

Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe

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Summary

1. Resilience-based approaches are increasingly being called upon to inform ecosystem management, particularly in arid and semi-arid regions. This requires management frameworks that can assess ecosystem dynamics, both within and between alternative states, at relevant time scales.

2. We analysed long-term vegetation records from two representative sites in the North American sagebrush-steppe ecosystem, spanning nine decades, to determine if empirical patterns were consistent with resilience theory, and to determine if cheatgrass *Bromus tectorum* invasion led to thresholds as currently envisioned by expert-based state-and-transition models (STM). These data span the entire history of cheatgrass invasion at these sites and provide a unique opportunity to assess the impacts of biotic invasion on ecosystem resilience.

3. We used univariate and multivariate statistical tools to identify unique plant communities and document the magnitude, frequency and directionality of community transitions through time. Community transitions were characterized by 37–47% dissimilarity in species composition, they were not evenly distributed through time, their frequency was not correlated with precipitation, and they could not be readily attributed to fire or grazing. Instead, at both sites, the majority of community transitions occurred within an 8–10 year period of increasing cheatgrass density, became infrequent after cheatgrass density peaked, and thereafter transition frequency declined.

4. Greater cheatgrass density, replacement of native species and indication of asymmetry in community transitions suggest that thresholds may have been exceeded in response to cheatgrass invasion at one site (more arid), but not at the other site (less arid). Asymmetry in the direction of community transitions also identified communities that were ‘at-risk’ of cheatgrass invasion, as well as potential restoration pathways for recovery of pre-invasion states.

5. *Synthesis and applications.* These results illustrate the complexities associated with threshold identification, and indicate that criteria describing the frequency, magnitude, directionality and temporal scale of community transitions may provide greater insight into resilience theory and its application for ecosystem management. These criteria are likely to vary across biogeographic regions that are susceptible to cheatgrass invasion, and necessitate more in-depth assessments of thresholds and alternative states, than currently available.

Key-words: *Artemisia*, community transitions, dynamic regime, ecological resilience, ecosystem management, invasive species, rangelands, resilience-based management, thresholds

Introduction

Rangelands occupy *c.* 40% of the Earth’s land area, primarily in arid and semi-arid regions, and provide diverse ecosystem services to large human populations (Scurlock & Hall 1998; Reynolds *et al.* 2007). Effective rangeland stewardship and restoration, amidst numerous environmental

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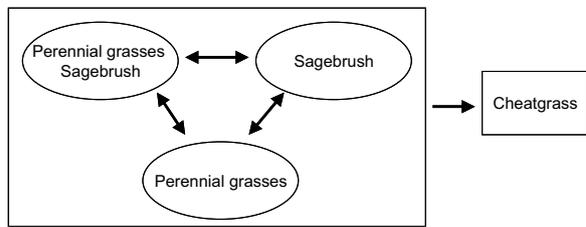
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and socio-economic challenges, require a comprehensive understanding of ecosystem dynamics and their response to episodic and chronic disturbances. Initial studies on North American rangelands, including the sagebrush-steppe that cover 6×10^5 km² of the Intermountain West and Great Basin eco-regions, were conducted within the Clementsian model (Dyksterhuis 1949) that emphasized predictable and reversible changes in vegetation composition, either towards or away from a reference climax plant community (e.g. Pechanec, Pickford & Stewart 1937; Mueggler 1950; Harniss & West 1973). However, subsequent investigations found that vegetation dynamics, particularly large fluctuations in the abundance of perennial grasses, were often inconsistent with this model (Anderson & Holte 1981; Anderson & Inouye 2001). This highlighted the need to consider resilience-based frameworks that accommodate multiple alternative states and thresholds (Westoby, Walker & Noy-Meir 1989) to inform ecosystem management (Briske, Fuhlendorf & Smeins 2003).

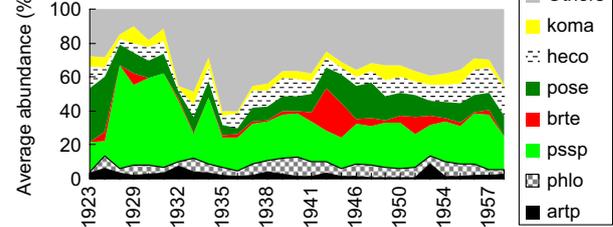
Over the past century, invasion by cheatgrass *Bromus tectorum* has posed an additional challenge for management and restoration of the sagebrush-steppe (Mack 1981; Reisner *et al.* 2013). This invasion has had a number of direct and indirect effects, including a shortening of fire return intervals from 60–110 years to 3–5 years (Brooks *et al.* 2004; Chambers *et al.* 2007; Baker 2011), and modification of soil structure and biogeochemical cycling (Kulmatiski, Beard & Stark 2006; Shinneman & Baker 2009) that can have important consequences for ecosystem services and human livelihoods. Cheatgrass is widely perceived to have influenced the resilience of the sagebrush-steppe, and create threshold conditions that yield an alternative state (Stringham, Krueger & Shaver 2003; Davies *et al.* 2012). Current management models, developed through expert opinion, consider cheatgrass as an alternative stable state that is irreversible without management prescriptions (Fig. 1a). However, the presence of thresholds is challenged by scattered evidence suggesting cheatgrass populations to be less persistent than widely assumed (West & Yorks 2002; Mata-González *et al.* 2007; Bradley & Wilcove 2009). This establishes a need to investigate the influence of cheatgrass on resilience of the sagebrush-steppe with empirical patterns that exist in historical vegetation records.

Conceptually, state-and-transition models (STM) are founded upon the theory of multiple equilibria and they accommodate alternative states in order to operationalize resilience concepts for ecosystem management (Westoby, Walker & Noy-Meir 1989; Briske *et al.* 2008). STMs account for vegetation dynamics as transitions within and between alternative states (Stringham, Krueger & Shaver 2003; Bestelmeyer *et al.* 2004). States consist of one or more phases, or closely related vegetation communities, that may show frequent and reversible transitions. States, however, are assumed to be separated by biophysical thresholds originating from the relative strength of

(a) Expert STM



(b) USSES



(c) INEEL

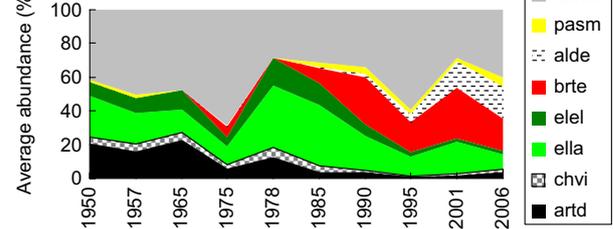


Fig. 1. Representative expert STM developed by the Natural Resource Conservation Service depicting community transitions within and between stable states in sagebrush-steppe ecosystem (a). Summary of vegetation dynamics at two representative sites of the sagebrush-steppe ecosystem, at US Sheep Experiment Station, USSES (b) and Idaho National Engineering and Environmental Laboratory, INEEL (c), represented as changes in average density of common plant species through time. Species names are abbreviated as – achy: *Achnatherum hymenoides* (grass), alde: *Alyssum desertorum* (forb), arfu: *Arnica fulgens* (forb), artd: *Artemisia tridentata* (shrub), artp: *Artemisia tripartita* (shrub), brte: *Bromus tectorum* (invasive annual grass), chvi: *Chrysothamnus viscidiflorus* (shrub), elal: *Elymus albicans* (grass), elal: *Elymus elymoides* (grass), ella: *Elymus lanceolatus* (grass), erco: *Erigeron corymbosus* (forb), heco: *Hesperostipa comata* (grass), koma: *Koeleria macrantha* (grass), laoc: *Lappula occidentalis* (forb), meal: *Mentzelia albicaulis* (forb), oppo: *Opuntia polyacantha* (cactus), phho: *Phlox hoodii* (forb), phlo: *Phlox longifolia* (forb), pose: *Poa secunda* (grass), pssp: *Pseudoroegneria spicata* (grass), pasm: *Pascopyrum smithii* (grass), saka: *Salsola kali* (forb).

negative and positive feedback mechanisms. Transitions and thresholds are linked with causal anthropogenic and natural events and drivers to interpret and anticipate outcomes of management actions qualitatively, but the incorporation of additional empirical information, including trends seen in long-term historical records, would further strengthen the STM framework (Bestelmeyer 2006; Knapp *et al.* 2011; Bagchi *et al.* 2012).

Here, we quantify the historical response of resident species to cheatgrass invasion, along with other plausible drivers of vegetation change, and identify the temporal

scale at which these dynamics occurred. Limited knowledge of temporal aspects is recognized as a serious omission in STMs by researchers and managers alike (Knapp *et al.* 2011). We use long-term records of vegetation dynamics at two sites from the sagebrush-steppe in Idaho, USA (Table 1). Collectively, these data sets span nine decades and cover the entire history of cheatgrass invasion in these regions. The first data set (1923–1973) is from the US Sheep Experiment Station near Dubois, Idaho (USSES, 113 km² area) and the second data set (1950–2006) is from the Idaho National Engineering and Environmental Laboratory near Idaho Falls, Idaho (INEEL, 2315 km² area). Specifically, we (i) identify vegetation communities and represent long-term dynamics as transitions between communities through time, (ii) derive quantitative information regarding the frequency, magnitude and directionality of transitions, as evidence of thresholds and alternative stable states (iii) investigate the incidence of community transitions in relation to precipitation patterns and the extent of cheatgrass invasion, and (iv) compare empirical patterns of community transitions with those identified in representative expert STMs for the sagebrush-steppe ecosystem.

Materials and methods

STUDY AREAS AND LONG-TERM DATA SETS

The sagebrush-steppe is characterized by various species and subspecies of the shrub *Artemisia* alongside many perennial grasses, a few of which are of Eurasian origin and were introduced in the 19th century. USSES and INEEL are representatives of the sagebrush-steppe and show broad similarity in their climatic regime, edaphic and topographic features, and life forms of common plants (Table 1). Long-term data for USSES were compiled from mapped chart-quadrats (Zachmann, Moffet & Adler 2010); the INEEL data were compiled by Anderson & Inouye (2001) for

1950–1995, and by Forman, Blew & Hafla (2010) for 2001–2006. Data from the two sites were analysed separately. At USSES, vegetation data are density of plants in 13–26 permanently marked plots (1-m² quadrats) that were sampled 29 times between 1923 and 1973 (Fig. 1b). At INEEL, the data are density of plants in 34 permanently marked plots (1-m² quadrats), which were all sampled 10 times between 1950 and 2006 (Fig. 1c). We did not include plots that were infrequently sampled over the duration of the data sets. Further details can be found in previous studies related to these data sets (Table 1). Use of density as a metric is a common feature of such historical data sets in North America and reflects the methodological emphasis during the early part of the 20th century. While data on other metrics are much more limited, density and cover have been previously seen to present qualitatively consistent trends (Anderson & Inouye 2001). To our knowledge, these are the only available long-term data sets that record the entire period of cheatgrass expansion, although several short-term records do exist (e.g. Allen-Diaz & Bartolome 1998; Davies *et al.* 2012).

Invasion history

Cheatgrass was initially recorded at USSES in the 1920s, but remained at low densities until the late 1930s. It attained maximum density in the 1940s, and thereafter occurred at moderate abundance during the 1950s (Fig. 1b). A similar pattern was evident at INEEL where cheatgrass was first recorded in 1950 (Anderson & Inouye 2001), but it did not appear in the sampled plots until 1965 and remained at low density until 1985; it increased to peak abundance over the next 15 years, and thereafter occurred at intermediate density (Fig. 1c).

Grazing history

Historically, livestock grazing in the 19th century is likely to have influenced vegetation composition at these sites, but quantitative information on past grazing intensities does not exist. However, following the establishment of the research stations, livestock grazing continued at moderate intensities at USSES, and was

Table 1. Comparison of salient features of two sites from the sagebrush-steppe ecosystem, USSES and INEEL that provide the vegetation data used our analyses

	USSES	INEEL
Location	44°N, 112°W	43°N, 112°W
Average elevation	1650 m (1465–3084 m)	1500 m (1460–1620 m)
Average temperature	6.1 °C (–31–38 °C)	5.6 °C (–30–37 °C)
Frost-free days	120 yr ⁻¹	90 yr ⁻¹ (68–123 yr ⁻¹)
Average precipitation	282 mm yr ⁻¹ (183–417 mm)	199 mm yr ⁻¹ (83–360 mm)
Wettest months	May–June	May–June
Soils	Aeolian loess, Calcic agrikeroll, loamy and sandy-loam formations	Aeolian deposits, Calciorthids, loamy and sandy formations
Major native species	<i>Artemisia tripartita</i> , <i>Balsamorhiza sagittata</i> , <i>Chrysothamnus viscidiflorus</i> , <i>Crepis acuminata</i> , <i>Phlox longifolia</i> , <i>Pseudoroegneria spicata</i> , <i>Elymus albicans</i>	<i>Artemisia tridentata</i> (var. <i>wyomingensis</i> and <i>tridentata</i>), <i>Chrysothamnus viscidiflorus</i> , <i>Phlox hoodi</i> , <i>Elymus lanceolatus</i> , <i>Elymus elymoides</i> , <i>Pseudoroegneria spicata</i>
Invasive species	<i>Bromus tectorum</i>	<i>Bromus tectorum</i>
Data coverage	1923–1973 (29 samples)	1950–2006 (10 samples)
Sampling	13–26 plots yr ⁻¹	34 plots yr ⁻¹
Key references	Pechanec, Pickford & Stewart (1937), Mueggler (1950), Zachmann, Moffet & Adler (2010)	Harniss & West (1973), Anderson & Holte (1981), Anderson & Inouye (2001)

removed at INEEL with only minimal herbivory by native ungulates (Anderson & Inouye 2001). If ensuing vegetation responses were largely due to a release from livestock grazing, then it would be evident in the early part of the vegetation record, prior to the arrival of cheatgrass. Alternatively, major dynamics occurring later in the vegetation record, following the arrival and establishment of cheatgrass, are likely to be a response to the invasion.

Fire history

Fire was largely absent from these sites during the period of the vegetation records. Prior to 1950, only two plots were affected by fire at INEEL, and only six plots were affected by fire in 2000; none of the plots at USSES were known to have burned during the span of the data set. This probably reflects long fire return intervals characteristic of the eco-region prior to cheatgrass invasion (Balch *et al.* 2013). Therefore, these data sets allow us to assess the influence of cheatgrass invasion relatively uninfluenced by alterations in fire regimes; previous studies have found that cheatgrass can invade even in the absence of fire (Bangert & Huntly 2010), but restoration may become more difficult with increasing fire frequency.

Precipitation history

Average precipitation during the periods covered by the data set was 282 mm yr⁻¹ (range 183–417 mm yr⁻¹) at USSES and 199 mm yr⁻¹ (range 83–360 mm yr⁻¹) for INEEL. Precipitation for the 10 years for which data were collected at INEEL averaged 211 mm yr⁻¹ (range 85–328 mm yr⁻¹), indicating that sampling was not systematically biased towards unusually wet or dry periods.

STATISTICAL ANALYSIS

Since the operational unit in the STM framework is a state comprised of one or more closely related plant communities (Briske, Fuhlendorf & Smiens 2005; Bagchi *et al.* 2012), we determined the number of statistically distinguishable plant communities in the vegetation records over time. We used the relatively common species for analysis: those that occurred in at least 2% of samples. Following the analytical protocol developed by Bagchi *et al.* (2012), we used a model-based clustering approach to derive parsimonious estimates of the number of constituent plant communities, based on Bayesian Information Criteria (Fraley & Raftery 2002). We tabulated community membership of individual samples using Ward's linkage over Bray–Curtis dissimilarity, and verified that these were indeed distinguishable from one another using Analysis of Similarity (ANOSIM). Once all plots were assigned to their respective communities, we tracked their history through time to record the frequency, dissimilarity and directionality of transitions that resulted in the reassignment of a plot to an alternative community (Bagchi *et al.* 2012).

To assess whether transitions were related to precipitation, we investigated potential covariation between the incidence of community transitions and precipitation during the 12 months preceding individual sampling periods (July–June water year, Anderson & Inouye 2001). For cluster analysis, we used packages Mclust and vegan in R 2.8.1 (R Development Core Team 2008), and PRIMER 5 (Plymouth Marine Laboratory, Plymouth, UK) for ANOSIM.

We compared the patterns of community transitions against the pathways included in a representative STM (Fig. 1a) that

captures the salient features of expert models developed for loamy and sandy ecological sites that are characteristic of this eco-region (see Figs S1 and S2 in Supporting Information). These expert models envision two generalized alternative states separated by an implicit biophysical threshold: (i) sagebrush and perennial grasses that contain multiple phases differing in their relative abundances and (ii) a cheatgrass-dominated state. Auto-genic succession, climate, disturbances due to fire and/or grazing, and management interventions are potential drivers of dynamics within and between states. So, in our analysis, when groups of communities show frequent and bidirectional transitions between them (i.e. phases), but not with other groups, these could indicate alternative states separated by thresholds. Transitions between communities that belong to separate states, however, are expected to be infrequent and unidirectional.

Results

VEGETATION DYNAMICS AT USSES

Temporal change in cheatgrass density at USSES was poorly correlated with that of several common native species (Fig. 2a–e), with $-0.29 < R < 0.19$, and $0.09 < P < 0.87$. Change in vegetation composition, or species dissimilarity relative to initial conditions, showed gradual divergence between 1920s and 1940s (Fig. 3a). Thereafter, species dissimilarity declined, and vegetation composition began to approach the initial conditions during the 1950s, suggesting a recovery following the decline in cheatgrass (Fig. 3a). This trend at USSES was adequately described by a unimodal function ($R^2 = 0.27$, $P < 0.001$, AIC = 36.58), rather than by a monotonic saturating function ($R^2 = 0.11$, $P < 0.05$, AIC = 54.78).

Model-based clustering identified five plant communities at USSES (Fig. 3b), and ANOSIM verified their compositional distinctiveness (Global $R = 0.46$, $P < 0.001$, and $P < 0.005$ for each pairwise comparison). While three tipped sagebrush *Artemisia tripartita*, bluebunch wheatgrass *Pseudoroegneria spicata* and Sandberg bluegrass *Poa secunda* occurred uniformly in all communities (Fig. 3b), abundance of other grasses such as needle-and-thread *Hesperostipa comata*, prairie Junegrass *Koeleria macrantha* and Montana wheatgrass *Elymus albicans*, and forbs such as fleabane *Erigeron corymbosus* and foothill arnica *Arnica fulgens*, varied substantially among communities (Fig. 3b). High cheatgrass density was characteristic of only one of the five communities (i.e. [C], Fig. 3b); this community, [C], appeared in the 1930s and accounted for about a quarter of the plots in the 1940s and 1950s, but subsequently declined in prominence (Fig. 3b).

These five communities at USSES could result in a total of 20 types of transition pathways; for example 2 ($C_2^5 = 5!/[2!(5-2)!] = 20$; viz., [A]→[B], [B]→[A], [A]→[C], and so on. But, only nine types of transition pathways were recorded with a combined total of 40 transition events between communities (Fig. 4). Community [A] appeared most susceptible to cheatgrass invasion, [B] and [D] were less susceptible, and [E] was not susceptible

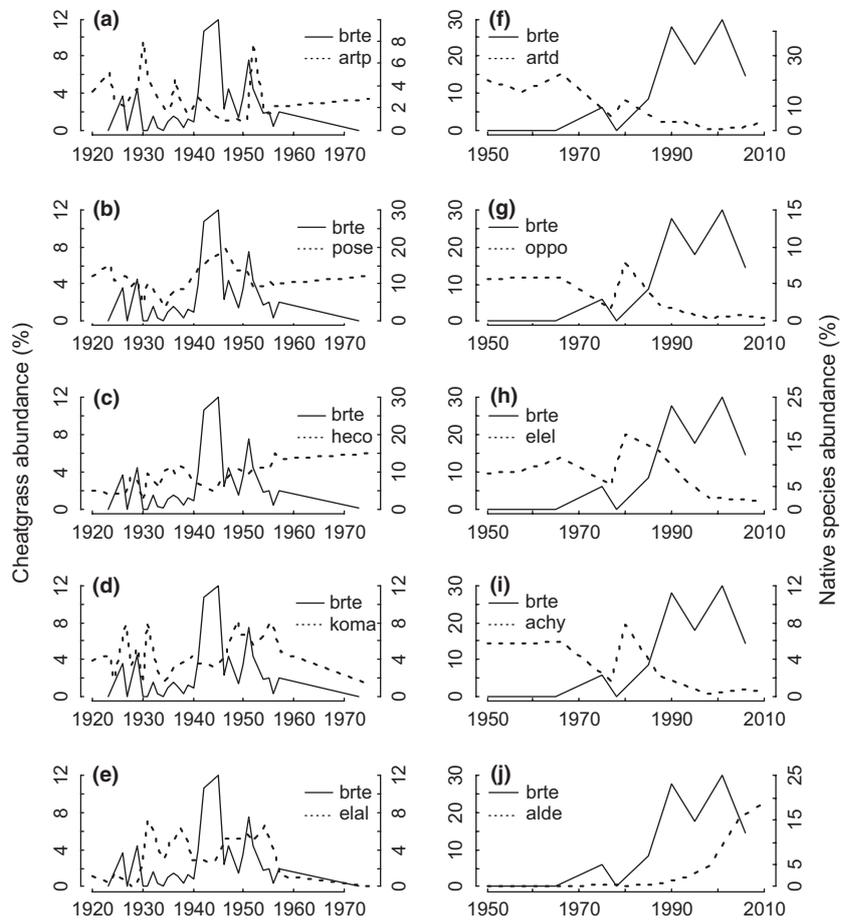


Fig. 2. Illustrative examples of temporal change in the average relative abundance of native species and cheatgrass. The first column (a–e) represents average trends in USSES, where densities of five common native species (a shrub and four grasses) were not correlated with that of cheatgrass. The second column (f–i) represents average trends in INEEL, where the densities of four common species (a shrub, cactus and two grasses) were negatively correlated with that of cheatgrass, but density of another invasive species (desert madwort) was positively related to cheatgrass (j). Abbreviations for species names follow Fig. 1.

(Fig. 4). Communities with relatively greater species dissimilarity (Fig. 3b) showed few or no transitions between them (Fig. 4). For example, community [E], characterized by a mix of perennial grasses and forbs such as longleaf fleabane and foothill arnica was most distant, relative to the other communities, and yielded only a single transition (Fig. 4). However, communities [A], [B] and [C] shared several species and they underwent frequent transitions (Fig. 4). Compositional dissimilarity expressed during transitions (0.37 ± 0.03 SE) was greater than compositional dissimilarity when transitions were not assigned (0.17 ± 0.01 SE, $F_{1,501} = 174.12$, $P < 0.001$), and this indicated that a lack of transitions did not necessarily imply complete stasis.

VEGETATION DYNAMICS AT INEEL

Temporal change in cheatgrass density at INEEL was negatively correlated with that in several resident species (Fig. 2f–i), with $-0.79 < R < -0.65$, $0.005 < P < 0.02$. Interestingly, temporal change in cheatgrass density was positively correlated with another annual invasive species: desert madwort *Alyssum desertorum* (Fig. 2j, $R = 0.60$, $P = 0.06$). Temporal change in species dissimilarity relative to initial conditions showed consistent divergence between 1950 and 2006, with little indication for recovery

of initial composition at INEEL (Fig. 3d). A unimodal quadratic function ($R^2 = 0.35$, $P < 0.001$, $AIC = 184.53$) and a monotonic saturating function ($R^2 = 0.35$, $P < 0.001$, $AIC = 182.50$) for this trend were virtually indistinguishable.

Six communities were identified at INEEL (Fig. 3e), each having distinct species composition (Global $R = 0.62$, $P < 0.003$, and $P < 0.01$ for each pairwise comparison in ANOSIM). Desert madwort, cheatgrass, thickspike wheatgrass *Elymus lanceolatus*, Russian thistle *Salsola kali*, big sagebrush *Artemisia tridentata*, Hood’s phlox *Phlox hoodii*, whitestem blazingstar *Mentzelia albicaulis* and rabbitbrush *Chrysothamnus viscidiflorus* were the primary species that varied in relative abundances among these communities (Fig. 3e). Two communities, [F] and [J], were characterized by cheatgrass, and these did not appear until 1965 (Fig. 3f). Their relative occurrence across the landscape increased after 1980s and coincided with declines in communities [H], [I] and [K], while community [G] was relatively unaffected (Fig. 3f).

Six communities at INEEL could yield a total of 2 ($C_2^6 = 6!/[2!(6-2)!] = 30$) types of transition pathways, of which only 17 were recorded, with a total of 130 transition events between communities (Fig. 5). Frequent transitions were observed between the community pairs of [J] and [G], [K] and [G], [I] and [J]. Communities [H] and [I]

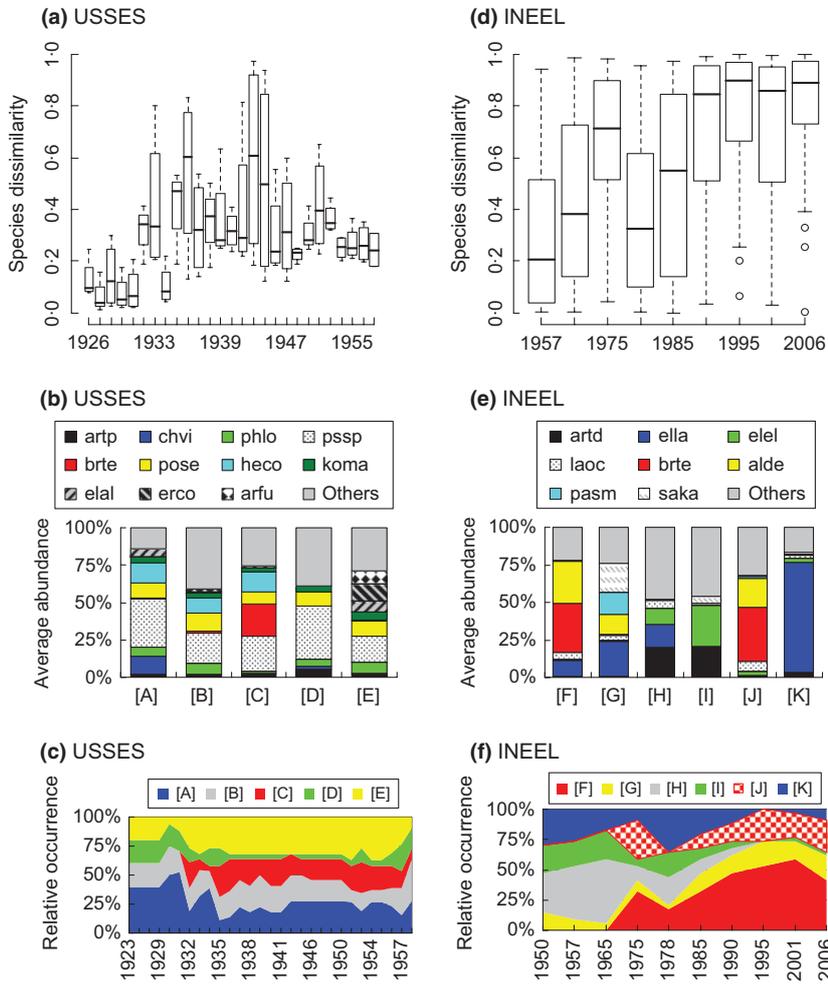


Fig. 3. Change in vegetation composition over time, expressed as species dissimilarity relative to starting conditions, at USSES (a). Relative abundance of key plant species in five plant communities ([A] through [E]) at USSES in (b). Relative occurrence of five plant communities ([A] through [E]) through time at USSES (c). Change in vegetation composition over time, expressed as species dissimilarity relative to starting conditions, at INEEL (d). Relative abundance of key plant species in six plant communities ([F] through [K]) at INEEL in (e), and relative occurrence of six plant communities ([F] through [K]) through time at INEEL (f). Species names and abbreviations follow Fig. 1.

appeared highly susceptible to cheatgrass invasion, while the others were less susceptible. As in USSES, compositional dissimilarity expressed during transitions at INEEL (0.47 ± 0.03) was greater than dissimilarity in absence of transitions (0.32 ± 0.01 , $F_{1,304} = 102.58$, $P < 0.001$).

FREQUENCY OF TRANSITIONS

The frequency of community transitions was not temporally uniform at either site. At USSES, the majority of the transitions occurred between 1932 and 1938, whereas previous and subsequent decades experienced very few transitions (Fig. 6a). Likewise, transitions were initially rare at INEEL, the majority of transitions occurred between 1975 and 1985 (Fig. 6a), and their occurrence declined thereafter. Frequency of transitions was unrelated to annual precipitation at both USSES ($R = 0.10$, $P = 0.31$, Fig. 6b) and INEEL ($R = 0.08$, $P = 0.25$, Fig. 6b); instead they occurred before cheatgrass attained maximum abundance at either site (Figs 1, 2 and 6).

COMPARISON WITH EXPERT MODELS

These historical dynamics corroborate the overall structure of expert models for this eco-region, but evidence

supporting the existence of cheatgrass-induced thresholds was mixed, and differed between sites. Our analyses suggest the existence of two primary states: one comprised of sagebrush and perennial grasses, and the other characterized by cheatgrass – as also indicated by the expert models (Fig. 1a). But, importantly, a substantial number of bidirectional transitions between these two purported states indicate that the potential for reversibility exists at USSES, but less so at INEEL (Figs 4 and 5). This is only partially consistent with the prevailing interpretation and usage of threshold concepts in the STM framework.

Discussion

CORRESPONDENCE WITH RESILIENCE THEORY

The statistical protocol identified unique communities and revealed temporal transitions within the long-term vegetation records (Figs 1, 4 and 5). Community transitions were not evenly distributed through time, their frequency was not correlated with precipitation, and they could not be readily attributed to fire or grazing regimes. Previous studies have also found that cheatgrass invasion can proceed in the sagebrush-steppe in the absence of fire

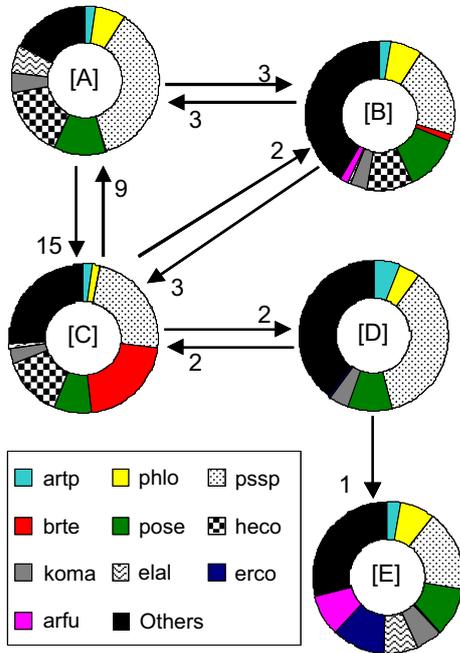


Fig. 4. Empirical patterns of transitions between five plant communities identified in USSES represented as [A] through [E] ($n = 40$ cases). Arrows indicate transition between a pair of communities and numbers represent the frequency of a particular transition between a pair of communities.

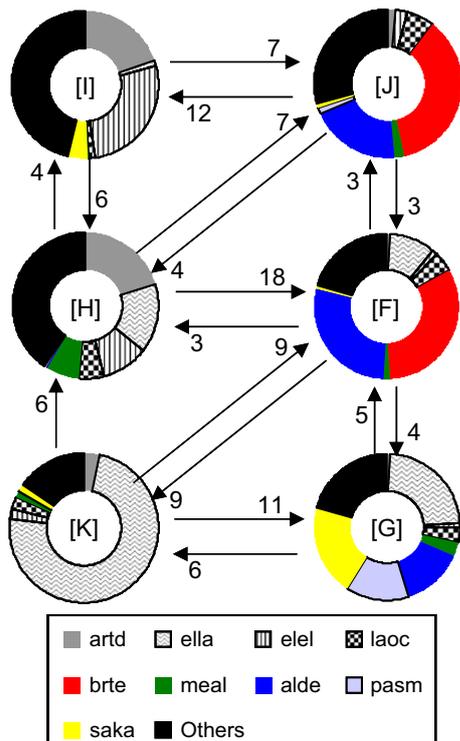


Fig. 5. Patterns of transitions between six plant communities identified in INEEL represented as [F] through [K] ($n = 130$ cases). Arrows indicate transitions between a pair of communities and numbers represent the frequency of a particular transition between a pair of communities.

(Bangert & Huntly 2010), and that fire has weak and transient effects on the native species in absence of cheatgrass (Seefeldt, Germino & DiCristina 2007). While infrequent fires can promote cheatgrass establishment, cheatgrass can eventually be displaced by native perennial vegetation over decadal timescales (West & Yorks 2002; Mata-González *et al.* 2007). But, in areas where cheatgrass invasion has changed fire return intervals (Baker 2011; Balch *et al.* 2013), it can suppress fire intolerant native species (Davies *et al.* 2012). Instead, in both of these records without major fires, the majority of transitions occurred within an 8–10 year window coincident with increasing cheatgrass density, and then became infrequent after cheatgrass density peaked and thereafter transition frequency declined. Cheatgrass invasion at INEEL was associated with a reduction in the densities of several resident species (Fig. 2f–i), as well as with an increase in another invasive annual (desert madwort, Fig. 2j). In contrast, increasing cheatgrass densities were not associated with concomitant responses in the resident species at USSES (Fig. 2a–e). Cheatgrass invasion at USSES appears to be a case where an invasive species was simply added to the ecosystem, at low or moderate density, perhaps without modifying the pre-existing species interactions (Besaw *et al.* 2011). These contrasting responses may represent variation in susceptibility among eco-regions featuring different species and subspecies of *Artemisia* (Davies & Bates 2010).

Only about half of the potential transition pathways were recorded (nine of potential 20 at USSES, and 17 of 30 at INEEL); some transition pathways were clearly more prevalent than others (Figs 4 and 5), suggesting that certain types of dynamics are either exceedingly rare, or implausible (Bagchi *et al.* 2012). The absence of specific transition pathways may indicate the presence of strong negative feedbacks that increase resilience of the current states. While transitions between a pair of communities could be bidirectional, the frequency of transitions in one direction was not necessarily matched in the reverse direction. For example, communities, [H] and [I] at INEEL, were characterized by a large number of transitions into cheatgrass communities (Fig. 6). Asymmetric transitions were less pronounced at USSES (community [A], Fig. 4), which is consistent with the more transient nature of compositional change and the partial recovery of pre-invasion status after cheatgrass declined (Fig. 3a). Expectedly, if communities shared similar physiognomy and dominant species (Fig. 3b–e), they also exhibited frequent transitions (Figs 4 and 5). Otherwise, transitions were either infrequent or nonexistent among communities that differed greatly in species composition.

Greater dissimilarity of community composition following cheatgrass invasion at INEEL compared to USSES corresponds with higher cheatgrass density (Fig. 1b–c). A maximum relative density of 30% (maximum absolute density 3200 individuals m^{-2}) at INEEL, appeared to

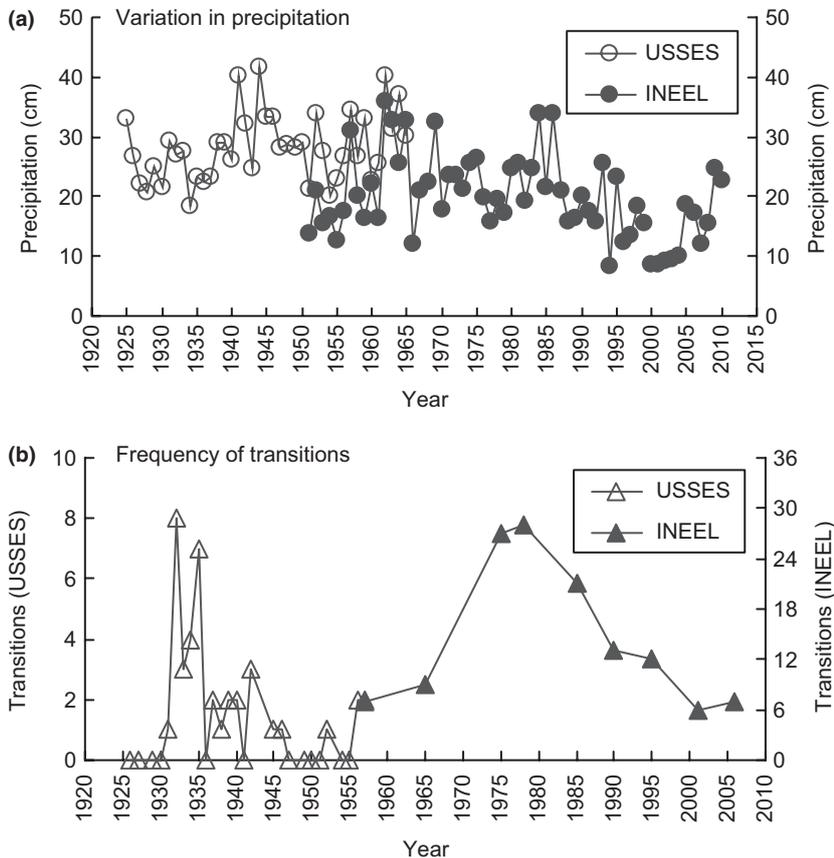


Fig. 6. Temporal pattern in long-term precipitation records at USSES and INEEL in (a). Temporal patterns in frequency of community transitions at USSES and INEEL in (b).

have been sufficient to modify composition of the resident species, even in the absence of an accelerated fire regime. This reiterates the point that cheatgrass invasion can occur successfully in the absence of fire (Bangert & Huntly 2010) to establish conditions that are, at least partially, consistent with prevalent interpretations of thresholds, as evident at INEEL. In comparison, a maximum relative density of 24% (and maximum absolute density 700 individuals m^{-2}) at USSES may have been insufficient to modify composition of the resident species and cheatgrass density declined after 8–10 years, which is inconsistent with the occurrence of thresholds.

If removal or reduction in livestock grazing at the two research sites had been a key driver of vegetation dynamics, we would have anticipated that most transitions would have occurred early in the vegetation record, but this was not the case. Neither was the incidence of community transitions correlated with precipitation, at either site, indicating that fluctuations in precipitation, at this sampling scale, either had a weak influence on the observed dynamics, or involved more complex time-lags not included in our analysis (Fig. 6). Previous studies have also noted a similar absence of simple correlation between precipitation and the dynamics of common plant species (Anderson & Inouye 2001; Adler, HilleRisLambers & Levine 2009).

Cheatgrass establishment at both sites (Fig. 1b–c) appears to coincide with periods of average to below-average annual

precipitation (Fig. 6a). At USSES, precipitation during the 1930s was about 250 $mm\ yr^{-1}$, compared with 300 $mm\ yr^{-1}$ in the subsequent two decades (Fig. 6a). Similarly, Anderson & Inouye (2001) have also noted that precipitation at INEEL during the 1950s and 1960s was about 190 $mm\ yr^{-1}$, compared with 220 $mm\ yr^{-1}$ in the 1970s (Fig. 6a). The initial period of cheatgrass establishment appears to coincide with a period of average to below-average precipitation, and cheatgrass subsequently attained peak density during years of average to above-average precipitation, at both sites (Fig. 1b,c); the invasion may have been influenced by subtle climate variation at both sites. Also, frequency of precipitation events, especially in the fall and early spring, are likely to be related to cheatgrass growth and fecundity (Concilio, Loik & Belnap 2013), rather than annual total precipitation. Feedback mechanisms involving plant–soil interactions, seed banks and soil-resource acquisition may also be relevant to ecosystem resilience following cheatgrass invasion, in addition to fire, climate and grazing (Humphrey & Schupp 2001; Boxell & Drohan 2009; Leffler, Monaco & James 2011).

Community composition at USSES appeared to recover towards the initial conditions that were prevalent during the 1920s and 1930s following peak cheatgrass density during the 1940s (Fig. 3a), but there was no evidence for a similar recovery at INEEL (Fig. 3d). This inconsistency between sites may reflect: (i) a time-lag in relation to the

continued existence of moderate cheatgrass densities at INEEL (Fig. 1) and/or (ii) the alteration of prevalent feedback mechanisms, or development of novel feedbacks, in response to occurrence of high cheatgrass density at INEEL. The decreasing number of community transitions following peak cheatgrass density can be interpreted as recovery of the former stable state at USSES (Bradley & Wilcove 2009), but as strengthening of the alternative state containing cheatgrass at INEEL where communities [F] and [J] could be separated from the others by a threshold (Fig. 5).

ASSESSMENT OF EXPERT STMs

Communities identified in the vegetation record correspond, in large part, with those identified by the expert STMs. For USSES, communities [A], [B], [D] and [E] appear to correspond with community phases in the sagebrush and perennial grass state of the expert models, and community [C] matches the alternative state containing cheatgrass (Figs 1a and 4). However, there were frequent, and often bidirectional, transitions between these communities (Fig. 4), which are inconsistent with the interpretation of thresholds in expert models. Frequency and directionality of transitions between communities at USSES indicate that cheatgrass invasion may not represent a distinct alternative state defined by an irreversible threshold. But, for INEEL, communities [G], [H], [I] and [K] correspond well with different community phases comprising perennial grasses and sagebrush, while communities [F] and [J] correspond with a cheatgrass state (Figs 1a and 5). Transitions involving communities [G] and [K] were bidirectional and mostly symmetrical, which, once again, is inconsistent with the interpretation of thresholds. However, transitions to the cheatgrass communities were asymmetrical for communities [I] and [H] and indicate that a biophysical threshold may separate them from other states. These historical records highlight complex and varied dynamics, and clarify some practical challenges associated with threshold identification. The STM framework accounts for only broad approximations of these complexities and in so doing may overlook valuable information related to resilience and threshold conditions.

The ecological consequences of cheatgrass invasion were expressed within unexpectedly short temporal scales and with different effects on resident plant communities. Evidence for large temporal fluctuations in cheatgrass density is consistent with bioclimatic projections that cheatgrass dominance may last only a few decades at specific sites, although invasion may simultaneously expand into previously unoccupied areas (Bradley & Wilcove 2009). These temporal patterns emphasize a recurring dilemma with threshold interpretation, in that cheatgrass densities at USSES were ecologically reversible, but only in time frames that may seriously constrain management options (West & Yorks 2002; Mata-González *et al.* 2007).

Distinctions between 'ecological' and 'managerial' thresholds have previously been recognized (Brown, Herrick & Price 1999) and may represent a viable solution to the recurring dilemma over temporal scale in threshold identification for STMs.

IMPLICATION FOR RESILIENCE-BASED ECOSYSTEM MANAGEMENT

Long-term vegetation records, when analysed to represent unique communities and temporal transitions between them (Figs 4 and 5), provide a valuable source of information for construction and interpretation of STMs that is not accessible from other sources (Knapp *et al.* 2011). Specifically, these historical records quantitatively define four criteria – frequency, magnitude, directionality and temporal scale of community transitions – that may increase insight into resilience theory and its application to ecosystem management. Such quantitative information can inform the STM framework to refine procedures and guidelines to identify triggers, feedback mechanisms, temporal scales, at-risk communities and restoration pathways. For example, these records suggest that communities containing a moderate proportion of Montana wheatgrass (10–17% average relative density) may be 'at-risk' for cheatgrass invasion, as it had a high number of unidirectional transitions to the cheatgrass state. Recognition of 'at-risk' communities may be especially relevant because lack of clear early-warning signals constrain the ability to respond to ecological indicators of imminent dynamics. As a corollary, a high frequency of bidirectional transitions between communities [E] and [D] could be further investigated as potential restoration pathways which represent communities that have a high probability for recovery to a pre-invasion state (Stringham, Krueger & Shaver 2003; Ray Mukherjee *et al.* 2011).

In conclusion, analyses of historical vegetation records promise to enrich the STM framework with empirical patterns and relationships that can refine their construction rules and management value. These records clarify that community transitions can be induced by natural events and autogenic drivers, in addition to management actions that are frequently emphasized in STMs (Bagchi *et al.* 2012). Despite similar population trends, cheatgrass invasion yielded different outcomes at the two sites; it invaded specific communities, but not others; concentration of transitions within an 8–10 year window, collectively show the complexity of thresholds. Practical assessment and interpretation of ecological thresholds will benefit from consideration of a set of criteria describing community transitions. These criteria are likely to vary across biogeographic regions susceptible to cheatgrass invasion that are characterized by various *Artemisia* species and subspecies (Davies & Bates 2010), and necessitate more in-depth assessments of thresholds and alternative stable states.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Detailed description of expert STMs specific to loamy topo-edaphic conditions across the sagebrush-steppe in Idaho, USA.

Fig. S2. Detailed description of expert STMs specific to sandy topo-edaphic conditions across the sagebrush-steppe in Idaho, USA.