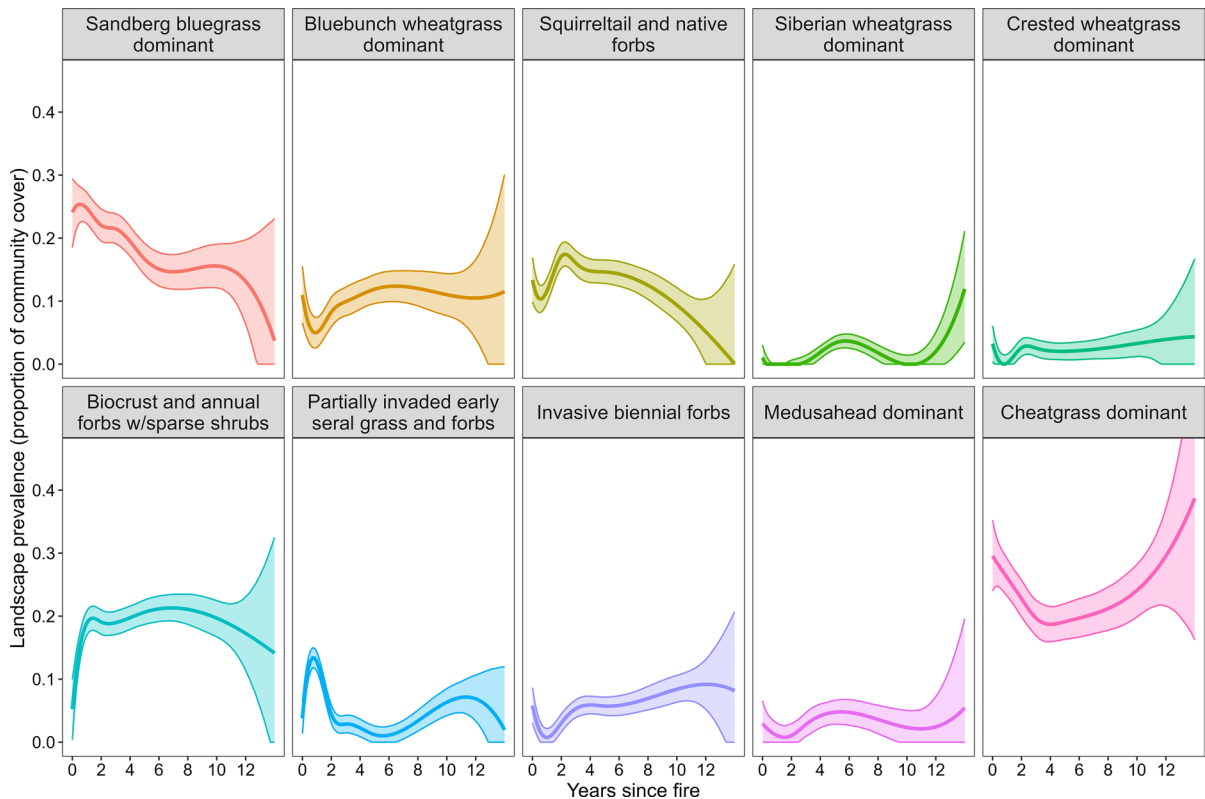


Fig. 3 The relationship between years since fire (x-axis) and landscape prevalence, i.e. the proportion of all plant cover comprised of a given association. The estimates are derived

STRUTMO and are averaged across sites. Dashed lines display the 95% confidence interval

biennial forb” association increased, generally by a landscape prevalence of ~1% (Fig. 3). The “Sandberg bluegrass-dominant” association tended to gradually decrease as time since fire elapsed, mirrored by an initial subsequent increase and then stabilization in the “Bluebunch wheatgrass-dominant” association; both associations had a landscape prevalence of around 12% at year twelve, after which time, “Bluebunch wheatgrass-dominant” stayed fairly stable and the “Sandberg bluegrass-dominant” association continued to decrease (Fig. 3). Following initial post-fire decreases, the “Crested wheatgrass-dominant” association increased by <1%/year until the 10th or more post-fire year. The “Cheatgrass-dominant” association comprised a high proportion of cover in the first several years after fire (landscape prevalence of ~25–30% of total plant community), declined at about 3 years after fire to a landscape prevalence of ~22% of total plant community, and changed little until increasing ~2–3%/year after 10 years post-fire

(Fig. 3). The “Squirrealtail and native forb” association declined ~1%/year after about 8 years post fire (Fig. 3). The “Biocrust and annual forbs w/sparse shrubs” association was stable at ~20% landscape prevalence over the time course. The uncertainty of estimates increased after the 10th year post-fire because of a reduction in the number of plots sampled (data exclusively sampled at Murphy).

In a case study of the Soda wildfire, how often are major association interannual changes apparent at the plot-level scale and between which associations do changes occur?

Within the first five years of the Soda wildfire, large abrupt changes (defined here as $\geq 10\%$ change in the relative cover of any association from year-to-year) were very common and occurred in 87% of plot-year changes (4023 total observations out of 4644 year-to-year changes considered). Instances of

concurrent positive and negative large abrupt changes ($> 10\%$) in different associations occurred about 76% of the time (3512 total observations out of 4644 year-to-year changes). Many transitions involved multiple associations changing at once. Perennial associations transitioned to other perennial associations more frequently (occurred in $\sim 57\%$ of transitions) than mixed or annual-dominant associations transitioned to other mixed or annual-dominant associations (occurred in $\sim 34\%$ of transitions, Fig. 4). However, mixed or

annual-dominant associations were more likely to transition towards perennial associations (in $\sim 64\%$ of transitions) than the reverse transition (perennial towards annual/mixed in 50% of transitions), likely due to successful restoration treatments (Fig. 4).

Mixed association changes occurred infrequently, however, these association types were uncommon to begin with on the Soda wildfire and the lack of change may be due to lower abundances (Fig. 4). The most common conversions involving mixed

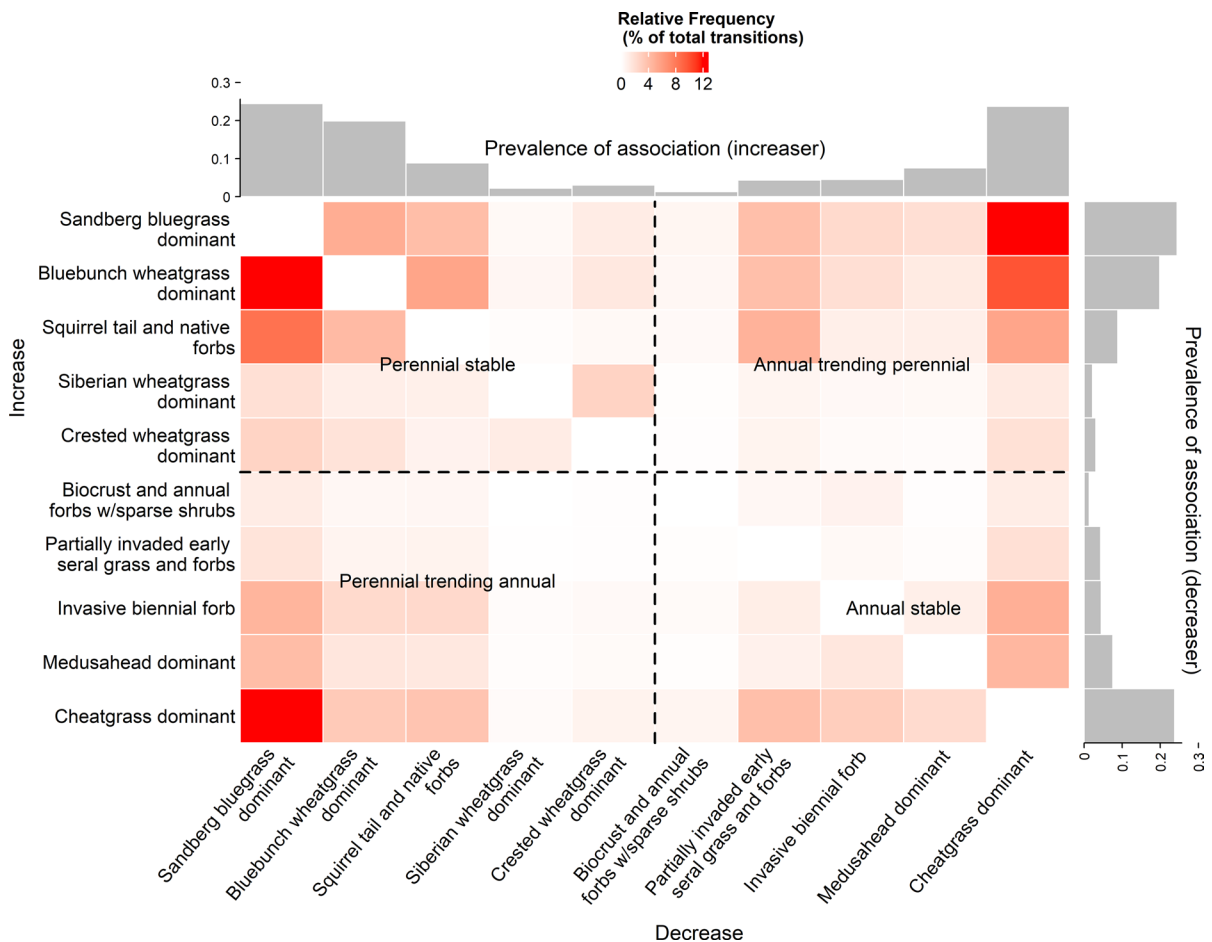


Fig. 4 Relative frequency of transitions between associations (defined as concurrent $\geq 10\%$ increase in one association and $\geq 10\%$ decrease in another within the same year) during the first five years after the 2015 Soda wildfire. For each transition type, the association on the x-axis decreased and the association on the y-axis increased. Darker colors indicate a greater number of times that the association on the x-axis decreased by $\geq 10\%$, while the association on the y-axis increased by $\geq 10\%$ in the same year. The four quadrants of the figure describe the trend; bottom-left corner are instances of

perennial associations trending towards annual, top-left corner are instances of perennial associations remaining perennial, top right corner is annual associations trending towards perennial and bottom right is annual associations remaining annual. Matrix totals sum to more than 100% because many transitions involved more than two association types (and thus would get counted in multiple rows or columns at once). The grey bar charts show the across-year average landscape prevalence of the increasing association (top) or decreasing association (left)

associations were from the “Sandberg bluegrass-dominant” or “Cheatgrass-dominant” association to the “Invasive biennial forb” association (each occurring in ~5% of transitions). The “Cheatgrass-dominant” association transitioned more frequently than other mixed or invasive-dominant associations and bidirectional changes between the “Sandberg bluegrass-dominant” and “Cheatgrass-dominant” association were common (~12% of total transitions each) (Fig. 4). Conversions from “Cheatgrass-dominant” to “Bluebunch wheatgrass-dominant” or “Squirrel-tail and native forb” associations were also common, occurring in ~10% and ~6% of transitions, respectively. The “Medusahead-dominant” association appeared less likely to transition to other community types, but overall tended to increase more often than decrease (~15% vs ~9% of transitions), most often from “Sandberg bluegrass-dominant” or “Cheatgrass-dominant” associations (~4% of transitions for each, Fig. 4).

Discussion

Our study is one of very few to assess long-term restructuring of whole communities after fire and subsequent active land management. STRUTMO identified plant associations and temporal variation among association during the immediate and crucial recovery years after fire. Although we only assessed change over time here, the same model could be applied to any environmental gradient of interest including soil characteristics, weather, or topography. Many of the plant associations identified were distinct and dominated by single species, supporting many descriptive state classifications of post-fire sagebrush steppe communities (e.g. Davies et al. 2012; Ellsworth et al. 2020). We identified both frequent and abrupt small-scale change and landscape (multiple megafires)-scale gradual change over time between associations, indicating the need for analysis methods such as STRUTMO that are flexible enough to accommodate both types of change. Because we only analyzed post-fire communities, our results do not preclude threshold-like community change occurring across the landscape scale at the time of disturbance (i.e. major change from before to after the fire such as that seen in some community types in Wainwright et al. 2020). Together, these results suggest

that post-fire rates of community change vary with scale (in agreement with Turner 1989) and that analytical approaches that have flexibility across scales and rates of change (such as STRUTMO) can provide insight about post-fire dynamics that are not possible with deterministic classification methods.

Community types

Some of the association types that were identified by STRUTMO are similar to commonly identified vegetation states within STMs for invaded, annual, or seeded states that occur after disturbances such as fire (e.g. Holmes and Miller 2010; Davies et al. 2012; Chambers et al. 2014; Ellsworth et al. 2020). For example, the “Cheatgrass-” and “Medusahead-dominant” associations we identified agree with the annual-grass, degraded states within most STMs which portray them as being unlikely to have natural or assisted recovery of perennial plants (Hemstrom et al. 2002; Stringham et al. 2003; Bestelmeyer et al. 2003, 2004; Chambers et al. 2014; Ellsworth et al. 2020). Although the “Medusahead-dominant” association was stable (not frequently replaced) throughout time after the Soda wildfire, we did find semi-frequent occurrences of the “Cheatgrass-dominant” association being replaced with “Sandberg bluegrass-dominant”, “Bluebunch wheatgrass-dominant” or “Squirreltail and native forb” associations. Many of these transitions likely occurred as a result of significant land-management intervention (herbicide and seeding) and further analysis is needed to assess the specific management and landscape conditions under which these changes occurred.

Sandberg bluegrass has high genetic and taxonomic variability across our study region (Johnson et al. 2015), but the ecological patterns of this community type were relatively uniform and distinctive. The “Sandberg bluegrass-dominant” association was an unstable association compared to the other associations, tending to be replaced by large-statured bunchgrass-dominant associations as time since fire increased but also frequently replaced by mixed or annual-dominant associations, which is expected because Sandberg bluegrass is a short-lived ruderal species (Baethke et al. 2020). Our observations of interchangeability between Sandberg bluegrass and cheatgrass communities and their co-occurrence in some communities corroborated observations from a

smaller site by Davies et al. (2012) and with results from Applestein and Germino (2022b). Furthermore, the negative relationship between medusahead and Sandberg bluegrass found in Applestein and Germino (2022b) agrees with our findings from this analysis in that Sandberg bluegrass composed a negligible proportion of the “Medusahead-dominant association” and that the transitions were more often unidirectional (from “Sandberg bluegrass-dominant” to “Medusahead-dominant”) than bidirectional. We did not consider elevational gradient in this analysis and Anthony and Germino (2023) observed that Sandberg bluegrass was negatively associated with cheatgrass at lower elevations, indicating factors correlated with elevation (i.e. temperature, precipitation) can influence species interactions.

Some generalized regional STMs (e.g. Chambers et al. 2014) recognize a stable “seeded state” of introduced, naturalized species, such as Siberian or crested wheatgrass that may inhibit native perennial reestablishment and growth. In agreement with these conceptual models, we found that both species formed distinct associations that were very stable and did not change much over time. A recent study suggested that intact sagebrush-steppe communities are competitive with crested wheatgrass and can recover even when seeded with crested wheatgrass (Davies et al. 2023). Although this may be true of unburned systems, Siberian or crested wheatgrasses are often seeded into burned sagebrush steppe rangelands (Knutson et al. 2014), because they sometimes exert more competitive pressure on invasive annual grasses than native species (Davies and Johnson 2017). We found minimal evidence of native associations replacing Siberian or crested wheatgrass following the wildfires we evaluated, which agrees with Nafus et al. (2015), who found that crested wheatgrass tended to outcompete co-planted native perennial bunchgrasses. The stability and dominance of these non-native perennial species are well documented, even following treatments to remove them and reestablish native species (Hulet et al 2010; Fansler and Mangold 2011).

Prior research has indicated that recovery time required for big sagebrush to approach pre-fire cover on a burn site is variable among ecological sites and subspecies. Recovery of mountain big sagebrush cover can take anywhere from 20 to 60 years (occasionally less if a burn is patchy), while recovery of Wyoming big sagebrush can take 50 years or much

more and sometimes does not occur (Baker 2006; Ziegenhagen and Miller 2009; Bates et al. 2020). Therefore, it was not surprising that we did not observe a sagebrush dominant-association across sites where the maximum time since fire was 14 years. Although sagebrush was rare throughout our study, it was most abundant within the “Biocrust and annual forb w/sparse shrub” association, which may indicate potential for long-term recovery of sagebrush. A prior study found that post-fire sagebrush cover was higher in areas with poorly developed biological crusts (but not with strongly developed or mature biocrusts), which may indicate facilitation of sagebrush by some types of biocrust, but further research is needed to elucidate this relationship (Barnard et al. 2019).

Our analysis covers a broader spatial scale while still highlighting some important distinctions between associations dominated by different species. Different associations, including those that would be classified within the same generalized vegetation STM state (i.e. “seeded”, “invaded”, “perennial grassland”) varied in their propensity to change. Furthermore, many of the classifications, such as those used to describe states within STMs, are limited in their ability to describe communities of mixed plant associations or associations composed of many mixed species. STRUTMO offers a method of exactly quantifying mixtures of species in distinct associations (such as intermediary successional types) or mixed associations at single plots (which allows for incorporation of ecotones).

Plant communities as gradients rather than discrete units

Quantitative classification methods that rely on discrete community types (1) can only model abrupt change at the point in time when a plant community type meets a specific classification criterion, and (2) do not allow for quantification of gradual underlying continuous gradients (McGarigal and Cushman 2005). The error associated with misclassification can often be larger than error associated with continuous metrics, a concept well recognized within remote sensing context (e.g. Arnot et al. 2004; Shao and Wu 2008; Lechner et al. 2012), and occasionally in other realms of ecology (e.g. Evans and Cushman 2009). Meanwhile, distinguishing between gradual and abrupt change in distinct, interpretable communities is

difficult with existing ordination methods like NMDS and PCA. We have shown here how STRUTMO can incorporate identification of distinct plant community types dominated by a few species (as in Clements successional theory), identification of mixed community types, and/or gradual or abrupt non-equilibrium dynamics (as in Gleasonian model of plant community organization). By modeling prevalence and composition as continuous metrics, STRUTMO avoids the risk of large misclassification error attributable to incorrectly characterizing a plot as a single community type. While our analysis largely agrees with Bagchi et al. (2013), who found frequent ephemeral transitions between associations in sagebrush steppe communities, we also found evidence of more gradual change occurring across a landscape or regional scale.

Identifying whether the change in post-fire community composition is abrupt or gradual over time is important to management and the understanding of temporal windows in which managers can affect change. The majority of intensive management of sagebrush steppe occurs in the first few years after fires (Pilliod et al. 2007, Germino et al. 2022). Our analysis suggests that within the context of a major management interventions, there is the potential for community fluctuation and longer-term change in early post-fire communities, especially when cheatgrass is the dominant invader. Given the frequency of transition from “Cheatgrass-dominant” association to perennial associations, our findings suggest that this particular “invaded state” has potential for conversion back to perennial states with herbicide and seedling. Further analysis will focus on specific treatment effects on association compositions and differences across the landscape. Additional research could focus on understanding how recovery trajectories compare between passive restoration (natural recovery) and active restoration, in order to assist with prioritizing management activities.

Conclusions

Many benchmarks and objectives for post-fire restoration in sagebrush steppe focus on functional group metrics and not species per se. However, we found that the propensity of a plant community to transition depended on the species composition, and that

species composition should be considered when setting objectives for restoration aimed at increasing resistance and resilience. Our analysis provides empirical evidence to support many of the conceptual classifications and transitions with regional STMs. However, our unique analytical approach was also able to characterize small-scale ephemeral plant community changes to show how rapid ecological restructuring occurs in initial post-disturbance years. Our results suggest that year-to-year change may not be a good indicator of longer term processes.

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Data availability Data from the OCTC is the property of the Department of Defense. Authors can arrange communication with data owners upon reasonable request for the data. The remaining data will be released and available on U.S. Geological Survey ScienceBase website.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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