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Quantifying long-term plant community dynamics with movement models: implications for ecological resilience

Sumanta Bagchi,[1,6] Navinder J. Singh,[2] David D. Briske,[3] Brandon T. Bestelmeyer,[4]
Mitchel P. McClaran,[5] and Karthik Murthy[1]

[1]*Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012 India*
[2]*Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå SE-90183 Sweden*
[3]*Department of Ecosystem Science and Management, Texas A&M University, 2120 TAMU, College Station, Texas 77843 USA*
[4]*USDA-ARS, Jornada Experimental Range, New Mexico State University, Las Cruces, New Mexico 88003 USA*
[5]*School of Natural Resources and the Environment, University of Arizona, P.O. Box 210137, Tucson, Arizona 85719 USA*

Abstract. Quantification of rates and patterns of community dynamics is central for understanding the organization and function of ecosystems. These insights may support a greater empirical understanding of ecological resilience, and the application of resilience concepts toward ecosystem management. Distinct types of dynamics in natural communities can be used to interpret and apply resilience concepts, but quantitative methods that can systematically distinguish among them are needed. We develop a quantitative method to analyze long-term records of plant community dynamics using principles of movement ecology. We analyzed dissimilarity of species composition through time with linear and nonlinear statistical models to assign community change to four classes of movement trajectories. Compositional change in each sampled plot through time was classified into four classes, stability, abrupt nonlinear change, transient reversible change, and gradual linear drift, each representing a different aspect of ecological resilience. These competing models were evaluated based on estimated coefficients, goodness of fit, and parsimony. We tested our method's accuracy and robustness through simulations, or the ability to distinguish among trajectories and classify them correctly. We simulated 16,000 trajectories of four types, of which 94–100% were correctly classified. Next, we analyzed 13 long-term vegetation records from North American grasslands (annual grasslands with warm-season and cool-season communities, shortgrass, mixedgrass, and tallgrass prairies, and sagebrush steppe), and a record of primary succession at Mt. St. Helens volcano. Collectively, we analyzed 14,647 observations from 775 plots, between 1915 and 2012. Dynamics could be reliably assigned for 705 plots (91%), and overall statistical fit was high (goodness of fit, 0.77 ± 0.15 SD). Among the perennial grasslands, stability was most common (44% of all plots), followed by gradual linear (22%), abrupt nonlinear (17%), and reversible (6%) change. Among annual grasslands, abrupt nonlinear shifts (33%) were more common in the warm-season community than in the cool-season (20%). As expected, abrupt nonlinear change was common during primary succession (51%) while reversible change was rare (3%). Generally, reversible dynamics often required 2–3 decades. Analysis of long-term community change, or trajectories, with principles of movement ecology provides a quantitative basis to compare and interpret ecological resilience within and among ecosystems.

Key words: long-term monitoring; model selection; multiple equilibria; nonlinear regression; parsimony; resilience indicators; time series; tipping points; vegetation change.

Introduction

Species composition in plant communities varies through time in response to a variety of factors, both natural and anthropogenic. It may also change in response to endogenous processes unrelated to any external forcing. Distinguishing between different trajectories of community change, their associated timescales, and the ability to predict future trajectories, has important implications for ecosystem ecology and management (Fukami and Nakajima 2011). Trajectories of community change provide insights into ecological resilience by revealing whether an ecosystem is resistant to change, undergoes abrupt and persistent change, or whether it can recover its previous composition after disturbance (Beisner et al. 2003, Standish et al. 2014). Measurements of these trajectories can clarify the temporal scales of dynamics when long-term records exist (Suding et al. 2008, Thrush et al. 2009).

We explore whether rates and patterns of dynamics in native plant communities can be categorized into four fundamental trajectories that relate to distinct resilience concepts (Table 1, Figs. 1, 2; Holling 1973, Beisner et al. 2003, Nolting and Abbott 2016):

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[6] E-mail: sbagchi@ces.iisc.ernet.in

TABLE 1. Summary of four vegetation trajectories quantitatively identified by our analysis and their corresponding resilience concepts that are illustrated with familiar ball-and-cup heuristic.

Vegetation trajectory	Corresponding resilience concepts	Ball-and-cup heuristic
Stability	resistance, or asymptotic state with strong attractor	Fig. 2a
Reversible change	engineering resilience, transient dynamics near an attractor of intermediate strength	Fig. 2b
Abrupt nonlinear change	state transition, threshold, regime shift, tipping point	Fig. 2c
Gradual linear change	nonequilibrium, phase shift, lack of strong attractor, change in basins of attraction	Fig. 2d

1. *Stability*: species composition does not undergo any appreciable change over time (c.f. "resistance"), and species' abundances in initial and subsequent observations remain similar.
2. *Abrupt nonlinear shift*: a relatively sudden community change in which compositional dissimilarity between initial and subsequent observations persists through time.
3. *Reversible change*: major community changes that later return to a former configuration, reflected as initial increases in compositional dissimilarity that are followed by increasing similarity with initial composition.
4. *Gradual linear shift*: slow incremental community change in which species composition progressively trends away from initial conditions.

We propose that metrics used to quantify animal movement paths are broadly analogous to trajectories of plant community change, and we draw on these principles to analyze long-term records of vegetation dynamics (Nathan et al. 2008, Schick et al. 2008, Bunnefeld et al. 2011, Singh et al. 2012). Movement metrics may provide a robust means for classifying the trajectory of composition change in plant communities (Fig. 1, Table 1). In animal ecology, movement paths (i.e., change in location over time) can be migratory, nomadic, or dispersive, while lack of movement is residence (Bunnefeld et al. 2011, Singh et al. 2012). Mathematical and statistical properties of these movement paths can characterize and differentiate these trajectories. A number of theoretical models, such as random walks, first passage time, and Lévy flights, have been developed over the past decades to distinguish these movement paths (Turchin 1998, Schick et al. 2008). Recent advances include the use of displacement as a time-dependent metric (Borger and Fryxell 2012). This represents the distance from an initial location to each subsequent location along a documented movement path through time (Borger and Fryxell 2012, Singh et al. 2012). When used in combination with linear and nonlinear statistical models, these metrics can quantify rates and patterns of both animal movement and vegetation change over time.

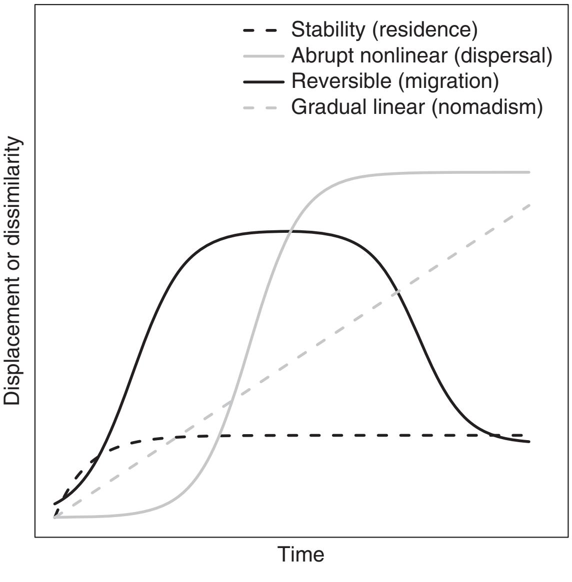

FIG. 1. Concept diagram of four categories of animal movement trajectories (Bunnefeld et al. 2011, Singh et al. 2012), and their correspondence with trajectories of vegetation change.

We propose that models of animal movement paths can approximate recognized plant community trajectories over time in multivariate space of species composition, and apply these models to data from 14 long-term vegetation monitoring sites. The magnitude and direction of species composition change can be represented with distance-based metrics such as a dissimilarity index of species composition (e.g., Bray-Curtis dissimilarity). Such indices are robust representations of ecological distance (Faith et al. 1987). When depicted as a time series, the distance between each successive sample, relative to initial conditions, corresponds to community displacement in multivariate space, or the trajectory of change (Fig. 1). We fit linear and nonlinear statistical models to time series data on change in plant community species composition in order to classify each plot to one of four trajectories (Fig. 1, Table 1; Bunnefeld et al. 2011, Singh et al. 2012). Stability in plant communities is analogous to residence in animal movement because dissimilarity changes little over time. Abrupt nonlinear shifts are analogous to animal dispersal because dissimilarity increases abruptly and it persists through time. Reversible change is analogous to animal migration as the community eventually returns toward a reference composition. Finally, gradual linear drift is analogous to animal nomadism in which dissimilarity gradually increases as different species appear and disappear from the community (Fig. 2, Table 1). Collectively, these behaviors encompass various aspects of plant community dynamics

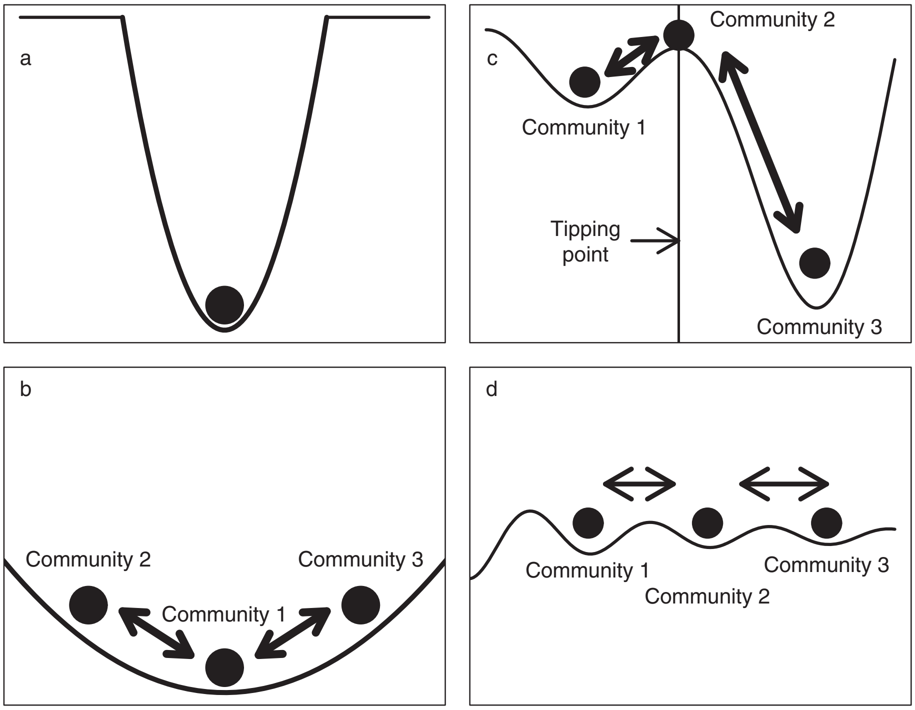

FIG. 2. Illustrative ball-and-cup diagrams corresponding to resilience concepts listed in Table 1: (a) stability, (b) reversible change, (c) abrupt nonlinear change, and (d) gradual linear change.

(Beisner et al. 2003, Bestelmeyer 2006, Bestelmeyer et al. 2011*a*, Bagchi et al. 2012, 2013). By considering the relative frequency of these behaviors among a collection of plots within a monitoring site, we can draw inferences about the resilience characteristics of those sites and develop hypotheses to interpret the potential underlying mechanisms.

When depicted as a time series, the distance between each successive sample, relative to initial conditions, corresponds to community displacement in multivariate space, or the trajectory of change (Fig. 1). Our goals are (1) to develop a simple analytical method to classify long-term time series data to one of the four trajectories, (2) evaluate our method using 14 long-term data sets of vegetation change, including a well-known example of primary succession (Table 2), and (3) relate these trajectories to concepts of ecological resilience (Fig. 2). As proof of concept, we use simulations to evaluate the accuracy and robustness of this method, or the ability to classify trajectories correctly for data where parameters are known. Additionally, we compare our results against available methods to quantify rates and patterns of vegetation change through time.

We expected the relative frequency of different trajectories to vary predictably across the sites (Table 2). Dynamics at Mt. St. Helens (*Lawetlat'la*) should reflect abrupt nonlinear dynamics due to the intransient nature of primary succession in the plots affected by the volcano in 1980, but should show stability in the control plots that were from unaffected areas. Stability and reversible dynamics would be common in prairies and steppes, as these change little or recover from perturbations quickly (Bestelmeyer et al. 2013, Porensky et al. 2017). Gradual linear and abrupt nonlinear dynamics would be most common in the annual grasslands that are thought to be dominated by nonequilibrium behaviors (Bartolome et al. 2009); the warm season community was expected to be more changeable than the cool season community. Abrupt nonlinear changes related to thresholds (or tipping points) should also be represented in the desert grasslands that have experienced shrub encroachment (Ratajczak et al. 2014) and/or prolonged droughts (Bestelmeyer et al. 2011*a*).

MATERIALS AND METHODS

Long-term data sets

We use long-term vegetation records of plant species abundance from 14 sites across North America, including primary succession at Mt. St. Helens (Table 2). They included prairies, desert grasslands, and sagebrush steppe, spanning a broad latitudinal gradient across North America, and covering a wide range of mean annual precipitation and temperature, as well as plant growth form and life histories. These data sets used permanent quadrats or transects to census density of plant species, and represent the efforts of ecologists beginning in the early 20th century (Clements 1907).

Grazing is the predominant land use across most of these sites, and many experienced intensive livestock

Table 2. Summary of long-term vegetation records used in our analysis.

	Site	Description	Precipitation (mm/yr)	Data span	Plot size	Plots	Temporal replicates	Key data source
1	Staveley, Alberta, Canada	northern prairie	334 ± 10	1949–1981	1 m^2	14 ± 1 (17)	28	Douwes and Willms (2012)
2	Ft. Keough, Montana, USA	northern prairie	310 ± 27	1932–1945	1 m^2	38 ± 1 (44)	14	Anderson et al. (2011)†
3	U.S. Sheep Experiment Station, USSES, Idaho, USA	sagebrush steppe	282 ± 12	1923–1973	1 m^2	24 ± 3 (26)	29	Zachmann et al. (2010)‡
4	Idaho National Lab, INL, Idaho, USA	sagebrush steppe	199 ± 13	1950–2006	1 m^2	34 (34)	10	Anderson and Inouye (2001), Forman et al. (2010)
5	Nunn, Colorado, USA	shortgrass prairie	332 ± 28	1997–2010	1 m^2	23 ± 1 (24)	14	Chu et al. (2013)§
6	Fort Hays, Kansas, USA	mixedgrass prairie	595 ± 26	1932–1972	1 m^2	41 ± 1 (47)	41	Adler et al. (2007)¶
7	Foraker, Oklahoma, USA	tallgrass prairie	940 ± 75	1998–2009	1 m^2	80 (80)	12	McGlinn et al. (2010)#
8	Sonora, Texas, USA	mixedgrass prairie	555 ± 39	1949–1993	1 m^2	92 ± 6 (119)	17	Fuhlendorf et al. (2001)
9	Jornada Basin, New Mexico, USA	Chihuahuan Desert (perennial)	230 ± 10	1915–1979	1 m^2	38 ± 3 (69)	59	Chu et al. (2014)‖
10	Santa Rita (q), Arizona, USA	Sonoran Desert	364 ± 32	1915–1947	1 m^2	15 ± 1 (54)	22	Anderson et al. (2012)††
11	Santa Rita (*t*), Arizona, USA	Sonoran Desert	364 ± 32	1953–2012	30.5 m	65 ± 1 (68)	27	Bagchi et al. (2012)
12	Portal, Arizona, USA (summer)	Chihuahuan Desert (annual)	435 ± 35	1983–2002	1 m^2	24 (24)	20	Ernest et al. (2009) and Ernest et al. (2016)‡‡,§§
13	Portal, Arizona, USA (winter)	Chihuahuan Desert (annual)	435 ± 35	1983–2002	1 m^2	23 ± 1 (24)	20	Ernest et al. (2009)‡‡,§§
14	Mt. St. Helens, Washington, USA	primary succession	~1100	1980–2009	0.25 m^2	51 ± 2 (55)	30	del Moral (2010)¶¶

Note: Precipitation values are mean ± SE; plots are number of plots sampled per year, with total number of plots in the data set in parentheses; temporal replicates refer to the number of times data were collected each year.

† Ecological Archives: https://dx.doi.org/10.1890/11-0193.1.

‡ Ecological Archives: https://dx.doi.org/10.1890/10-0404.1.

§ Ecological Archives: https://dx.doi.org/10.1890/13-0121.1.

¶Ecological Archives: https://dx.doi.org/10.1890/0012-9658(2007)88[2673:lmqfkp]2.0.co;2.

#Ecological Archives: https://dx.doi.org/10.1890/09-2017.1.

‖https://dx.doi.org/10.1111/jvs.12106.

††Ecological Archives: https://dx.doi.org/10.1890/11-2200.1.

‡‡Ecological Archives: https://dx.doi.org/10.1890/08-1222.1.

§§Ecological Archives: https://dx.doi.org/10.1890/15-2115.1.

¶¶Ecological Archives: https://dx.doi.org/10.1890/09-2357.1.

grazing in the early 20th century. Many sites are currently grazed by livestock at moderate intensities, and also support native grazers. Some sites were also affected by the major droughts of the 1930s and 1950s, especially the southern and central grasslands and deserts. These sites also have a history of invasion by nonnative species and encroachment by native woody plants in the past century (e.g., cheatgrass *Bromus tectorum* in the Intermountain West, mesquite *Prosopis glandulosa* and *P. velutina* and creosotebush *Larrea tridentata* in the southern deserts). Nonnative perennial grasses were introduced at several sites to provide additional livestock forage: Lehmann's lovegrass *Eragrostis lehmanniana* in the southern regions and crested wheatgrass *Agropyron cristatum* in the northern prairies (for more historical details see Weaver and Albertson 1936, Albertson and Tomanek 1965, Buffington and Herbel 1965, Mack and Thompson 1982, Gibbens et al. 2005, McClaran et al. 2010).

Data analysis

We used the net displacement approach, combined with linear and nonlinear statistical models, to distinguish stable (residence), abrupt nonlinear (dispersal), reversible (migratory), and gradual linear (nomadic) vegetation dynamics (Bunnefeld et al. 2011, Singh et al. 2012). From species abundance data in individual plots (quadrats, or transects, Table 2), we calculated Bray-Curtis dissimilarity index as a time series, for each successive observation relative to initial conditions, or net ecological displacement. Data from the Oklahoma site were in presence/absence form, and here we used Sorensen dissimilarity index.

Many indices exist to calculate species dissimilarity, and the Bray-Curtis index is bounded between 0 and 1 (i.e., between 0% and 100% species dissimilarity, as is the Sorensen index). Alternative indices are unbounded, e.g., Euclidean distance. Consequently, choice of index may have an influence on overall interpretation. We found both indices, Bray-Curtis and Euclidean, to be strongly correlated (r = 0.54–0.88, and $P < 0.001$, for different sites), and report results from the Bray-Curtis index; we briefly discuss the congruence between bounded (Bray-Curtis) and unbounded (Euclidean) indices in the Supplementary Material (Appendix S1: Fig. S1). For all data sets, we included species that occurred in >2% of samples, and excluded the rarer species.

Next, we fit the dissimilarity estimates from each plot to mathematical functions defined for each behavior (Fig. 1, Table 1). Both linear and nonlinear aspects of community dynamics are adequately addressed by this approach (Bunnefeld et al. 2011, Borger and Fryxell 2012). Stability (Fig. 1) is defined using an asymptotic model from the onset of movement as $\varphi_1[1 - \exp(\varphi_2 t)]$, where ϕ_1 is the asymptote at the steady-state equilibrium and ϕ_2 is the logarithm of the rate constant. Abrupt nonlinear shift (Fig. 1) is defined by a logistic model as $\frac{\delta}{1+\exp\left(\frac{\theta-t}{\varphi}\right)}$, where δ is the asymptotic height, θ is the time at which dispersal reaches half δ, φ is the time between reaching one-half and three-quarters of migration, and t is the time since beginning. Reversible change (Fig. 1) is defined by a double sigmoid mathematical function that estimates the distance, timing of onset and return phases (θ_o and θ_r, respectively), and duration of onset and return (φ_o and φ_r, respectively) as $\frac{\delta_o}{1+\exp\left(\frac{\theta_o-t}{\phi_o}\right)} - \frac{\delta_r}{1+\exp\left(\frac{\theta_r-t}{\phi_r}\right)}$. Here δ_o and δ_r are the asymptotic height for onset and return phases of migration, θ_o and θ_r are the time of onset and return phases at which migration reaches one-half of its asymptotic height, φ_o and φ_r are the time elapsed between reaching one-half and three-quarters of the migration distance for onset and return phases, and t is time interval since beginning of the record. Since reversibility in plant community composition may not be exact, and former relative abundance of all participant species may not be perfectly recovered, we considered the asymptote may differ between the onset and return phases of migration, such that $\delta_o \neq \delta_r$ (Bunnefeld et al. 2011). Finally, gradual linear change (Fig. 1) is defined with a linear model as $\alpha t + \varepsilon$, where α is the diffusion constant and t denotes the time since beginning of the record, and ε is an error term representing the intercept. The model parameters for shape correspond to relative time spent in different stages of various movement trajectories (Bunnefeld et al. 2011, Singh et al. 2012). It is possible that reversible dynamics can be the result of two consecutive regime shifts, where the latter counteracts the former. While such instances would likely be rare, they cannot be easily distinguished from typical transient dynamics in our analysis with a double sigmoid mathematical function. Also, with sudden modifications to drivers of change, it is possible that a plot is placed into a new trajectory. For example, a plot that starts on a linear trajectory can undergo a shift into an abrupt nonlinear trajectory. So, in addition to the four ideal types (Fig. 1, Table 1), there are rare possibilities of encountering mixed trajectories in real data; these mixed trajectories would not be correctly classified by our method.

Displacement, or the time series of Bray-Curtis dissimilarity, from all plots were fitted to each mathematical function in package nlme for R environment (Pinheiro and Bates 2000). The time series for each site, including all replicates, were analyzed separately. Since long-term data represent a time series, we performed the analysis with serial autocorrelation through time (first-order autoregressive), as this is a simple covariance structure that involves only a few parameters (Cryer and Chan 2008). Best-fit model for each plot was evaluated using a combination of participant coefficient values, goodness of fit, and parsimony (Bastille-Rousseau et al. 2016, de Grissac et al. 2016, Singh et al. 2016). We judged goodness of fit with the concordance criterion (i.e., CC; Vonesh et al. 1997, Huang et al. 2009), because traditional estimators for linear models, e.g., r^2 based on least-squares calculations, are unsuitable for nonlinear models (Spiess and Neumeyer 2010). CC measures the level of agreement between the observed and predicted values for linear and nonlinear models. CC ≤ 0 indicates lack of fit, and CC $= 1$ indicates perfect fit, where

$$\mathrm{CC}_i = 1 - \frac{\sum_{j=1}^{n_i}\left(y_{ij} - \hat{y}_{ij}\right)^2}{\sum_{j=1}^{n_i}\left(y_{ij} - \bar{y}\right)^2 + \sum_{j=1}^{n_i}\left(\hat{y}_{ij} - \bar{\hat{y}}\right)^2 + n_i\left(\bar{y} - \bar{\hat{y}}\right)^2}$$

Here $\bar{y}$ and $\bar{\hat{y}}$ are the mean of the observed (y_{ij}) and predicted ($\bar{\hat{y}}_{ij}$) values for sample i and n_i is the sample-specific number of observations in the time series. We judged parsimony with the Akaike information criterion (AIC), with ΔAIC = 2 between competing models. First, we checked whether the fitted model yields meaningful coefficient estimates. Here, we verified if the coefficients were of the correct sign, and whether they were distinguishable from zero at $P = 0.10$. (For example, whether parameter $\alpha > 0$ for the fitted linear model.) Second, we checked if the model with highest CC was also supported by AIC. If not, then we checked the model with second-highest CC and its corresponding support from AIC. If no winning model emerged at this third step, then we considered the plot to be unresolved. This three-step screening to identify the best-fit model ensures that (1) a model is built with meaningful coefficients, (2) the coefficients describe the data well, and (3) that all coefficients are necessary. From coefficients, CC, and AIC of each model, we assigned the plots (Table 2) as stable, reversible, abrupt nonlinear, or gradual linear. We also identified the plots where the best-fit model was poor-fit (>2 SD below the mean CC-score across the data sets). Example computer code for model fitting is provided in the Supplementary Material (Appendix S2).

Checking accuracy and robustness through simulations

We used a simulation approach to verify the accuracy and robustness of this method, or the ability to classify trajectories correctly and consistently. We simulated data that mimic the real data sets, but with known model coefficients. Next, we performed the analysis to evaluate if samples were correctly assigned to their respective types. We simulated $n = 40$ samples (i.e., plots) over $t = 40$ time steps (i.e., years) for each of the four trajectories. We repeated this set of simulations 100 times to estimate average accuracy (i.e., consistency) of our method in successful classification.

Comparison with time lag analysis method

Collins et al. (2000) introduced time lag analysis (TLA) as a distance-based approach to quantify rates and patterns of vegetation change. Briefly, community dissimilarity is regressed against increasing time-lags to allow inference over trajectories of change. An increasing trend (positive slope) represents a directional shift away from initial conditions. No slope (zero) represents stability. A decreasing trend (negative slope) represents convergence toward a former state. More recent methods include principal coordinate of neighborhood matrices combined with redundancy analysis (PCNM-RDA; Angeler et al. 2009). However, general performance of more complex PCNM-RDA models and the simpler TLA models are comparable for species-rich communities undergoing weakly deterministic changes (Angeler et al. 2009). Therefore, we compare our results against corresponding TLA models. Admittedly, TLA was not designed to differentiate between the different linear and nonlinear dynamics as envisioned in Table 1. Rather, TLA offers a summary of whether directional changes are occurring at a site; it can also enable assessments of variation in behaviors among replicates at a site in a comparative framework (Collins and Xia 2015).

RESULTS

With simulations ($n = 40$ plots, $t = 40$ yr, of each of the four trajectories for 100 iterations), we evaluated a total of 16,000 trajectories (40 × 4 × 100). The simulated data contained adequate noise and mimicked the patterns in real data sets (Fig. 3). Overall, classification was very accurate and consistent (between 94% and 100% accurate classification, Table 3).

We found evidence of all four trajectories (Fig. 4) in several data sets. In comparison, trends from time-lag analysis were often unable to distinguish between these trajectories (Fig. 5). Across the sites, 70 plots (9%) either showed poor convergence, or showed comparable fit to more than one model and remained unresolved. Model fit was high overall, with CC score 0.77 ± 0.15 (mean ± SD; Fig. 6). The best-fit models had poor fit (2 SD units below mean CC, Fig. 6) in only eight plots (1%). These few instances of unresolved behaviors, and poor-fit models were not restricted to any single data set.

Abrupt nonlinear (51%) and stable (44%) trajectories were most common at Mt. St. Helens; reversible change was rare (3%). Relative prominence of these trajectories varied considerably across the other 13 grassland sites (Fig. 7a). Among the perennial grasslands, stability was the most common trajectory (45% of all plots); followed by gradual linear (21%), abrupt nonlinear (16%), and reversible trajectories (6%). In the remaining cases, either the best-fit model had poor fit, or no clear distinction could be made between different trajectories. In the Chihuahuan Desert annual grasslands, abrupt nonlinear shifts (33%) were more common in the warm-season (summer) community than in the cool-season community (20%). The two sagebrush steppes in Idaho, INL and USEES (Table 2), differed in the relative prominence of the trajectories. Gradual linear change was more prominent at INL (38%) than at USSES (4%). The northern grassland in Alberta (also Montana) was characterized by stability. Grasslands in Kansas and the

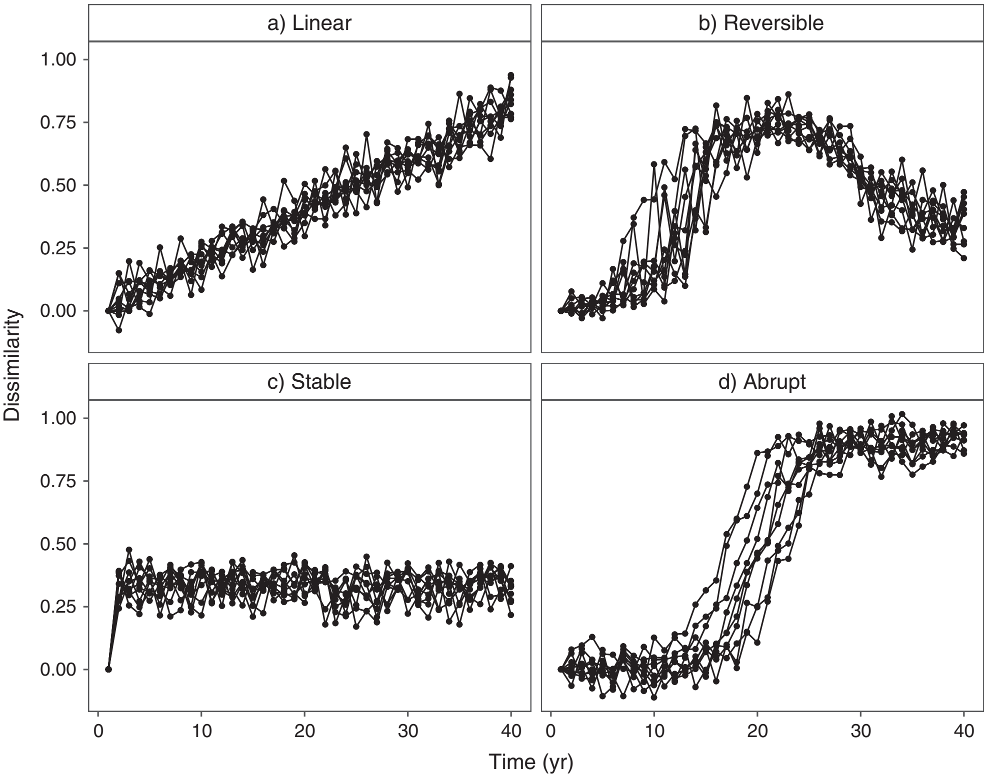

FIG. 3. Illustrative examples of simulated data used in verifying accuracy of the regression-based method to classify trajectories. For this, $n = 40$ samples (plots) over $t = 40$ time steps (years) of each of the four trajectories were simulated, and 100 iterations were run. For clarity, only 10 samples of each trajectory from one iteration are shown.

desert grassland at Jornada showed varied occurrence of all types of trajectories (Fig. 7a). The two data sets from desert grasslands of Santa Rita, Arizona, differed in the relative prominence of trajectories. Abrupt nonlinear shifts were less common in the older data set (1915–1947, Santa Rita q), than in the more recent data set (1953–2012, Santa Rita *t*).

Coefficients estimated from the best-fit models (Table 4) show four key patterns. First, even though inter-annual fluctuations can result in dissimilarity index >0.5, the plot can be considered stable in the long run (i.e., parameter φ_1). Second, in general, the northern prairies were more stable than the southern desert grasslands (i.e., parameter φ_1). Third, plots can recover former composition (reversible) even after the occurrence of considerable dissimilarity >0.8 (i.e., parameter δ_o). Finally, some reversible dynamics may take 2–3 decades (i.e., parameters θ_o and θ_r).

In comparison, results from time lag analysis were unable to detect differences among trajectories, and patterns among sites. Overwhelmingly, plots were assigned as divergent, with little or no resolution of within-site and cross-site patterns (Fig. 7b). Model fit for TLA also appeared lower (mean r^2 ± SD): Alberta (0.22 ± 0.16), Montana (0.08 ± 0.10), USSES (0.15 ± 0.15), INL (0.09 ± 0.06), Colorado (0.16 ± 0.13), Kansas (0.16 ± 0.13), Oklahoma (0.06 ± 0.03), Jornada (0.26 ± 0.09), SRER (q) (0.13 ± 0.15), SRER (*t*) (0.39 ± 0.21), Texas (0.12 ± 0.14), Arizona (summer, 0.16 ± 0.06, and winter 0.13 ± 0.09), and Mt. St. Helens (0.55 ± 0.17).

TABLE 3. Summary of accuracy and robustness of model-based classification into respective behaviors, based on simulations.

	Model output (%)				
Simulated input	Linear	Reversible	Stable	Abrupt	Unresolved
Linear	94 ± 2	0	2.75 ± 0.75	4.25 ± 2	3.75 ± 2.5
Reversible	0	100 ± 0	0	0	0
Stable	2.5 ± 0.25	0	97.25 ± 2.5	2.75 ± 0.75	2.5 ± 1.75
Abrupt	4.5 ± 1.25	0	0	94 ± 2.75	0

Note: Data were simulated ($n = 40$ plots over $t = 40$ yr, for each of the four behaviors, with 100 iterations) with known parameters (Fig. 3), and cross checked to determine overall classification success (mean ± SD in 100 iterations).

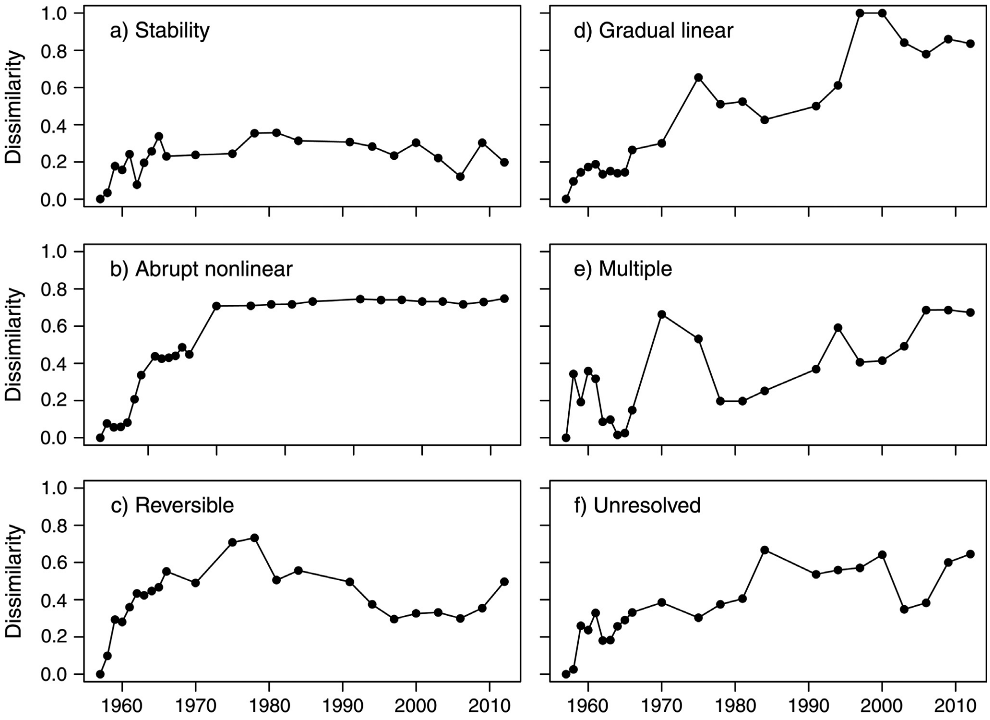

Fig. 4. Illustrative examples from six plots from Santa Rita data set that show different trajectories over 60 yr. These include (a) relative stability, (b) abrupt nonlinear shift, (c) reversible change over two to three decades, (d) gradual linear change, (e) instances of multiple behaviors, and (f) behaviors that remained statistically unresolved as they were explained by more than one model.

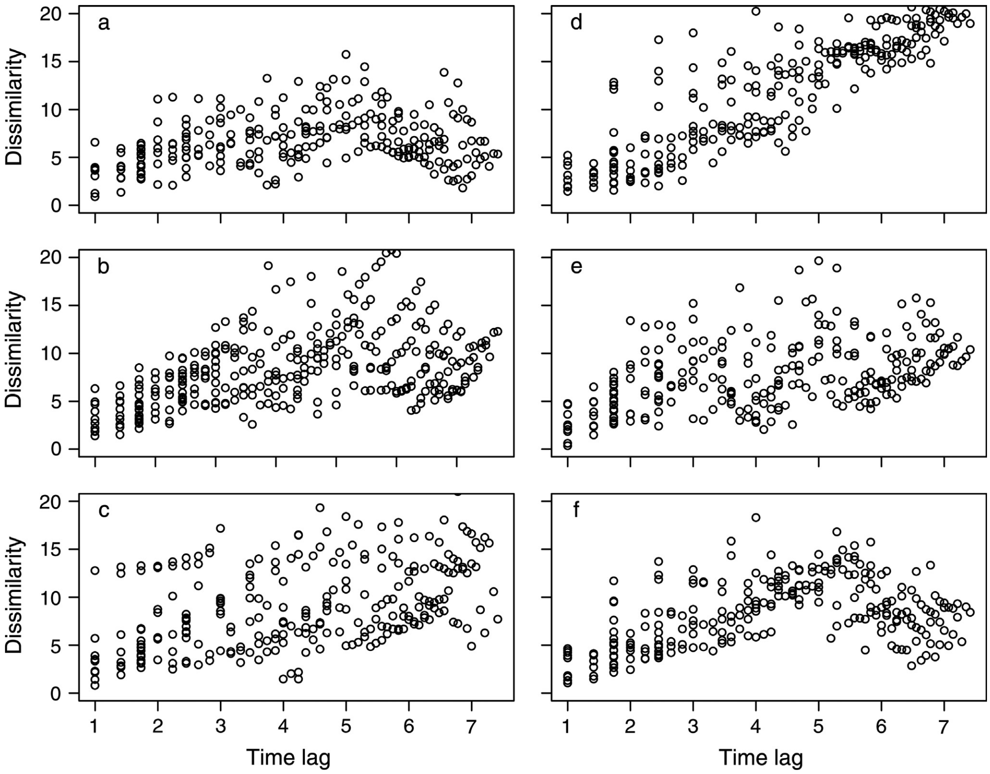

Fig. 5. Species dissimilarity patterns over increasing time lags for the six plots from Santa Rita depicted in Fig. 4. Patterns of time lag show lower ability to differentiate between trajectories in Fig. 4. Note that time lag was square-root transformed.

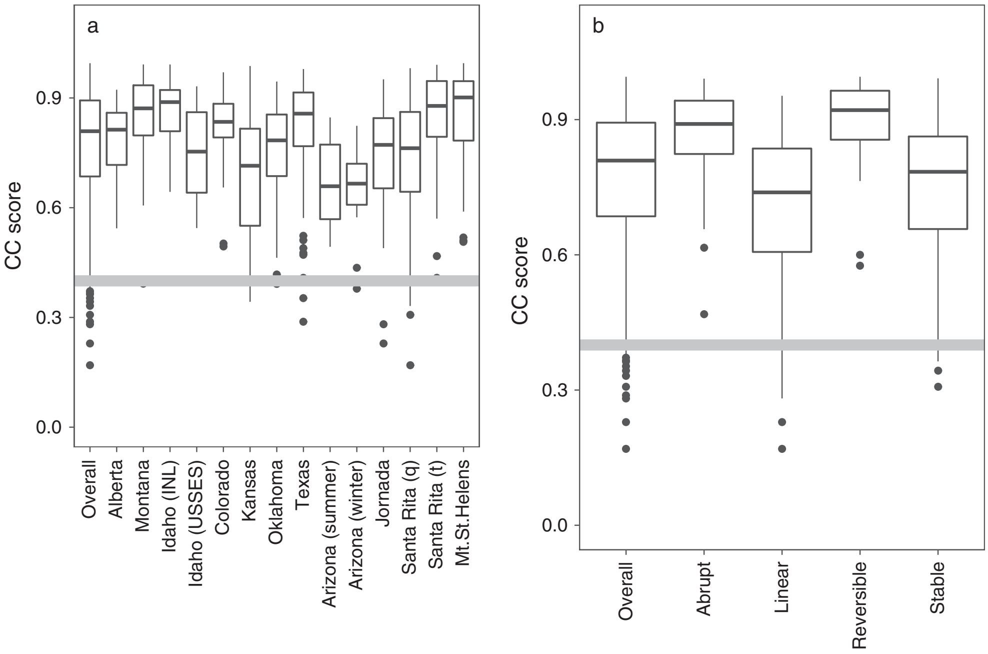

FIG. 6. Boxplot summary showing median and interquartile range of model performance measured by concordance criterion (CC) scores of the best-fit model. CC scores are shown for (a) different sites and for (b) different trajectories. Overall, model fit was generally high; poor fit winning models, which fall 2 SD units below the mean, are indicated by the gray line. Box plots show median and inter-quartile range, alongside outliers.

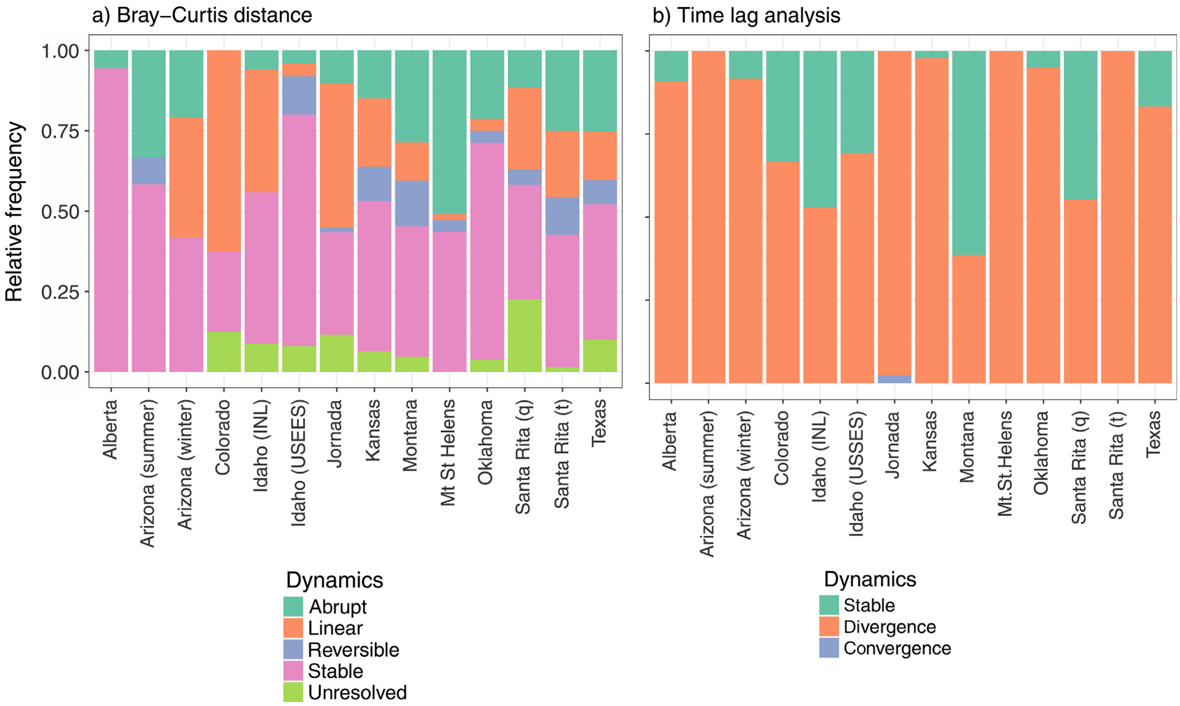

FIG. 7. (a) Relative frequency of trajectories of vegetation change derived from long-term records of North American ecosystems based on Bray-Curtis distance. Relative frequency of instances where trajectories could not be reliably classified (i.e., unresolved) are also shown. (b) Relative frequency of stable, divergent, and convergent trajectories at the different sites based on time lag analysis (TLA). [Color figure can be viewed at wileyonlinelibrary.com]

Table 4. Summary of model coefficients (mean ± SD) of for best-fit models from 14 long-term data sets across North America.

Site	Linear	Reversible	Stable	Abrupt
Alberta	NA	NA	$\varphi_1 = 0.43 \pm 0.05$ $\varphi_2 = -0.37 \pm 0.17$	$\delta = 0.44 \pm 0$ $\theta = 1.43 \pm 0$ $\varphi = 7.25 \pm 0$
Arizona (summer)	NA	$\delta_o = 0.68 \pm 0.01$ $\delta_r = 0.11 \pm 0.01$ $\theta_o = 2.15 \pm 0.03$ $\theta_r = 9.37 \pm 3.03$ $\varphi_o = 0.43 \pm 0.06$ $\varphi_r = 0.27 \pm 0.12$	$\varphi_1 = 0.64 \pm 0.03$ $\varphi_2 = -0.50 \pm 0.03$	$\delta = 0.64 \pm 0.02$ $\theta = 2.15 \pm 0.11$ $\varphi = 0.45 \pm 0.06$
Arizona (winter)	$\alpha = 0.01 \pm 0.002$	$\delta_o = 0.68 \pm 0.01$ $\delta_r = 0.11 \pm 0.01$ $\theta_o = 2.15 \pm 0.03$ $\theta_r = 9.37 \pm 3.03$ $\varphi_o = 0.43 \pm 0.06$ $\varphi_r = 0.27 \pm 0.12$	$\varphi_1 = 0.64 \pm 0.03$ $\varphi_2 = -0.59 \pm 0.03$	$\delta = 0.64 \pm 0.02$ $\theta = 2.15 \pm 0.11$ $\varphi = 0.45 \pm 0.06$
Colorado	$\alpha = 0.03 \pm 0.01$	NA	$\varphi_1 = 0.55 \pm 0.04$ $\varphi_2 = -0.20 \pm 0.12$	NA
Idaho (INL)	$\alpha = 0.01 \pm 0.001$	NA	$\varphi_1 = 0.74 \pm 0.13$ $\varphi_2 = -0.08 \pm 0.05$	$\delta = 0.89 \pm 0.14$ $\theta = 25.55 \pm 11.78$ $\varphi = 11.89 \pm 7.05$
Idaho (USSES)	$\alpha = 0.01 \pm 0$	$\delta_o = 0.62 \pm 0.17$ $\delta_r = 0.23 \pm 0.18$ $\theta_o = 5.75 \pm 3.48$ $\theta_r = 20.08 \pm 6.97$ $\varphi_o = 2.81 \pm 2.21$ $\varphi_r = 0.62 \pm 0.40$	$\varphi_1 = 0.48 \pm 0.22$ $\varphi_2 = -0.35 \pm 0.19$	$\delta = 0.44 \pm 0$ $\theta = 7.12 \pm 0$ $\varphi = 2.85 \pm 0$
Jornada	$\alpha = 0.01 \pm 0.006$	$\delta_o = 1.00 \pm 0$ $\delta_r = 0.33 \pm 0$ $\theta_o = 15.58 \pm 0$ $\theta_r = 13.13 \pm 0$ $\varphi_o = 6.10 \pm 0$ $\varphi_r = 0.07 \pm 0$	$\varphi_1 = 0.82 \pm 0.35$ $\varphi_2 = -0.31 \pm 0.38$	$\delta = 0.76 \pm 0.30$ $\theta = 11.72 \pm 3.04$ $\varphi = 9.76 \pm 5.77$
Kansas	$\alpha = 0.01 \pm 0.003$	$\delta_o = 0.98 \pm 0.25$ $\delta_r = 0.31 \pm 0.27$ $\theta_o = 9.68 \pm 7.18$ $\theta_r = 17.18 \pm 1.60$ $\varphi_o = 3.78 \pm 2.87$ $\varphi_r = 0.87 \pm 0.74$	$\varphi_1 = 0.61 \pm 0.40$ $\varphi_2 = -0.40 \pm 0.25$	$\delta = 0.72 \pm 0.30$ $\theta = 2.89 \pm 1.14$ $\varphi = 0.78 \pm 0.55$
Montana	$\alpha = 0.03 \pm 0.02$	$\delta_o = 0.67 \pm 0.18$ $\delta_r = 0.23 \pm 0.10$ $\theta_o = 3.71 \pm 1.04$ $\theta_r = 9.59 \pm 1.14$ $\varphi_o = 1.58 \pm 0.94$ $\varphi_r = 0.31 \pm 0.33$	$\varphi_1 = 0.55 \pm 0.11$ $\varphi_2 = -0.28 \pm 0.06$	$\delta = 0.56 \pm 0.14$ $\theta = 3.42 \pm 0.82$ $\varphi = 1.01 \pm 0.41$
Mt St Helens	$\alpha = 0.01 \pm 0$	$\delta_o = 0.64 \pm 0.21$ $\delta_r = 0.07 \pm 0.06$ $\theta_o = 2.50 \pm 0.71$ $\theta_r = 22.40 \pm 5.12$ $\varphi_o = 0.35 \pm 0.03$ $\varphi_r = 0.46 \pm 0.55$	$\varphi_1 = 0.37 \pm 0.04$ $\varphi_2 = -0.70 \pm 0.15$	$\delta = 0.59 \pm 0.23$ $\theta = 2.65 \pm 1.34$ $\varphi = 0.73 \pm 0.48$
Oklahoma	$\alpha = 0.03 \pm 0.004$	$\delta_o = 0.59 \pm 0.12$ $\delta_r = 0.26 \pm 0.11$ $\theta_o = 3.84 \pm 0.47$ $\theta_r = 6.10 \pm 0.67$ $\varphi_o = 1.81 \pm 0.26$ $\varphi_r = 0.37 \pm 0.39$	$\varphi_1 = 0.40 \pm 0.07$ $\varphi_2 = -0.49 \pm 0.19$	$\delta = 0.42 \pm 0.10$ $\theta = 2.17 \pm 0.50$ $\varphi = 0.62 \pm 0.35$
Santa Rita (*t*)	$\alpha = 0.02 \pm 0.002$	$\delta_o = 0.58 \pm 0.09$ $\delta_r = 0.12 \pm 0.09$ $\theta_o = 4.17 \pm 2.78$ $\theta_r = 9.90 \pm 4.04$ $\varphi_o = 0.95 \pm 1.00$ $\varphi_r = 0.30 \pm 0.37$	$\varphi_1 = 0.40 \pm 0.11$ $\varphi_2 = -0.39 \pm 0.19$	$\delta = 0.59 \pm 0.23$ $\theta = 16.29 \pm 10.02$ $\varphi = 6.94 \pm 3.78$

TABLE 4. (Continued)

Site	Linear	Reversible	Stable	Abrupt
Santa Rita (q)	$\alpha = 0.02 \pm 0.002$	$\delta_o = 0.58 \pm 0.09$ $\delta_r = 0.12 \pm 0.09$ $\theta_o = 4.17 \pm 2.78$ $\theta_r = 9.90 \pm 4.04$ $\varphi_o = 0.95 \pm 1.00$ $\varphi_r = 0.30 \pm 0.37$	$\varphi_1 = 0.40 \pm 0.11$ $\varphi_2 = -0.39 \pm 0.19$	$\delta = 0.67 \pm 0.09$ $\theta = 3.26 \pm 1.74$ $\varphi = 0.79 \pm 0.66$
Texas	$\alpha = 0.01 \pm 0.005$	$\delta_o = 0.71 \pm 0.44$ $\delta_r = 0.67 \pm 0.98$ $\theta_o = 6.86 \pm 5.82$ $\theta_r = 29.4 \pm 17.68$ $\varphi_o = 2.05 \pm 1.76$ $\varphi_r = 3.73 \pm 6.20$	$\varphi_1 = 0.50 \pm 0.15$ $\varphi_2 = -0.17 \pm 0.08$	$\delta = 0.58 \pm 0.14$ $\theta = 5.15 \pm 2.30$ $\varphi = 1.63 \pm 1.36$

Notes: Model coefficients correspond to parameters used in regression analysis. All coefficients are defined in text (*Methods*).

DISCUSSION

Our results demonstrate that analysis of movement paths developed in animal ecology (Schick et al. 2008, Bunnefeld et al. 2011, Singh et al. 2012) can advance the understanding and interpretation of long-term vegetation dynamics in diverse ecoregions. Our objective was not to establish a unifying theme that connects mobile animals with plant community change. Rather, we highlight that both can be studied under a common statistical framework. Quantification of long-term records of vegetation change as movement trajectories provides a means to disentangle transient and persistent vegetation dynamics, both within and among sites. Consequently, this method may facilitate greater insight into the interpretation and application of resilience concepts by defining patterns, reversibility, and rates of vegetation change (Bestelmeyer 2006, Standish et al. 2014). Specifically, it can help ascertain the degree to which an ecosystem is stable, or is prone to persistent transitions, and enables quantitative comparisons among ecosystems.

Overall, our method provided more detailed characterization of patterns of community change than time lag analysis (Fig. 7). While our approach offers more detailed insights into resilience concepts, broad characterization of general ecosystem behavior can still be achieved through TLA; detailed interpretation through regressions can be the next step. Statistical fit of empirical patterns to the best models was generally high (Fig. 6). This supports a close mathematical correspondence between rates and patterns of community dynamics (Friedel et al. 1993, Bagchi et al. 2012) and theoretical models of movement paths. We found that an overwhelming majority of plots could be reliably classified with a high degree of fit with empirical data. Sometimes, classification success and fit have been observed to be low when models are applied to animal movement paths (Singh et al. 2016). Our use of a combination of model coefficient values, goodness of fit, and parsimony, together in a three-step screening process, while simultaneously accounting for the temporal autocorrelation, may improve the applicability of these models (Bastille-Rousseau et al. 2016, de Grissac et al. 2016). Plots with poor fit to data were rare (Fig. 6) and involved cases where multiple behaviors occurred in the time series (e.g., reversible change followed by linear drift, Fig. 4).

Interestingly, multiple vegetation trajectories were observed in nearly every data set, while ambiguous cases were rare. Such pluralism is consistent with recent studies that emphasize variation in dynamics among replicates, rather than considering a composite or average response for a site (Avolio et al. 2015, Collins and Xia 2015). If the dominant trajectory at a site is identifiable, it can be used to represent the general resilience characteristics of the ecosystem over a relevant time period. However, it is important to acknowledge that community dynamics may exhibit a wide range of behaviors. Frequent persistent directional change and rarity of transient change (indicating the trajectories of plots affected by the volcano), and stability (indicating the control plots), is consistent with existing analyses of primary succession at Mt. St. Helens (Wood and del Moral 1987, del Moral and Wood 1993). When instances of reversible change were detected in other data sets, they usually encompassed time scales of two to three decades or more (Table 4). Time scales associated with reversible change may reflect life-history traits of participant species, such as life span. For this reason, contrasting the annual communities (short lived grasses) with perennials (long lived grasses) is informative.

Other regression-based approaches could also be considered as alternative options for describing these dynamics. For example, an intercept-only (i.e., flat-line) model could also capture stability, but yields low goodness of fit because dissimilarity is zero at the start of the time series (i.e., true intercept is zero at the beginning of the time series), and this not particularly well suited for real-world data (Bunnefeld et al. 2011, Borger and Fryxell 2012). Also, one could use segmented regressions to represent different phases of the alternative trajectories (see Appendix S1: Fig. S2). The number of statistically significant segments would indicate the shape of the trajectory. While heuristically appealing, this approach is not likely to be very useful for classification because the number of breakpoints cannot be determined objectively. But, once a plot has been classified, segmented regressions could be useful to identify change-points for further inference. One could also consider use of a single generic model where the coefficient values determine whether the behavior is linear, asymptotic, sigmoidal, or hump-shaped. E.g., $f(x) = \frac{a_1+a_2x^c}{a_3+a_4x+a_5x^2}$is such a generic form (see Appendix S1: Fig. S2), where the values of the different coefficients determine the shape of the relationship (often used in models of prey–predator interactions, Ranjan and Bagchi 2016). But, since this oversimplifies the expected trajectories, the interpretation of the coefficients is not straightforward, and it contains a larger number of estimated coefficients, such a generic model is less suitable than the development of four separate models (Bunnefeld et al. 2011).

Collectively, these data sets indicate that transient dynamics can also be a distinct feature of ecosystems (Fukami and Nakajima 2011), but it is possible to misinterpret them as permanent vegetation transitions when temporal scales are limited. An ecosystem may be erroneously considered to be irreversibly altered, when it is just slow to recover from disturbance (Bestelmeyer et al. 2013). These data caution against the underestimation of time scales involved in transient dynamics (two to three decades, parameters θ_o and θ_r, Table 4), which may result in the misapplication of resilience concepts (Bestelmeyer 2006, Bagchi et al. 2012).

Abrupt nonlinear trajectories were detected in the Chihuahuan Desert annual grasslands, particularly regarding the expression of summer dominants, and in the more recent data set from the Sonoran Desert (Santa Rita *t*, Fig. 7), but they were comparatively less common in the older Santa Rita (q) data set. This may reflect fundamental differences in the population dynamics of cool-season and warm-season annuals. At Santa Rita (q), abrupt nonlinear trajectories may reflect an initial phase of woody encroachment in the Sonoran Desert, which started in the early 20th century (McClaran et al. 2010). The low incidence of abrupt nonlinear trajectories in perennial grassland may imply that they are either uncommon, or they were not effectively detected in the long-term records. Frequently, vegetation dynamics that are consistent with thresholds or regime shifts are often associated with woody plant encroachment (Ratajczak et al. 2014). In our analysis, woody encroachment may also have led to abrupt nonlinear trajectories at Santa Rita (*t*). However, woody encroachment generally occurs as a spatially contagious process, and permanent plots may not always effectively capture expansion of woody plants (Bestelmeyer et al. 2011*b*). Nevertheless, abrupt nonlinear trajectories were detected in data sets where woody encroachment is a known feature, such as at the Jornada desert grassland site (Bestelmeyer et al. 2011*a*).

On the other hand, reversible change also occurs in many grasslands (Fukami and Nakajima 2011, Bagchi et al. 2012, Hughes et al. 2013). Limited expression of reversible change is best illustrated by the Mt. St. Helens site and the two sagebrush steppe sites (INL and USEES). Vegetation dynamics were strongly influenced by successional processes and cheatgrass invasion, *Bromus tectorum,* respectively, at these sites. Previously, we have found that cheatgrass invasion was comparatively more persistent and extensive at INL compared to USEES (Bagchi et al. 2013). USSES not only had a lower overall abundance of cheatgrass than at INL, but the duration of peak cheatgrass abundance was also shorter (Bagchi et al. 2013). Presumably, greater cheatgrass density and a longer period of occupation contributed to greater directional compositional change at INL than at USSES.

Terms such as "stable," "resilient," "nonequilibrial," and "threshold-prone" are frequently used in management decisions, often without reference to empirical measurements and quantitative criteria. Moreover, there remains a widely held concern regarding the ability to draw quantitative inferences about resilience from real-world ecological data (Carpenter et al. 2001, Thrush et al. 2009, Standish et al. 2014). In particular, thresholds and regime-shifts are frequently identified, even though supporting empirical evidence for their occurrence is often weak or lacking (Bestelmeyer et al. 2013, Mac Nally et al. 2014, Capon et al. 2015). Our approach provides an accurate and robust method to distinguish vegetation dynamics that provide insights into characteristics of ecosystem resilience, and its interpretation. Our results also indicate that researchers and managers should use caution when referencing ecosystems as irreversibly altered, when they are perhaps just slow to recover (Bestelmeyer et al. 2013), taking longer than two to three decades (Table 4). In other words, analyses of these vegetation records indicate that transient community composition may persist for long periods (Fukami and Nakajima 2011, Bagchi et al. 2013).

The potential implications of these analyses may be best illustrated through the correspondence of vegetation trajectories with theorized resilience landscapes (Table 1, Fig. 2, Holling 1973, Beisner et al. 2003, Nolting and Abbott 2016). Stability is often associated with communities located in a relatively narrow and deep basin where dynamics are constrained by strong feedback mechanisms and controlling variables (i.e., resistance). Reversible dynamics suggests comparatively broader basins of attraction with gradual slopes that allow for large compositional shifts that corresponds to engineering resilience. *Gradual linear* change may be visualized as either very broad basins that do not allow for stability (i.e., diffuse attractor), or chronic change in feedback mechanisms and controlling variables that modify basin configuration (i.e., moving attractor). In either of these cases, the resultant trajectory may correspond with non-equilibrium dynamics. Abrupt nonlinear change is consistent with multiple equilibria where distinct basins of attraction are separated by thresholds. A general correspondence between dynamic behaviors within long-term vegetation change and the attributes of ecological resilience further corroborates the tenets of this basin-of-attraction heuristic (Nolting and Abbott 2016). Quantitative assessments of long-term vegetation trajectories may represent an important tool for understanding resilience theory and implementing resilience-based ecosystem management. Specific benefits include identification of multiple trajectories in vegetation records and disentangling transient and persistent dynamics by evaluating time periods associated with their occurrence.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1544/full

Data Accessibility

Publicly available data sets are listed in Table 2.