Methods for tracking sagebrush-steppe community trajectories and quantifying resilience in relation to disturbance and restoration

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Understanding how plant community dynamics are impacted by altered disturbance regimes is a pressing challenge for restoration ecology. Most assessments of community dynamics involve computationally intensive statistical techniques, while management often defers to derived, qualitative “state-and-transition” models. Here, we demonstrate an intermediate approach to track and predict community resilience, diversifying the tools available to assess ecosystem change. First, we develop indices of sagebrush-steppe community structure in permanent monitoring plots based on plant functional types and our conceptual understanding of the ecosystem. The indices define a bivariate space within which the trajectories of permanent monitoring plots can be tracked. Second, we quantify two metrics of community resilience: resistance (overall change during the time period) and stability (average amount of movement per monitoring period). Plots dominated by obligate seeders shrubs displayed low resilience relative to those dominated by grasses and forbs or resprouting shrubs. Resilience was strongly related to initial plant functional type composition and elevation. Our results suggest restoration objectives should consider how plant traits control ecosystem responses to disturbance. We suggest that the approach developed here can help assess longer-term resilience, evaluate restoration success, and identify communities at risk of state transitions.

Key words: plant functional types, resilience, resistance, restoration, sagebrush-steppe, stability

Implications for Practice

• Practitioners often want to describe ecosystem resilience following disturbance and restoration, but need a “middle ground” between computationally intensive multivariate techniques and derived qualitative state-and-transition models that often have limited generalizability.
• Complex vegetation dynamics can be summarized using indices of plant functional type dominance. These indices are easily calculated, generalizable, and can easily be updated with new monitoring data.
• The indices define a bivariate trait-based space within which one can assess community trajectories of change, such as by calculating resistance and stability. This assessment can enhance restoration success by providing a mechanistic link between community resilience and disturbance, and making it easier to identify communities at risk of state transitions.

Introduction

One of the grand challenges for restoration ecology is developing methods to quantify, model, and predict vegetation community dynamics in relation to disturbance (Brudvig et al. 2017). Meeting this challenge is vital as we are currently limited in our ability to manage post-disturbance successional pathways that govern critical ecosystem services. Many ecosystems display nonequilibrium dynamics in response to altered disturbance regimes (Schröder et al. 2005). Such alterations may be linked to sudden and dramatic shifts in ecosystem state, and thus impact long-term community composition and ecosystem function (Scheffer et al. 2001). Ecosystems displaying such fundamental changes are argued to have undergone a state transition in community composition and, in the absence of restoration, are unlikely to recover to their initial composition (Briske et al. 2003).

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Three key concepts are useful for evaluating whether an ecosystem has undergone a state transition: resilience, resistance, and stability. We define resilience as the ability of an ecosystem to maintain structure and function following alteration to the prevailing disturbance regime (e.g. Holling 1973; SER 2004; Bestelmeyer & Briske 2012; Standish et al. 2014). Resilience is influenced by resistance, the extent to which an ecosystem retains its structure and function in the face of disturbance regime alteration (SER 2004), and by stability, the ability of an ecosystem to maintain its successional trajectory despite disturbance regime alteration (SER 2004). Importantly, resilience can be either “helpful” (i.e. indicative of recovery from disturbance regime alteration) or “unhelpful” (i.e. indicative of a degraded community remaining degraded rather than recovering following disturbance regime alteration; Standish et al. 2014). Unhelpful resilience is thus symptomatic of a system having transitioned into a less desirable state from a land management perspective.

A variety of approaches have been used to quantify processes of vegetation change and resilience in relation to disturbance. These include ordination-based approaches (nonmetric multidimensional scaling [NMDS; e.g. Davies et al. 2012], principal response curves [e.g. Máren et al. 2008], and cluster analysis [e.g. Mitchell et al. 2017]). State-and-transition models, which are based on site-specific descriptions of observed ecological patterns and processes, have been adopted among rangeland ecologists (Bagchi et al. 2013; Chambers et al. 2014a; Bestelmeyer et al. 2017). Others have proposed using digital imagery to characterize key parameters such as changes in shrub canopy cover and spacing (e.g. Karl et al. 2012). These existing approaches vary in analytical intensity, site-specificity, and ability to capture ecosystem responses of interest. Data-driven, evidence-based ecosystem restoration, will, as a process, be more successful when it incorporates a diversity of tools with varying computational complexity, system specificity, and flexibility.

Davies et al. (2012) proposed a straightforward, qualitative method to track shifts in the broad structure of sagebrush-steppe plant communities based on the relative abundance of key plant functional types. Their approach emphasized consideration of species traits rather than species identities alone. Trait-based approaches provide a number of advantages including: (1) generality across ecological sites (sensu Bestelmeyer et al. 2016) with different species pools; (2) a more mechanistic understanding of community change (e.g. Lavorel & Garnier 2002; Zirbel et al. 2017); (3) synergy with other broad-based modeling approaches, e.g. dynamic vegetation models (Isabelle et al. 2012); and (4) applicability to situations in which species are not identified consistently or to the same taxonomic resolution.

Here, we extend the qualitative model proposed by Davies et al. (2012) by expressing community dynamics within a trait space defined by two axes of variation, and by quantifying two metrics of community resilience. Existing ordination-based approaches are quantitative but can be difficult to interpret. We sought a simpler method that would reflect the ecology of our study system and result in axis values that are readily interpretable and static. For example, managers could use this system to track succession following disturbance or restoration, and to distinguish phase changes from permanent shifts in state. We thus defined two key axes of variation: the relative abundance of shrubs and the relative abundance of nonnative herbaceous species. Shrubs are an important component of native vegetation structure and habitat integrity in sagebrush-steppe ecosystems and are vulnerable to depletion by increasing wildfire frequencies linked to invasion by nonnative herbaceous species (Davies et al. 2012). Describing ecosystem structure as such is supported by the mass ratio hypothesis (Grime 1998), which posits that ecosystem function is primarily an expression of the attributes of dominant species. Additionally, describing communities in terms of their dominant species is similar to vegetation classification systems commonly used by land managers (e.g. The U.S. National Vegetation Classification System; usnvc.org). The position of a community $i$ in a given year along each axis is determined by an index:

$$\text{Shrub Index} (Si) = \frac{S}{S + H}$$

$$\text{Herbaceous "Invadedness" Index} (II) = \frac{I}{I + N}$$

where $S =$ total cover of shrub species, $H =$ total cover of nonshrub species (i.e. herbaceous species: grasses and forbs), $I =$ total cover of nonnative herbaceous species, and $N =$ total cover of native herbaceous species. These indices correspond to key plant functional type dominances and are bounded by 0 and 1. Together, they form a bivariate “S-I space” that can describe community structure and can enable the movement of communities to be tracked over time.

We used the S-I space to quantitatively express resistance and stability, the two aspects of community resilience. More resistant communities will have changed less and therefore will have smaller distances between their positions at the beginning and end of a time interval. We express this as the distance

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**Tracking Sagebrush-Steppe Community Dynamics**

Transitions in ecosystem state have been well-documented in sagebrush (Artemisia spp.)-steppe ecosystems of North America (e.g. Allen-Diaz & Bartolome 1998; Bagchi et al. 2013) and producing knowledge systems to support resilience-based restoration is thus a high priority (Bestelmeyer & Briske 2012). Sagebrush-steppe ecosystems have declined by more than half from their historic range (Davies et al. 2011), primarily due to anthropogenic disturbance. Key processes driving this decline include conversion to agricultural crops (Hann et al. 1998) and over-grazing by livestock (Davies et al. 2016). Additionally, invasion by cheatgrass (Bromus tectorum L.) has led to increasingly frequent and extensive wildfires that have pushed many sagebrush-steppe ecosystems into a new stable state dominated by exotic annual plants (Knapp 1996). In many areas, big sagebrush (Artemisia tridentata Nutt.), an obligate seeder with a short-lived soil seedbank (Wijayratne & Pyke 2012), has been effectively extirpated.
between the two positions. More stable communities will have less fluctuation over time. We express this as the sum of the distance a community moves in each time interval divided by the number of time intervals. In other words, this is the average movement across consecutive monitoring periods. If a community has only been monitored twice, its resistance and stability are equivalent. Comparisons of stability among communities will only be equitable if the communities have been monitored in the same years. However, it is not necessary that communities be monitored every year.

In this article, we use data from permanent monitoring plots to illustrate these two quantitative approaches. Specifically, we track community trajectories in plots in a sagebrush-steppe ecosystem in central Washington State, U.S.A., that vary in their wildfire and restoration histories. Our objectives are to: (1) assess whether metrics based on broad species functional types capture sagebrush-steppe community responses to disturbance and restoration; (2) quantify how communities differ in resilience (measured via resistance and stability); and (3) test whether community resilience is contingent on predisturbance abiotic and biotic conditions, and on fire and restoration history.

**Methods**

**Study Site**

Research was completed on the Fitzner-Eberhardt Arid Lands Ecology Reserve (hereafter ALE), which lies within the Hanford Reach National Monument in Benton County, Washington (46°30′N, 119°39′W), U.S.A. The site lies in the Columbia Basin. Elevations range from 130–1,060 m above sea level. Average total annual precipitation ranges from 120 mm at the lowest elevations to 300 mm along the crest of Rattlesnake Mountain (US DOE-RL 2017). Soils are predominantly sand or sandy loams at low elevations, silt loams at mid-elevations, and lithosols at the highest elevations.

At the start of this study (in 1994), shrub-dominated communities were dominated by *Artemisia tridentata* Nutt., likely ssp. *wyomingensis* Beetle & Young (McArthur & Sanderson 1999), at low and middle elevations and *Artemisia tripartita* Rydb. (three-tip sagebrush) at higher elevations (Wilderman 1994). *Chrysothamnus viscidiflorus* (Hook.) Nutt. (green rabbitbrush), *Eriocameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird (gray rabbitbrush), *Gravia spinosa* (Hook.) Moq. (spiny hogsage), and *Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit (winterfat) were also locally important. Shrubland understoreys were dominated by large native bunchgrasses including *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass) and, at higher elevations, *Festuca idahoensis* Elmer (Idaho fescue). A small native bunchgrass, *Poa secunda* J. Presl (Sandberg’s bluegrass), was ubiquitous. A diverse array of hemi-shrubs and forbs was also present.

In the decades before 1994, wildfires reduced the shrub-dominated portion of ALE to less than 20% of its mid-20th century extent (Soll et al. 1999). Perennial and/or annual grasses dominated burned areas and shrubs were largely absent. Bluebunch wheatgrass-Sandberg’s bluegrass was the most common perennial grassland association. *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle and thread) grassland associations occurred at lower to middle elevations, often on sandy soils. *Bromus tectorum* (hereafter “cheatgrass”) was widespread at low elevations. ALE experienced additional wildfires between 1994 and 2010, most notably the 24 Command Fire in 2000 and the Wautoma-Milepost 17 fire complex in 2007. Both fires burned >75% of ALE and were followed by restoration treatments such as aerial application of pre- and postemergence herbicides, aerial and drill seeding of native species, and outplanting of big sagebrush seedlings. Details of these treatments and plot fire histories are provided in Table S1.

**Field Survey**

We used survey data from 32 permanent plots established on ALE in 1994 (Soll et al. 1999). The plots were established in stands chosen to represent major native plant community types (Wilderman 1994). Areas that were highly disturbed or dominated by invasives in 1994 were generally avoided during plot establishment. Each plot was 5 m × 20 m. Plots were resurveyed annually from 2001 to 2004 (Evans & Lih 2005) and in 2009 and 2010 (Bakker et al. 2011). In total, therefore, each plot was monitored seven times, for a total of 224 plot-years. Monitoring consisted of estimating the cover of each vascular plant species, using 12 classes: <1% (expressed as 1%); 1–5%; 6–15%; 16–25%; 26–35%; 36–45%; 46–55%; 56–65%; 66–75%; 76–85%; 86–95%; and 96–100% (Wilderman 1994). During data entry, the 100% class was expressed as 100%. Across all plots and years, 148 taxa were recorded. Species nomenclature follows USDA NRCS (2018).

**Data Analysis**

All analyses were completed using R 3.5.0 (R Core Team 2018). An adaptable version of our R code can be found in Supplement S1.

**Categorizing Species Functional Types.** Prior to analysis, we performed several taxonomic adjustments on our species composition dataset. This included combining congeneric species that are easily misidentified in the field (e.g. *Ansineckia* species were combined) or collapsing subspecies to observations at the species level. These changes resulted in retention of 139 of 148 taxa, and are detailed in Table S2.

We then classified taxa into functional types defined on the basis of five attributes: plant life-form (graminoid, shrub, forb [which included sub-shrubs]), longevity (annual, perennial), postfire regeneration strategy for shrubs (resprouters, obligate seeders), plant size for bunchgrasses (large, small), and origin (native, nonnative). This classification scheme was also used in Davies et al. (2012). We recognize that the nativity distinction does not represent a specific trait per se, and that nonnative species exert various impacts on native communities, but this distinction provides an ecologically conservative, objective way to define nonnative species. There is a range of nonnative taxa in our system, including those which tend to rapidly colonize...
disturbed sites, such as cheatgrass, and those generally considered to be of lesser ecological concern (e.g. Draba verna L., Holosteum umbellatum L.). Species in the latter case usually had low cover and thus limited impact on the results. No native, annual grasses (Vulpia spp.) or small, invasive, perennial grasses (Poa bulbosa L.) were recorded in 1994. These functional types composed a relatively small proportion of the overall vegetation dataset (never > 3% or 1%, respectively, of standardized cover [see next section] in any plot in any year). For this reason we created a single “annual grass” functional type (i.e. B. tectorum plus Vulpia spp.) and excluded the “small, invasive perennial grass” (i.e. P. bulbosa) type.

Together, these attributes defined nine plant functional types that encapsulated most taxa (134 of 139); five taxa could not be classified into these types and were omitted from analyses (Table S2), but were <0.2% of the total cover recorded in the entire 148-species dataset. The covers of all taxa within each functional type in each plot-year were summed for analyses.

Classifying Community Groups. To assess the effect of initial composition on the extent and direction of subsequent community changes, we classified the plots into groups based on the relative abundance of plant functional types in 1994. Data were standardized by functional type maxima (across all plots) and by plot totals (“wisconsin” function from package vegan; Oksanen et al. 2018). This standardization allowed us to focus on differences in relative abundance of each plant functional type irrespective of variation in absolute cover that might be caused by differences in site productivity or time since fire. It also minimized the effect of differences in observers within and across years. We expressed the standardized data as a Bray–Curtis dissimilarity matrix (“vegdist,” vegan) and applied hierarchical agglomerative cluster analysis to this matrix (“hclust” function with Ward’s clustering criterion). Scree plots of the proportion of information explained were examined to determine the appropriate number of groups to use in further analysis.

We compared the distribution of plots in S-I space (see below) to their distribution represented using a common multivariate approach, NMDS (e.g. Davies et al. 2012). We ran a two-dimensional NMDS (“metaMDS;” vegan) on the Bray–Curtis dissimilarity matrix obtained from Wisconsin standardized functional type abundances from all plots in all years. A two-dimensional (2D) solution was chosen as this allows explicit comparison of two dimensional representations of composition provided by the NMDS and S-I space methods. The final solution had a stress of 19.8 (indicative of a “fair” fit; Kruskal 1964) and was rotated (“MDSrrotate,” vegan) along both axes to maximize discrimination among sites in their invasive herbaceous (axis 1) and shrub (axis 2) relative cover. We then overlaid vectors corresponding to the two axes onto the ordination (“envfit,” vegan).

Quantifying the S, and I, Indices. As noted previously, $S_i$ and $I_i$ define the axes of our S-I space. We calculated $S_i$ and $I_i$ for all plot-year combinations and plotted them in this space. 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 2D kernel density estimates (“kde2d,” MASS; Venables & Ripley 2002). While kernel density estimation is an effective visualization tool to help objectively separate states, it is not required to assess changes in community state. Plotting plot-year $S_i$ and $I_i$ coordinates is sufficient to visually determine major changes in the distribution of plot-years in S-I space.

Controls on Community Resistance and Stability. Resistance was defined as the distance between a plot’s position in S-I space at the start and end of a time interval. Stability was defined as the average distance moved in S-I space between all consecutive monitoring years within the time interval. These metrics were based on the Euclidian distance between plots in S-I space. For example, the resistance of a plot between 1996 and 2010 was the distance between its positions in S-I space in these 2 years, while stability was the average of the distance it moved during the six monitoring intervals (1994–2001, 2001–2002, 2002–2003, 2003–2004, 2004–2009, 2009–2010). To provide a comparison with the data from the S-I space, we also calculated resistance and stability based on the NMDS axis scores. For each variable, the correlation between the values in the S-I space and the NMDS space was calculated (“cor.test,” stats; R Core Team 2018).

We tested whether community resistance and stability were products of biotic conditions (community group), abiotic conditions (plot elevation, which is highly correlated with soil type, temperature, and precipitation at our site), fire history (number of fires between 1994 and 2010, ranging from one to three), and postfire restoration (a binomial variable indicating whether or not a plot had been subject to one or more restoration treatments following any of the fires). We adopted this simple coding for restoration because specific restoration treatments could not be differentiated—e.g. many plots received herbicide followed by re-seeding. Elevation and community group are also somewhat confounded with restoration due to the nonrandom placement of restoration interventions by managers (Table S1, Fig. S1). However, examination of variance inflation factors (VIF) among predictors (“vif,” usdm; Babak 2015) did not identify significant collinearity (all VIF < 2).

We fitted general linear models of resistance and stability as a function of community group, elevation, fire history, and postfire restoration, and all possible interactions among these variables. Resistance and stability were calculated over the entire monitoring period (1994–2010). We used stepwise regression (“stepAIC,” MASS; Venables & Ripley 2002) to gauge the relative importance of variables, and the Bayesian information criterion to select final models that balanced complexity with explanatory power. When community group was retained in the final model, we ran pairwise contrasts to identify differences between groups (“contrast,” contrast; Kuhn et al. 2013). p Values were adjusted for multiple comparisons. Contrasts were based on least squares means from the final fitted models and thus accounted for the effect of any fitted covariates.

Finally, we examined whether temporal patterns in resistance and stability differed among groups. To do so, we calculated resistance and stability values in each time interval relative to
Table 1. Characteristics of the four community groups identified in 1994 (Fig. S1, Table S3).

| Group               | Abbreviation | n  | Shrub Description                                                                 | Herbaceous Description                                                                 | Elevation Range (m) |
|---------------------|--------------|----|-----------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|---------------------|
| Obligate seeder     | O-S          | 8  | Very high relative cover of obligate seeder shrubs (generally Artemisia tridentata) | High relative cover of Poa secunda but relatively little cover of large bunchgrasses; relatively few forbs. Mixed levels of invasive dominance; cheatgrass abundant in some plots. | 227–280             |
| Grass-forb          | G-F          | 10 | Absence or very low relative cover of shrubs                                        | High relative cover of large bunchgrasses and Poa secunda; high perennial and annual forb relative cover. | 184–906             |
| Invaded sprouter    | I-Sp         | 5  | Resprouting shrubs generally present. Obligate seeder shrubs absent.                | Low cover of large bunchgrasses. Invaded by annual and perennial forbs and cheatgrass. | 417–1,035           |
| Pristine sprouter   | P-Sp         | 9  | Resprouting shrubs generally present sometimes at high abundances. Obligate seeder shrubs absent. | Often no invasives present; relatively high cover of large bunchgrasses and native forbs. Very low or no cheatgrass cover. | 170–1,043           |

Figure 1. (A) Plot positions in S-I space, defined by a shrub index ($S_i$) and an invadedness index ($I_i$). Each symbol is a plot-year combination. Bands on the x- and y-axes indicate the density of observations for each index. (B) A two-dimensional NMDS ordination (stress = 19.8) based on abundance of nine functional groups in the same plot-year combinations. Fitted vectors denote $S_i$ and $I_i$. In both panels, 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.

1994. We then ran mixed-effects linear models (“lme,” nlme; Pinheiro et al. 2018). We modeled plot resistance and stability by time interval in years (continuous), community group, and their interaction, with plot identity specified as a random effect.

Results

Classifying Community Groups
Cluster analysis of plant functional type composition in 1994 identified four distinct groups (Tables 1, S3, & S4, Figs. S2 & S3). We refer to these as obligate seeder, grass-forb, pristine sprouter, and invaded sprouter on the basis of compositional differences such as the presence or absence of shrubs, the postfire regeneration strategy of shrubs, and prevalence of non-native species (Table 1). The groups were clearly separated when viewed in both the S-I space and the NMDS ordination (Fig. 1). These groups could also be distinguished by their restoration histories and elevational differences (Fig. S1, Table S5).

Differences in Community Group Trajectories in S-I Space
Trajectories in S-I space were generally consistent among plots within each community group (Figs. 2 & S4). Plots in the obligate seeder group displayed the largest movement in S-I space, and there were two clear basins of attraction: a basin
Tracks community trajectories and resilience

Figure 2. Plot positions in S-I space for each community group in all years (note differences in axis ranges for each group). These are the same data as in Figure 1A, but plotted separately for each group and with fill colors demarcating 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.

with high $S_i$ and low $I_i$, and a larger basin with low $S_i$ but large variation in $I_i$ (Fig. 2). Plots moved between these basins during the first monitoring interval, which included the 2000 wildfire (Fig. S5). In later years, there was some recovery by shrubs and a general decline in invadedness. For example, relative invasive cover was lower in 2009 and 2010, following the 2007 wildfire, than in some inter-fire years.

Unlike the obligate seeder group, the grass-forb group showed no clear separation in S-I space between pre- and postfire periods. Observations were instead organized along a gradient of invasion that related to earlier versus more recent observations (and thus earlier versus more recent disturbance). This group was relatively uninvaded prior to the fires but became more invaded over time. The relative cover of several shrub species increased in some plots in this group (Fig. 2) as well, including resprouters (*Chrysothamnus viscidiflorus* and *Eriocameria nauseosa*) and an obligate seeder (*Krascheninnikovia lanata*).

In the pristine sprouter group, shrub dominance remained relatively stable or was slightly reduced during the first period (1994–2001) though invasive herbaceous dominance increased markedly. Changes were limited during the early 2000s (Fig. S4). There was no clear separation of the monitoring years into separate basins.

The invaded sprouter group changed the least from initial to final monitoring but experienced substantial interim changes in invasive dominance (Fig. 2). The invaded sprouter group became much more invaded between 1994 and 2001 following the 2000 wildfire. Invasive herbaceous dominance decreased between 2003 and 2004 in this group, as in the pristine sprouter group (Fig. S4). Two separate basins of attraction emerged based predominantly on two plots with higher $S_i$ which nevertheless displayed temporal patterns in $I_i$ consistent with the other plots.

**Controls on Community Stability and Resistance**

Across all community groups there was a linear relationship between resistance and stability (Fig. 3A) over the entire monitoring period (1994–2010) ($r = 0.75$, $t_{30} = 6.23$, $p < 0.0001$). Most plots within the same community groups were clustered together when plotted against these two metrics. The noticeable
exception was the obligate seeder group, which showed a considerable range of stability and resistance values from 1994 to 2010 (Fig. 3).

Plot resistance was best explained by community group; the obligate seeder group was significantly less resistant than all other groups (Fig. 3B, Tables S5 & S6). Plot stability over this time period was best explained by community group and elevation (Fig. 3C, Tables S5 & S7). Stability increased with elevation. Relative to the obligate seeder group, the grass-forb group and pristine sprouter group were significantly more stable (Table S7).

Comparison Between S-I Space and NMDS Ordination
When calculated using NMDS axis scores, resistance and stability from 1994 to 2010 were less strongly correlated than they were when calculated from the $S_i$ and $I_i$ indices, though they remained positively correlated ($r = 0.54$, $p = 0.002$; Fig. S6). Model selection indicated that resistance still differed among community groups, being significantly lower in the obligate seeder group than in all other groups (all comparisons $p < 0.05$). Stability as calculated in this space was not related to any of the potential predictors.

Temporal Changes in Resistance and Stability
Resistance and stability varied depending on the temporal interval over which they were calculated, community group, and their interaction (Fig. 4, Tables S8 & S9). The obligate seeder group had low resistance overall, and resistance changed minimally over time. Relative to this group, the pristine sprouter group had high but declining resistance, whereas the invaded sprouter group had strongly increasing resistance over time. The grass-forb group had an intermediate level of resistance and its resistance did not change over time. Variability among plots also differed considerably among groups; generally, pristine sprouter group resistance was more consistent than other groups (Fig. 4).

Stability increased over time in the obligate seeder group (Fig. 4, Table S9). Although we fitted a linear model, the data appear to resemble a saturating function with large changes in the first few intervals and smaller changes thereafter. Compared to this group, all others showed very little change in stability over time.

Discussion
The approaches demonstrated here provide managers with methods to track community change, quantify resilience in relation to disturbance, and identify communities at risk of sustained state transitions. The approach we have developed is, in numerical terms, considerably simpler than more commonly used ordination-based approaches. Defining plant communities based on plant functional types facilitates generalizations across sites and ecosystems and may help us identify broad principles to guide ecological restoration. Our $S_i$ and $I_i$ indices graphically
Figure 4. Plot resistance and stability for each community group over time relative to 1994 (x-axis: end year of the interval). Both metrics of resilience are calculated from the S-I space (Fig. 1A). Resistance is defined as the distance between a plot’s position in 1994 and in the end year of the interval. Stability is defined as the average distance moved by a plot during consecutive monitoring periods between 1994 and the end year of the interval. Both metrics are expressed as negative values so that less negative values indicate higher resistance/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 (Tables S8 & S9).

depict community changes in this ecosystem, but managers working in other ecosystems could replace them with indices that reflect the key functional attributes in those systems. In addition, we have demonstrated the utility of quantifying resistance and stability.

The distribution of the community groups we identified resemble the patterns in an NMDS ordination and qualitative state-and-transition model that Davies et al. (2012) developed using a different set of permanent monitoring plots from the same study area. Ordination techniques like NMDS, or more recent analytical techniques to identify ecological thresholds (e.g. Foley et al. 2015; Bagchi et al. 2017), provide robust, detailed information on community change. They are, however, computationally intensive and can be difficult to interpret. Furthermore, incorporating new data into ordinations can alter the distribution of previous observations relative to one another. By contrast, our approach is computationally simpler and easier to update with new data. The approach can also provide efficiency in field data collection—e.g. in our case study observers would only have to distinguish shrubs from herbaceous species and key nonnative species from all other species. This approach does, however, aggregate data to the plant functional type level, which may not capture dynamics of individual species of conservation interest. Additionally, those adopting the approach should be aware of requirements for meaningful data interpretations: (1) at least three time steps are needed to distinguish resistance and stability; (2) plots still need to be classified in terms of their dominant species’ functional traits if their exhibited dynamics are to be understood; (3) assignment of some functional traits (e.g. longevity, regeneration strategy) may require identification of plants to species level.

Community Group Trajectories in S-I Space

Initial plant functional type composition played a significant role in determining community responses to disturbance. Obligate seeder communities experienced the largest changes in composition. The canopy of obligate seeder shrubs was lost in nearly all plots following the 2000 fire, and plots became more invaded. Interestingly, shrub relative abundance increased in some obligate seeder plots following the 2007 wildfire. This increase was partly explained by a decline in herbaceous cover, but also by the fact that several plots experienced some recovery of obligate seeder shrubs and limited impacts of fires on the cover of previously less important resprouting shrubs. Changes in the positions of obligate seeder plots in S-I space following the 2000 wildfire, notably their shift into a new relatively distant basin of attraction, suggest that these sites have undergone a state transition.
By contrast, plots in the grass-forb group lacked dominant shrub cover in 1994, and remained stable with regards to their shrub component. However, the wildfire in 2000 appeared to provide an opportunity for invasive herbaceous species to gain a foothold. These plots generally moved little in S-I space following the 2007 wildfire and were usually less invaded in subsequent years. This difference suggests the compounded disturbance of the 2007 wildfire, in combination with extensive invasive species control efforts, did not lead to further invasion in the short term. Plots dominated by resprouting shrubs (i.e. the invaded sprouter and pristine sprouter groups) were organized along a gradient of invadedness, but repeated fires had little impact on their shrub cover. Instead, the repeated fires and restoration appeared to drive changes in the abundance of invasive species over time. The difference in the effects of these repeated fires on compositional dynamics highlights the need to consider responses to disturbances both holistically and individually as the effects of a particular disturbance can vary with its abiotic and biotic circumstances (Paine et al. 1998).

Controls on Community Stability and Resistance

Community groups differed significantly in resistance and stability. In particular, the obligate seeder group had lower resistance than the other groups over the entire monitoring period. By contrast, average resistance over the entire monitoring period was greatest in the invaded sprouter group. This was likely because the dominant shrub species were able to resprout, and because invasion did not cause large compositional changes. These results confirm predictions from Davies et al. (2012), the results of state-and-transition models (e.g. Chambers et al. 2014), and recent studies demonstrating that community compositional change in response to altered disturbance regimes is often tightly linked to initial biotic conditions (Mitchell et al. 2017).

Previous research in other shrub-dominated ecosystems has identified species regenerative traits as being critical in determining resilience to fire and alteration to disturbance regimes (Keeley 1986; Clarke et al. 2013). Given that the pristine sprouter, invaded sprouter, and grass-forb groups all showed comparatively high stability and resistance relative to the obligate seeder group, we can distinguish whether these metrics constitute “helpful” or “unhelpful” resilience (sensu Standish et al. 2014) by examining their temporal trends. Resistance in the pristine sprouter group was high on average, indicative of “helpful” resilience due to rapid postfire recovery. This resistance, however, gradually declined over time relative to the pattern in the obligate seeder group (i.e. the distance moved in S-I space relative to initial conditions tended to increase gradually over time in the pristine sprouter group). This decline may represent a combination of natural temporal compositional change and effects of compounded disturbance. These results underscore the importance of long-term monitoring for detecting subtle state transitions over extended timescales in addition to abrupt changes. In contrast, community composition in the obligate seeder group changed dramatically in the years following the first major wildfire, and less so in subsequent years. As a result, this group tended to increase in both stability and resistance over time, reflecting a transition to a degraded state from which it did not recover despite restoration efforts. This pattern is indicative of “unhelpful” resilience. Similarly, resistance and stability trends in the grass-forb and invaded sprouter groups suggest a limited potential for these plots to escape from their degraded compositions, indicating opportunities for additional active management interventions.

Plot stability was also a function of elevation, with higher elevation plots showing greater stability. Previous research has found that variation in resilience in desert ecosystems in western North America can be explained in terms of regional environmental variation, with mesic, colder sites (such as at higher elevations) more resilient to invasion than xeric, hotter sites typical of lower elevations (Brooks & Chambers 2011; Chambers et al. 2014). Dominant shrubs at higher elevations in this system also tend to be fire tolerant (e.g. through the ability to resprout), potentially reflecting their adaptation to historic fire frequencies (Miller et al. 2011; Chambers et al. 2014). In addition to the effects of prefire composition, this increase in compositional stability with elevation may also have been due to reduced environmental stress associated with more productive conditions resulting from higher precipitation and finer-textured soils. These results are important in the context of climate change, as previous research has shown significant interactions between plant reproductive functional traits, moisture availability, and ecosystem resilience to fire (Enright et al. 2014).

Neither restoration nor fire frequency were strong predictors of resistance or stability. The signal of restoration on plot resistance and stability in the 1994–2010 interval was likely masked by the main effects of community group (models of resistance and stability) and elevation (model of stability). Restoration treatments may take extended periods of time to manifest, and 2010 may have been too early to detect effects on resistance and stability. Fire frequency may not have been retained as a significant predictor of resistance and stability between 1994 and 2010 because the fires in this period affected either the majority or a minority of plots when they occurred. Robustly testing links between community resilience, trait composition, and fire regime characteristics will require data from a wider range of sites with greater variation in historical fire regimes.

Our analyses in this study use initial plant community composition (i.e. \( S_i \) and \( I_i \) values in 1994) as a benchmark against which to evaluate resistance and stability. Other reference conditions may be of interest, however, depending on monitoring program goals. Managers may be interested in community departure relative to a specific reference condition, such as an \( S_i \) of >0.25 and \( I_i \) of <0.25. Plot positions in S-I space could be calculated relative to these specific targets, and could be used to evaluate community resistance and stability over time.

Implications for Sagebrush Steppe Monitoring, Restoration, and Management

Our findings add to mounting evidence that plant functional traits, particularly those associated with life history and growth form, play an important role in controlling the resilience of
vegetation communities to disturbance (e.g. Enright et al. 2014; Zirbel et al. 2017). However, responses of additional components of ecosystem resilience beyond the traits of dominant vascular plant functional groups should be taken into account (e.g. faunal and microbiotic soil crust communities), as they are not included in our resilience metrics and may respond differently to repeated fires. Here, we found that the resilience (as defined by plant functional type relative dominance) of shrub-steppe communities to repeated wildfire was contingent on prefire biotic conditions and underlying abiotic conditions. Specifically, low-elevation communities initially dominated by obligate seeders were less resistant to degradation following wildfire, but tended to become more stable over time, reflecting a transition to a degraded state from which they did not recover despite restoration efforts. Even so, the resilience of this community type may still be over-estimated as $S_i$ is calculated at the functional type level and does not account for species-specific compositional changes, particularly the loss of big sagebrush, a foundation species in this system (Knick et al. 2005).

These results suggest that difficult questions need to be asked about future targets for restoration in these types of highly fire-prone systems. Planting or seeding shrubs in environmentally stressful, low-elevation sites may be a costly (e.g. Dettweiler-Robinson et al. 2013) and largely fruitless exercise. Alternatively, restoration resources in these communities could prioritize fire risk management, with planting and seeding efforts focused in more environmentally amenable areas that already contain fire-tolerant species and that may be more resistant to invasion.

To assess the success of restoration interventions, managers need to be able to quickly and easily describe how ecosystems are changing. Generalized descriptions of ecosystem dynamics based on functional types have been proposed by a number of previous authors (e.g. Gondard et al. 2003) and other options for assessing ecosystem condition also exist—e.g. using Indicators of Rangeland Health (Kachergis et al. 2011) or developing species-based state-and-transition models for defined geographic areas (Bestelmeyer et al. 2016). Focusing on plant functional types derived from species traits may help identify differences in ecological function among sites while providing more readily comparable and generalizable descriptions of vegetation change (e.g. Boyd & Svejcar 2011). In our system, plant traits related to fire are key, though critical traits would likely differ in other ecosystems. An advantage of our approach is that while we use long-term data from a sagebrush-steppe ecosystem, it can be tailored to capture any functional differences among species that are of interest to restoration ecologists and practitioners in a variety of systems. The methodologies developed here provide a relatively straightforward method to track ecosystem change as evidenced in changes within dominant plant functional types, to assess community resilience over both short and long time intervals, and to evaluate restoration success.

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LITERATURE CITED

Allen-Diaz B, Bartolome JW (1998) Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. Ecological Applications 8:795–804

Babak N (2015) usdm: uncertainty analysis for species distribution models. R package version 1.1-15. https://CRAN.R-project.org/package=usdm (accessed 19 Oct 2019)

Bagchi S, Briske DD, Bestelmeyer BT, Ben Wu X (2013) Assessing resilience and state-transition models with historical records of cheatgrass Bromus tectorum invasion in North American sagebrush-steppe. Journal of Applied Ecology 50:1131–1141

Bagchi S, Singh NJ, Briske DD, Bestelmeyer BT, McClaran MP, Murthy K (2017) Quantifying long-term plant community dynamics with movement models: implications for ecological resilience. Ecological Applications 27:1514–1528

Bakker JD, Dunwiddie PW, Hall SA, Evans JR, Davies GM, Dettweiler-Robinson E (2011) Vegetation impacts of recurring fires on sagebrush ecosystems in Washington: implications for conservation and rehabilitation. Final Report to the Joint Fire Science Program for Project 08-1-5-20

Bestelmeyer BT, Briske DD (2012) Grand challenges for resilience-based management of rangelands. Rangeland Ecology & Management 65:654–663

Bestelmeyer BT, Williamson JC, Talbot CJ, Cates GW, Dunway MC, Brown JR (2016) Improving the effectiveness of ecological site descriptions: general state-and-transition models and the ecosystem dynamics interpretive tool (EDIT). Rangelands 38:329–335

Bestelmeyer BT, Ash A, Brown JR, Densambuu B, Fernández-Giménez M, Johanson J, et al. (2017) State and transition models: theory, applications, and challenges. Pages 303–345. In: Briske D (ed) Rangeland systems. Springer Series on Environmental Management. Springer, Cham, Switzerland

Boyd CS, Svejcar TJ (2011) The influence of plant removal on succession in Wyoming big sagebrush. Journal of Arid Environments 75:734–741

Briske DD, Fuhlendorf SD, Smeins FE (2003) Vegetation dynamics on rangelands: a critique of the current paradigms. Journal of Applied Ecology 40:601–614

Briske DD, Illius AW, Anderies JM (2017) Nonequilibrium ecology and resilience theory. In: Briske D (ed) Rangeland systems. Springer Series on Environmental Management. Springer, Cham, Switzerland

Brooks ML, Chambers JC (2011) Resistance to invasion and resilience to fire in desert shrublands of North America. Rangeland Ecology & Management 64:431–438

Brudvig LA, Barak RS, Bauer JT, Caughlin TT, Laughlin DC, Larios L, Matthews JW, Stuble KL, Turley NE, Zirbel CR (2017) Interpreting variation to advance predictive restoration science. Journal of Applied Ecology 54:1013–1017

Chambers JC, Miller RF, Board DI, Pyke DA, Rouny BA, Grace JB, Schupp EW, Tausch RJ (2014a) Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology & Management 67:440–454

Chambers JC, Bradley BA, Brown CS, D’Antonio C, Germino MJ, Grace JB, Hardegree SP, Miller RF, Pyke DA (2014b) Resilience to stress and
disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytologist 197:19–35

Davies KW, Bates JD & Boyd CD. (2016). Effects of intermediate-term grazing rest on sagebrush Communities with depleted under stories: evidence of a threshold. Rangel and Ecology & Management, 69, 173–178.

Davies KW, Boyd CS, Beck JL, Bates JD, Svejcar TJ, Gregg MA (2011) Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 44:2573–2584

Davies GM, Bakker JD, Dettweiler-Robinson E, Dunwiddie PW, Hall SA, Downs J, Evans JR (2012) Trajectories of change in sagebrush-steppe vegetation communities in relation to multiple wildfires. Ecological Applications 22:1562–1577

Dettweiler-Robinson E, Bakker JD, Evans JR, Newsome H, Davies GM, Wirth TA, Pyke DA, Easterly RT, Salstrom D, Dunwiddie PW (2013) Outplanting Wyoming big sagebrush following wildfire: stock performance and economics. Rangeland Ecology & Management 66:657–666

Enright NJ, Fontaine JB, Lamont BB, Miller BP, Westcott VC (2014) Resistance and resilience to changing climate and fire regime depend on plant functional traits. Journal of Ecology 102:1572–1581

Evans JR, Lih MP (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, Washington

Foley MM, Martone RG, Fox MD, Kappel CV, Mease LA, Erickson AL, Halpern BS, Selkoe KA, Taylor P, Scarborough C (2015) Using ecological thresholds to inform resource management: current options and future possibilities. Frontiers in Marine Science 2:1–12

Gondard H, Jauffret S, Aronson J, Lavorel S (2003) Plant functional types: a dynamic models of biodiversity: at the crossroads between functional and economics. Rangeland Ecology & Management 66:657–666

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910

Hann WJ, Jones J.L., Keane R.E., Hessburg P.F. & Gravenmier R.A. (1998). ICBEMP: Landscape Dynamics, Journal of Forestry, 96, 10–15

Holling CS (1973) Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23

Isabelle B, Pauline P, Sylvain A, Roland D, Luc G, Sébastien L, Lavorel S, Van Es J, Vittor P, Wilfried T (2012) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. Global Change Biology 8:3464–3475

Kacheris E, Roca ME, Fernandez-Gimenez ME (2011) Indicators of ecosystem function identify alternate states in the sagebrush steppe. Ecological Applications 21:2781–2792

Karl JW, Duniway MC, Schrader TS (2012) A technique for estimating range-land canopy-gap size distributions from high-resolution digital imagery. Rangeland Ecology & Management 65:196–207

Keeley JE (1986) Resilience of Mediterranean shrub communities to fires. Pages 95–112. In: Resilience in Mediterranean-type ecosystems. Springer, Dordrecht, The Netherlands

Knapp PA (1996) Cheatgrass (*Bromus tectorum*) dominance in the Great Basin desert: history, persistence, and influences to human activities. Global Environmental Change 6:37–52

Knick ST, Holmes AL, Miller RF (2005) The role of fire in structuring sagebrush habitats and bird communities. Pages 63–75. In: Saab VA, Powell DW (eds) Fire and avian ecology in North America. Studies in Avian Biology No. 30. Cooper Ornithological Society, Camarillo, California

Kraskul JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29:1–27

Kuhn M, Weston S, Wing J, Forester J, Thaler T (2013) contrast: A collection of contrast methods. R package version 0.19. https://CRAN.R-project.org/package=contrast (accessed 19 Oct 2019)

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556

Mären IE, Vandvik V, Ekelund K (2008) Restoration of bracken-invaded heathlands: effects on vegetation dynamics and non-target species. Biological Conservation 141:1032–1042

McArthur ED, Sanderson SC (1999) Cytogeography and chromosome evolution of subgenus *Tridentata* of *Artemisia* (Asteraceae). American Journal of Botany 86:1754–1775

Miller RF, Knick ST, Pyke DA, Meinke CW, Hanser SE, Wisdom MJ, Hild AL (2011) Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–185. In: Knick ST, Connelly JW (eds) Greater sage-grouse—ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California

Mitchell RM, Bakker JD, Vincent JB, Davies GM (2017) Relative importance of abiotic, biotic, and disturbance drivers of plant community structure in the sagebrush steppe. Ecological Applications 27:756–768

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solynos M, Stevens MHH, Szoecs E, Wagner H (2018) vegan: community ecology package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan (accessed 19 Oct 2019)

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. Ecosystems 1:535–545

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018) nlme: linear and nonlinear mixed effects models. R package version 3.1-137. http://CRAN .R-project.org/package=nlme (accessed 19 Oct 2019)

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R- project.org (accessed 19 Oct 2019)

Schefler M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591

Schröder A, Persson L, De Roos AM (2005) Direct experimental evidence for alternative stable states: a review. Oikos 110:3–19

Society for Ecological Restoration International Science & Policy Working Group (2004) The SER international primer on ecological restoration. Society for Ecological Restoration International, Washington, D.C. www.ser.org

Soll J, Hall JA, Pabst R, Soper C (1999) Biodiversity inventory and analysis of the Hanford site. Final report: 1994–1999. The Nature Conservancy, Seattle, Washington

Standish RJ, Hobbs RJ, Mayfield MM, Bestelmeyer BT, Suding KN, Battaglia LL, et al. (2014) Resilience in ecology: abstraction, distraction, or where the action is? Biological Conservation 177:43–51

USDA NRCS (2018) The PLANTS database. National Plant Data Team, Greensboro, NC 27401–4901 U.S.A. http://plants.usda.gov (accessed 15 Jul 2018)

Venables WN, Ripley BD (2002) Modern applied statistics with S. Fourth edition. Springer, New York

Wijayaratne UC, Pyke DA (2012) Burial increases seed longevity of two sagebrush steppe communities. Pages 95–112. In: Resilience in Mediterranean-type ecosystems. Springer, New York

Wijayaratne UC, Pyke DA (2012) Burial increases seed longevity of two *Artemisia tridentata* (Asteraceae) subspecies. American Journal of Botany 99:438–477

Wilderman DW (1994) Plant communities of the Fitzner/Eberhardt arid lands vegetation communities in relation to multiple wildfires. Ecological Applications 22:1562–1577

Yañez-Aldama J, Vélez H, Correa LF, Ceballos E, Garay-Echeverri L, et al. (2014) Tracking community trajectories and resilience of *Artemisia tridentata* (Asteraceae) subsp. *bochotensis*. Ecological Monographs 84:438–462

Yi YV, Wang Z, Song Y, Wang B, Zhang Z, et al. (2014) Tracking community trajectories and resilience of *Artemisia tridentata* (Asteraceae) subsp. *bochotensis*. Ecological Monographs 84:438–462

**Supporting Information**

The following information may be found in the online version of this article:

**Supplement S1:** R Script for calculating bivariate shrub and invadedness indices, and resilience metrics.

**Figure S1:** Relationship between elevation (y-axis), community group identity (x-axis), and restoration.
Figure S2. Wisconsin double-standardized cover values in 1994 of nine plant functional types in four community groups.
Figure S3. Dendrogram produced from hierarchical cluster analysis.
Figure S4. Plot positions (points) in S-I space.
Figure S5. (A) Photograph from a permanent plot on ALE in the obligate seeder group in 1994. (B) Photograph taken in the near vicinity of this plot in 2002, and (C) in 2009.
Figure S6. Relationship between stability and resistance for each plot (n = 32).
Table S1. Summary of plot fire and restoration histories.
Table S2. Details of the 148 taxa recorded during monitoring of permanent plots between 1994 and 2010.

Table S3. Average abundance (unstandardized estimate of percent cover based on cover classes.
Table S4. Species richness within each functional type within each community group.
Table S5. Summary of final linear models.
Table S6. Results of the post hoc pairwise contrasts following the linear model of resistance.
Table S7. Results of the post hoc pairwise contrasts following the linear model of stability.
Table S8. Summary of linear mixed-effects models of the effect of functional community group.
Table S9. Coefficients from mixed-effects models of resistance and stability.

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