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3 **Assessing resilience and state-transition models with historical records of cheatgrass**

4 ***Bromus tectorum* invasion in North American sagebrush-steppe**

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1 **Summary**

- 2 1. Resilience-based approaches are increasingly being called upon to inform ecosystem
3 management, particularly in arid and semiarid regions. This requires management
4 frameworks that can assess ecosystem dynamics, both within and between alternative states,
5 at relevant time scales.
- 6 2. We analysed long-term vegetation records from two representative sites in the North
7 American sagebrush-steppe ecosystem, spanning nine decades, to determine if empirical
8 patterns were consistent with resilience theory, and to determine if cheatgrass *Bromus*
9 *tectorum* invasion led to thresholds as currently envisioned by expert-based state-and-
10 transition models (STM). These data span the entire history of cheatgrass invasion at these
11 sites, and provide a unique opportunity to assess the impacts of biotic invasion on ecosystem
12 resilience.
- 13 3. We used univariate and multivariate statistical tools to identify unique plant communities and
14 document the magnitude, frequency, and directionality of community transitions through
15 time. Community transitions were characterized by 37–47% dissimilarity in species
16 composition, they were not evenly distributed through time, their frequency was not
17 correlated with precipitation, and they could not be readily attributed to fire or grazing.
18 Instead, at both sites, the majority of community transitions occurred within an 8–10 year
19 period of increasing cheatgrass density, became infrequent after cheatgrass density peaked,
20 and thereafter transition frequency declined.
- 21 4. Greater cheatgrass density, replacement of native species, and indication of asymmetry in
22 community transitions suggest that thresholds may have been exceeded in response to
23 cheatgrass invasion at one site (more arid), but not at the other site (less arid). Asymmetry in

1 the direction of community transitions also identified communities that were ‘at-risk’ of
2 cheatgrass invasion, as well as potential restoration pathways for recovery of pre-invasion
3 states.

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

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

13 **Introduction**

14 Rangelands occupy c. 40% of the Earth’s land area, primarily in arid and semi-arid regions, and
15 provide diverse ecosystem services to large human populations (Reynolds *et al.* 2007; Scurlock
16 & Hall 1998). Effective rangeland stewardship and restoration, amidst numerous environmental
17 and socio-economic challenges, require a comprehensive understanding of ecosystem dynamics
18 and their response to episodic and chronic disturbances. Initial studies on North American
19 rangelands, including the sagebrush-steppe that cover 6×10^5 km² of the Intermountain West and
20 Great Basin eco-regions, were conducted within the Clementsian model (Dyksterhuis 1949) that
21 emphasized predictable and reversible changes in vegetation composition, either toward or away
22 from a reference climax plant community (e.g. Harniss & West 1973; Mueggler 1950; Pechanec,
23 Pickford & Stewart 1937). However, subsequent investigations found that vegetation dynamics,

1 particularly large fluctuations in the abundance of perennial grasses, were often inconsistent with
2 this model (Anderson & Holte 1981; Anderson & Inouye 2001). This highlighted the need to
3 consider resilience-based frameworks that accommodate multiple alternative states and
4 thresholds (Westoby, Walker & Noy-Meir 1989) to inform ecosystem management (Briske,
5 Fuhlendorf & Smeins 2003).

6 Over the past century, invasion by cheatgrass *Bromus tectorum* has posed an additional
7 challenge for management and restoration of the sagebrush-steppe (Mack 1981; Reisner *et al.*
8 2013). This invasion has had a number of direct and indirect effects, including a shortening of
9 fire return intervals from 60–110 years to 3–5 years (Baker 2011; Brooks *et al.* 2004; Chambers
10 *et al.* 2007), and modification of soil structure and biogeochemical cycling (Kulmatiski, Beard &
11 Stark 2006; Shinneman & Baker 2009), that can have important consequences for ecosystem
12 services and human livelihoods. Cheatgrass is widely perceived to have influenced the resilience
13 of the sagebrush-steppe, and create threshold conditions that yield an alternative state (Davies *et*
14 *al.* 2012; Stringham, Krueger & Shaver 2003). Current management models, developed through
15 expert opinion, consider cheatgrass as an alternative stable state that is irreversible without
16 management prescriptions (Fig. 1a). However, the presence of thresholds is challenged by
17 scattered evidence suggesting cheatgrass populations to be less persistent than widely assumed
18 (Bradley & Wilcove 2009; Mata-González *et al.* 2007; West & Yorks 2002). This establishes a
19 need to investigate the influence of cheatgrass on resilience of the sagebrush-steppe with
20 empirical patterns that exist in historical vegetation records.

21 Conceptually, state and transition models (STM) are founded upon the theory of multiple
22 equilibria and they accommodate alternative states in order to operationalize resilience concepts
23 for ecosystem management (Briske *et al.* 2008; Westoby *et al.* 1989). STMs account for

1 vegetation dynamics as transitions within and between alternative states (Bestelmeyer *et al.*
2 2004; Stringham *et al.* 2003). States consist of one or more phases, or closely related vegetation
3 communities, that may show frequent and reversible transitions. States, however, are assumed to
4 be separated by biophysical thresholds originating from the relative strength of negative and
5 positive feedback mechanisms. Transitions and thresholds are linked with causal anthropogenic
6 and natural events and drivers to interpret and anticipate outcomes of management actions
7 qualitatively, but the incorporation of additional empirical information, including trends seen in
8 long-term historical records, would further strengthen the STM framework (Bagchi *et al.* 2012;
9 Bestelmeyer 2006; Knapp *et al.* 2011).

10 Here we quantify the historical response of resident species to cheatgrass invasion, along
11 with other plausible drivers of vegetation change, and identify the temporal scale at which these
12 dynamics occurred. Limited knowledge of temporal aspects is recognized as a serious omission
13 in STMs by researchers and managers alike (Knapp *et al.* 2011). We use long-term records of
14 vegetation dynamics at two sites from the sagebrush-steppe in Idaho, USA (Table 1).
15 Collectively, these datasets span nine decades and cover the entire history of cheatgrass invasion
16 in these regions. The first dataset (1923–1973) is from the US Sheep Experiment Station near
17 Dubois, Idaho (USSES, 113 km² area) and the second dataset (1950–2006) is from the Idaho
18 National Engineering and Environmental Laboratory near Idaho Falls, Idaho (INEEL, 2315
19 km² area). Specifically, we (1) identify vegetation communities and represent long-term
20 dynamics as transitions between communities through time, (2) derive quantitative information
21 regarding the frequency, magnitude, and directionality of transitions, as evidence of thresholds
22 and alternative stable states (3) investigate the incidence of community transitions in relation to
23 precipitation patterns and the extent of cheatgrass invasion, and, (4) compare empirical patterns

1 of community transitions with those identified in representative expert STMs for the sagebrush-
2 steppe ecosystem.

3

4 **Materials and Methods**

5 STUDY AREAS AND LONG-TERM DATASETS

6 The sagebrush-steppe is characterized by various species and sub-species of the shrub *Artemisia*
7 alongside many perennial grasses, a few of which are of Eurasian origin and were introduced in
8 the 19th century. USSES and INEEL are representatives of the sagebrush-steppe and show broad
9 similarity in their climatic regime, edaphic and topographic features, and life forms of common
10 plants (Table 1). Long-term data for USSES were compiled from mapped chart-quadrats
11 (Zachmann, Moffet & Adler 2010); the INEEL data were compiled by Anderson and Inouye
12 (2001) for 1950-1995, and by Forman *et al.* (2010) for 2001-2006. Data from the two sites were
13 analysed separately. At USSES, vegetation data are density of plants in 13–26 permanently
14 marked plots (1-m² quadrats) that were sampled 29 times between 1923 and 1973 (Fig. 1b). At
15 INEEL, the data are density of plants in 34 permanently marked plots (1-m² quadrats), that were
16 all sampled 10 times between 1950 and 2006 (Fig. 1c). We did not include plots that were
17 infrequently sampled over the duration of the datasets. Further details can be found in previous
18 studies related to these datasets (Table 1). Use of density as a metric is a common feature of such
19 historical datasets in North America, and reflects the methodological emphasis during the early
20 part of the 20th century. While data on other metrics are much more limited, density and cover
21 have been previously seen to present qualitatively consistent trends (Anderson & Inouye 2001).
22 To our knowledge, these are the only available long-term datasets that record the entire period of

1 cheatgrass expansion, although several short-term records do exist (e.g. Allen-Diaz & Bartolome
2 1998; Davies *et al.* 2012).

3
4 *Invasion history* – Cheatgrass was initially recorded at USSES in the 1920s, but remained at low
5 densities until the late 1930s. It attained maximum density in the 1940s, and thereafter occurred
6 at moderate abundance during the 1950s (Fig. 1b). A similar pattern was evident at INEEL
7 where cheatgrass was first recorded in 1950 (Anderson & Inouye 2001), but it did not appear in
8 the sampled plots until 1965 and remained at low density until 1985; it increased to peak
9 abundance over the next 15 years, and thereafter occurred at intermediate density (Fig. 1c).

10
11 *Grazing history* – Historically, livestock grazing in the 19th century is likely to have influenced
12 vegetation composition at these sites, but quantitative information on past grazing intensities
13 does not exist. However, following the establishment of the research stations, livestock grazing
14 continued at moderate intensities at USSES, and was removed at INEEL with only minimal
15 herbivory by native ungulates (Anderson & Inouye 2001). If ensuing vegetation responses were
16 largely due to a release from livestock grazing, then it would be evident in the early part of the
17 vegetation record, prior to the arrival of cheatgrass. Alternatively, major dynamics occurring
18 later in the vegetation record, following the arrival and establishment of cheatgrass, are likely to
19 be a response to the invasion.

20
21 *Fire history* – Fire was largely absent from these sites during the period of the vegetation
22 records. Prior to 1950, only two plots were affected by fire at INEEL, and only six plots were
23 affected by fire in 2000; none of the plots at USSES were known to have burned during the span

1 of the dataset. This probably reflects long fire return intervals characteristic of the eco-region
2 prior to cheatgrass invasion (Balch *et al.* 2013). Therefore, these datasets allow us to assess the
3 influence of cheatgrass invasion relatively uninfluenced by alterations in fire regimes; previous
4 studies have found that cheatgrass can invade even in the absence of fire (Bangert & Huntly
5 2010), but restoration may become more difficult with increasing fire frequency.

6

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

12

13 STATISTICAL ANALYSIS

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

1 we tracked their history through time to record the frequency, dissimilarity, and directionality of
2 transitions that resulted in the reassignment of a plot to an alternative community (Bagchi *et al.*
3 2012).

4 To assess whether transitions were related to precipitation, we investigated potential co-
5 variation between the incidence of community transitions and precipitation during the 12 months
6 preceding individual sampling periods (July-June water year, Anderson & Inouye 2001). For
7 cluster analysis we used packages Mclust and vegan in R 2.8.1 (R Development Core Team
8 2008), and PRIMER 5 (Plymouth Marine Laboratory, Plymouth, UK) for ANOSIM.

9 We compared the patterns of community transitions against the pathways included in a
10 representative STM (Fig. 1a) that captures the salient features of expert models developed for
11 loamy and sandy ecological sites that are characteristic of this eco-region (see Figs S1 and S2 in
12 Supporting Information). These expert models envision two generalized alternative states
13 separated by an implicit biophysical threshold: (1) sagebrush and perennial grasses that contain
14 multiple phases differing in their relative abundances, and (2) a cheatgrass-dominated state.
15 Autogenic succession, climate, disturbances due to fire and/or grazing, and management
16 interventions are potential drivers of dynamics within and between states. So, in our analysis,
17 when groups of communities show frequent and bi-directional transitions between them (i.e.
18 phases), but not with other groups, these could indicate alternative states separated by implicit
19 thresholds. Transitions between communities that belong to separate states, however, are
20 expected to be infrequent and uni-directional.

21

22

23

1 **Results**

2 *Vegetation dynamics at USSES* – Temporal change in cheatgrass density at USSES was poorly
3 correlated with that of several common native species (Fig. 2a–e), with $-0.29 < R < 0.19$, and
4 $0.09 < P < 0.87$. Change in vegetation composition, or species dissimilarity relative to initial
5 conditions, showed gradual divergence between 1920s and 1940s (Fig. 3a). Thereafter, species
6 dissimilarity declined, and vegetation composition began to approach the initial conditions
7 during the 1950s, suggesting a recovery following the decline in cheatgrass (Fig. 3a). This trend
8 at USSES was adequately described by a unimodal function ($R^2 = 0.27$, $P < 0.001$, AIC = 36.58),
9 rather than by a monotonic saturating function ($R^2 = 0.11$, $P < 0.05$, AIC = 54.78).

10 Model-based clustering identified five plant communities at USSES (Fig. 3b), and
11 ANOSIM verified their compositional distinctiveness (Global $R = 0.46$, $P < 0.001$, and $P <$
12 0.005 for each pair-wise comparison). While threetipped sagebrush *Artemisia tripartita*,
13 bluebunch wheatgrass *Pseudoroegneria spicata* and Sandberg bluegrass *Poa secunda* occurred
14 uniformly in all communities (Fig. 3b), abundance of other grasses such as needle-and-thread
15 *Hesperostipa comata*, prairie Junegrass *Koeleria macrantha* and Montana wheatgrass *Elymus*
16 *albicans*, and forbs such as fleabane *Erigeron corymbosus* and foothill arnica *Arnica fulgens*,
17 varied substantially among communities (Fig. 3b). High cheatgrass density was characteristic of
18 only one of the five communities (i.e. [C], Fig. 3b); this community, [C], appeared in the 1930s
19 and accounted for about a quarter of the plots in the 1940s and 1950s, but subsequently declined
20 in prominence (Fig. 3b).

21 These five communities at USSES could result in a total of 20 types of transition
22 pathways; e.g. $2(C_2^5) = 5!/[2!(5-2)!] = 20$; viz., [A]→[B], [B]→[A], [A]→[C], and so on. But,
23 only nine types of transition pathways were recorded with a combined total of 40 transition

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

11
12 *Vegetation dynamics at INEEL* – Temporal change in cheatgrass density at INEEL was
13 negatively correlated with that in several resident species (Fig. 2f-i), with $-0.79 < R < -0.65$,
14 $0.005 < P < 0.02$. Interestingly, temporal change in cheatgrass density was positively correlated
15 with another annual invasive species: desert madwort *Alyssum desertorum* (Fig. 2j, $R = 0.60$, $P =$
16 0.06). Temporal change in species dissimilarity relative to initial conditions showed consistent
17 divergence between 1950 and 2006, with little indication for recovery of initial composition at
18 INEEL (Fig. 3d). A unimodal quadratic function ($R^2 = 0.35$, $P < 0.001$, $AIC = 184.53$), and a
19 monotonic saturating function ($R^2 = 0.35$, $P < 0.001$, $AIC = 182.50$) for this trend were virtually
20 indistinguishable.

21 Six communities were identified at INEEL (Fig. 3e), each having distinct species
22 composition (Global $R = 0.62$, $P < 0.003$, and $P < 0.01$ for each pair-wise comparison in
23 ANOSIM). Desert madwort, cheatgrass, thickspike wheatgrass *Elymus lanceolatus*, Russian

1 thistle *Salsola kalii*, big sagebrush *Artemisia tridentata*, Hood's phlox *Phlox hoodii*, whitestem
2 blazingstar *Mentzelia albicaulis*, and rabbitbrush *Chrysothamnus viscidiflorus*, were the primary
3 species that varied in relative abundances among these communities (Fig. 3e). Two communities,
4 [F] and [J], were characterized by cheatgrass, and these did not appear until 1965 (Fig. 3f). Their
5 relative occurrence across the landscape increased after 1980s, and coincided with declines in
6 communities [H], [I] and [K], while community [G] was relatively unaffected (Fig. 3f).

7 Six communities at INEEL could yield a total of $2(C_2^6) = 6!/[2!(6-2)!] = 30$ types of
8 transition pathways, of which only 17 were recorded, with a total of 130 transition events
9 between communities (Fig. 5). Frequent transitions were observed between the community pairs
10 of [J] and [G], [K] and [G], [I] and [J]. Communities [H] and [I] appeared highly susceptible to
11 cheatgrass invasion, while the others were less susceptible. As in USSES, compositional
12 dissimilarity expressed during transitions at INEEL (0.47 ± 0.03) was greater than dissimilarity
13 in absence of transitions (0.32 ± 0.01 , $F_{1,304} = 102.58$, $P < 0.001$).

14
15 *Frequency of transitions* – The frequency of community transitions was not temporally uniform
16 at either site. At USSES, the majority of the transitions occurred between 1932 and 1938,
17 whereas previous and subsequent decades experienced very few transitions (Fig. 6a). Likewise,
18 transitions were initially rare at INEEL, the majority of transitions occurred between 1975 and
19 1985 (Fig. 6a), and their occurrence declined thereafter. Frequency of transitions was unrelated
20 to annual precipitation at both USSES ($R = 0.10$, $P = 0.31$, Fig. 6b) and INEEL ($R = 0.08$, $P =$
21 0.25 , Fig. 6b); instead they occurred before cheatgrass attained maximum abundance at either
22 site (Figs 1,2 & 6).

23

1 *Comparison with expert models* – These historical dynamics corroborate the overall structure of
2 expert models for this eco-region, but evidence supporting the existence of cheatgrass-induced
3 thresholds was mixed, and differed between sites. Our analyses suggest the existence of two
4 primary states: one comprised of sagebrush and perennial grasses, and the other characterized by
5 cheatgrass – as also indicated by the expert models (Fig. 1a). But, importantly, a substantial
6 number of bi-directional transitions between these two purported states indicate that the potential
7 for reversibility exists at USSES, but less so at INEEL (Figs 4 & 5). This is only partially
8 consistent with the prevailing interpretation and usage of threshold concepts in the STM
9 framework.

10

11 **Discussion**

12 *Correspondence with resilience theory* – The statistical protocol identified unique communities
13 and revealed temporal transitions within the long-term vegetation records (Figs 1, 4 & 5).
14 Community transitions were not evenly distributed through time, their frequency was not
15 correlated with precipitation, and they could not be readily attributed to fire or grazing regimes.
16 Previous studies have also found that cheatgrass invasion can proceed in the sagebrush-steppe in
17 the absence of fire (Bangert & Huntly 2010), and that fire has weak and transient effects on the
18 native species in absence of cheatgrass (Seefeldt, Germino & DiCristina 2007). While infrequent
19 fires can promote cheatgrass establishment, cheatgrass can eventually be displaced by native
20 perennial vegetation over decadal timescales (Mata-González *et al.* 2007; West & Yorks 2002).
21 But, in areas where cheatgrass invasion has changed fire return intervals (Baker 2011; Balch *et*
22 *al.* 2013), it can suppress fire intolerant native species (Davies *et al.* 2012). Instead, in both of
23 these records without major fires, the majority of transitions occurred within an 8–10 year

1 window coincident with increasing cheatgrass density, and then became infrequent after
2 cheatgrass density peaked and thereafter transition frequency declined. Cheatgrass invasion at
3 INEEL was associated with a reduction in the densities of several resident species (Fig. 2f–i), as
4 well as with an increase in another invasive annual (desert madwort, Fig. 2j). In contrast,
5 increasing cheatgrass densities were not associated with concomitant responses in the resident
6 species at USSES (Fig. 2a–e). Cheatgrass invasion at USSES appears to be a case where an
7 invasive species was simply added to the ecosystem, at low or moderate density, perhaps without
8 modifying the pre-existing species interactions (Besaw *et al.* 2011). These contrasting responses
9 may represent variation in susceptibility among eco-regions featuring different species and
10 subspecies of *Artemisia* (Davies & Bates 2010).

11 Only about half of the potential transition pathways were recorded (9 out of potential 20
12 at USSES, and 17 out of 30 at INEEL); some transition pathways were clearly more prevalent
13 than others (Figs 4 & 5), suggesting that certain types of dynamics are either exceedingly rare, or
14 implausible (Bagchi *et al.* 2012). The absence of specific transition pathways may indicate the
15 presence of strong negative feedbacks that increase resilience of the current states. While
16 transitions between a pair of communities could be bi-directional, the frequency of transitions in
17 one direction was not necessarily matched in the reverse direction. For example, communities
18 [H] and [I] at INEEL, were characterized by a large number of transitions into cheatgrass
19 communities (Fig. 6). Asymmetric transitions were less pronounced at USSES (community [A],
20 Fig. 4), which is consistent with the more transient nature of compositional change and the
21 partial recovery of pre-invasion status after cheatgrass declined (Fig. 3a). Expectedly, if
22 communities shared similar physiognomy and dominant species (Fig. 3b–e), they also exhibited

1 frequent transitions (Figs 4 &5). Otherwise, transitions were either infrequent or non-existent
2 among communities that differed greatly in species composition.

3 Greater dissimilarity of community composition following cheatgrass invasion at INEEL
4 compared to USSES corresponds with higher cheatgrass density (Fig. 1b–c). A maximum
5 relative density of 30% (maximum absolute density 3200 individuals m⁻²) at INEEL, appeared to
6 have been sufficient to modify composition of the resident species, even in the absence of an
7 accelerated fire regime. This reiterates the point that cheatgrass invasion can occur successfully
8 in the absence of fire (Bangert & Huntly 2010) to establish conditions that are, at least partially,
9 consistent with prevalent interpretations of thresholds, as evident at INEEL. In comparison, a
10 maximum relative density of 24% (and maximum absolute density 700 individuals m⁻²) at
11 USSES may have been insufficient to modify composition of the resident species and cheatgrass
12 density declined after 8–10 yrs, which is inconsistent with the occurrence of thresholds.

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

21 Cheatgrass establishment at both sites (Fig. 1b–c), appears to coincide with periods of
22 average to below-average annual precipitation (Fig 6a). At USSES, precipitation during the
23 1930s was about 250 mm yr⁻¹, compared to 300 mm yr⁻¹ in the subsequent two decades (Fig. 6a).

1 Similarly, Anderson & Inouye (2001) have also noted that precipitation at INEEL during the
2 1950s and 1960s was about 190 mm yr^{-1} , compared to 220 mm yr^{-1} in the 1970s (Fig. 6a). The
3 initial period of cheatgrass establishment appears to coincide with a period of average to below-
4 average precipitation, and cheatgrass subsequently attained peak density during years of average
5 to above average precipitation, at both sites (Fig. 1b–c); the invasion may have been influenced
6 by subtle climate variation at both sites. Also, frequency of precipitation events, especially in the
7 fall and early spring, are likely to be related to cheatgrass growth and fecundity (Concilio, Loik
8 & Belnap 2013), rather than annual total precipitation. Feedback mechanisms involving plant–
9 soil interactions, seed banks, and soil-resource acquisition, may also be relevant to ecosystem
10 resilience following cheatgrass invasion, in addition to fire, climate, and grazing (Boxell &
11 Drohan 2009; Humphrey & Schupp 2001; Leffler, Monaco & James 2011).

12 Community composition at USSES appeared to recover toward the initial conditions that
13 were prevalent during the 1920s and 1930s following peak cheatgrass density during the 1940s
14 (Fig. 3a), but there was no evidence for a similar recovery at INEEL (Fig. 3d). This
15 inconsistency between sites may reflect: (1) a time-lag in relation to the continued existence of
16 moderate cheatgrass densities at INEEL (Fig. 1), and/or (2) the alteration of prevalent feedback
17 mechanisms, or development of novel feedbacks, in response to occurrence of high cheatgrass
18 density at INEEL. The decreasing number of community transitions following peak cheatgrass
19 density can be interpreted as recovery of the former stable state at USSES (Bradley & Wilcove
20 2009), but as strengthening of the alternative state containing cheatgrass at INEEL where
21 communities [F] and [J] could be separated from the others by an implicit threshold (Fig. 5).

22

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

19 The ecological consequences of cheatgrass invasion were expressed within unexpectedly
20 short temporal scales and with different effects on resident plant communities. Evidence for large
21 temporal fluctuations in cheatgrass density is consistent with bioclimatic projections that
22 cheatgrass dominance may last only a few decades at specific sites, although invasion may
23 simultaneously expand into previously unoccupied areas (Bradley & Wilcove 2009). These

1 temporal patterns emphasize a recurring dilemma with threshold interpretation, in that cheatgrass
2 densities at USSES were ecologically reversible, but only in time frames that may seriously
3 constrain management options (Mata-González *et al.* 2007; West & Yorks 2002). Distinctions
4 between ‘ecological’ and ‘managerial’ thresholds have previously be recognized (Brown,
5 Herrick & Price 1999) and may represent a viable solution to the recurring dilemma over
6 temporal scale in threshold identification for STMs.

7
8 *Implication for resilience-based ecosystem management* – Long-term vegetation records, when
9 analysed to represent unique communities and temporal transitions between them (Figs 4 &5),
10 provide a valuable source of information for construction and interpretation of STMs that is not
11 accessible from other sources (Knapp *et al.* 2011). Specifically, these historical records
12 quantitatively define four criteria — frequency, magnitude, directionality and temporal scale of
13 community transitions — that may increase insight into resilience theory and its application to
14 ecosystem management. Such quantitative information can inform the STM framework to refine
15 procedures and guidelines to identify triggers, feedback mechanisms, temporal scales, at-risk
16 communities, and restoration pathways. For example, these records suggest that communities
17 containing a moderate proportion of Montana wheatgrass (10–17% average relative density) may
18 be ‘at-risk’ for cheatgrass invasion, as it had a high number of unidirectional transitions to the
19 cheatgrass state. Recognition of ‘at-risk’ communities may be especially relevant because lack of
20 clear early-warning signals constrain the ability to respond to ecological indicators of imminent
21 dynamics. As a corollary, a high frequency of bi-directional transitions between communities [E]
22 and [D] could be further investigated as potential restoration pathways which represent

1 communities that have a high probability for recovery to a pre-invasion state (Ray Mukherjee *et*
2 *al.* 2011; Stringham *et al.* 2003).

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

15

16 **Supporting Information**

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

18 Fig. S1. Detailed description of expert STMs specific to loamy topo-edaphic conditions across
19 the sagebrush-steppe in Idaho, USA. These expert models are from major land use areas B11 and
20 B12 as defined by the Natural Resource Conservation Service. Their salient features are
21 generalized in Fig. 1a.

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

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11

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19

1 Table 1. Comparison of salient features of two sites from the sagebrush-steppe ecosystem,
 2 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 to 3084 m)	1500 m (1460 to 1620 m)
Average temperature	6.1 °C (-31 to 38 °C)	5.6 °C (-30 to 37 °C)
Frost-free days	120 year ⁻¹	90 year ⁻¹ (68 to 123 year ⁻¹)
Average precipitation	282 mm year ⁻¹ (183 to 417 mm)	199 mm year ⁻¹ (83 to 360 mm)
Wettest months	May–June	May–June
Soils	Aeolian loess, Calcic agixeroll, 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 year ⁻¹	34 plots year ⁻¹
Key references	Pechanec <i>et al.</i> (1937), Mueggler (1950), Zachmann <i>et al.</i> (2010)	Harniss & West (1973), Anderson & Holte (1981), Anderson & Inouye (2001)

3

1 **Figure legends**

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

16
17 **Fig. 2.** Illustrative examples of temporal change in the average relative abundance of native
18 species, and cheatgrass. The first column (a–e) represents average trends in USSES, where
19 densities of five common native species (a shrub and four grasses) were not correlated with that
20 of cheatgrass. The second column (f–i) represents average trends in INEEL, where the densities
21 of four common species (a shrub, cactus, and two grasses) were negatively correlated with that
22 of cheatgrass, but density of another invasive species (desert madwort) was positively related to
23 cheatgrass (j). Abbreviations for species names follow Fig. 1.

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

9
10 **Fig. 4.** Empirical patterns of transitions between five plant communities identified in USSES
11 represented as [A] through [E] (n = 40 cases). Arrows indicate transition between a pair of
12 communities and numbers represent the frequency of a particular transition between a pair of
13 communities.

14
15 **Fig. 5.** Patterns of transitions between six plant communities identified in INEEL represented as
16 [F] through [K] (n = 130 cases). Arrows indicate transitions between a pair of communities and
17 numbers represent the frequency of a particular transition between a pair of communities.

18
19 **Fig. 6.** Temporal pattern in long-term precipitation records at USSES and INEEL in (a).
20 Temporal patterns in frequency of community transitions at USSES and INEEL in (b).

1 Fig. 1.

2

3 a) Expert STM

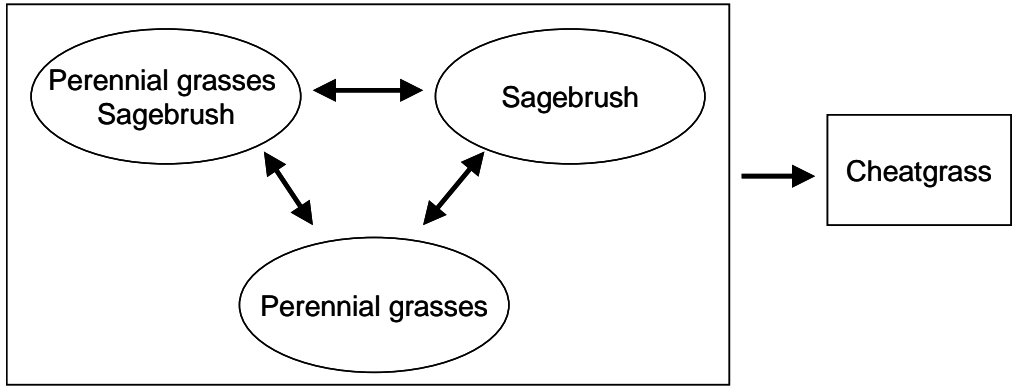
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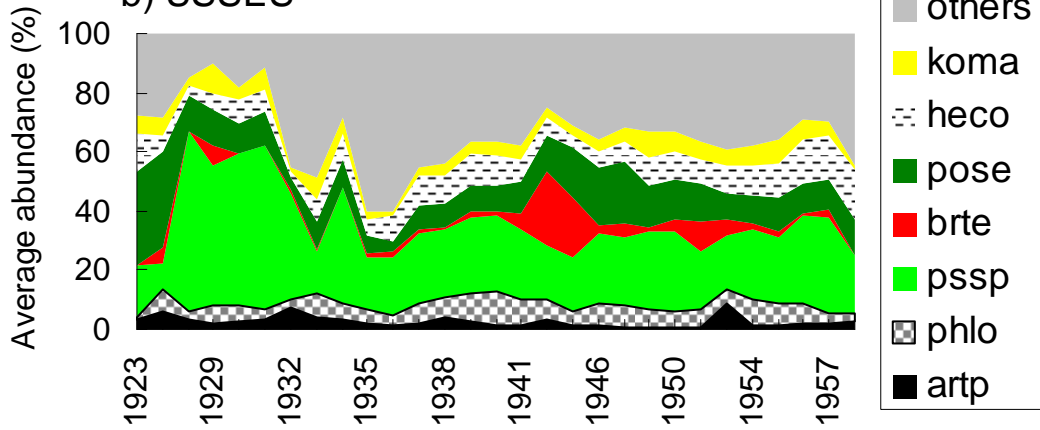
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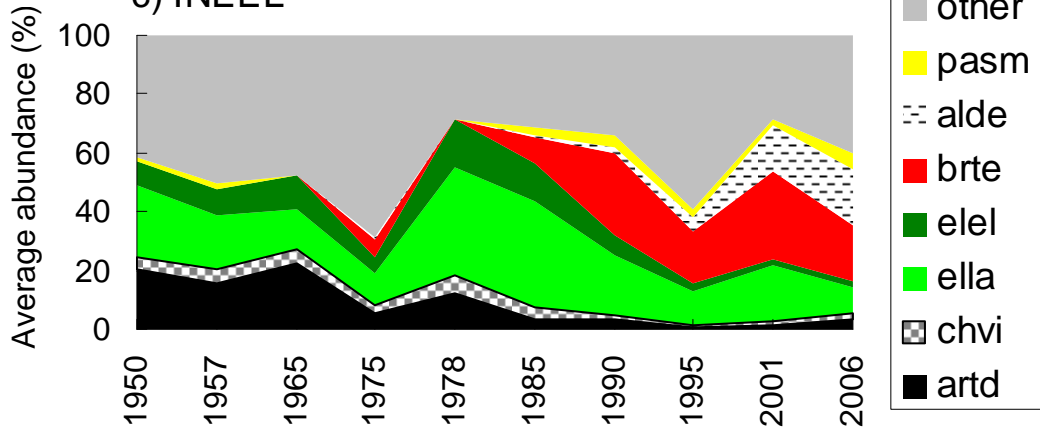
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10 b) USSES



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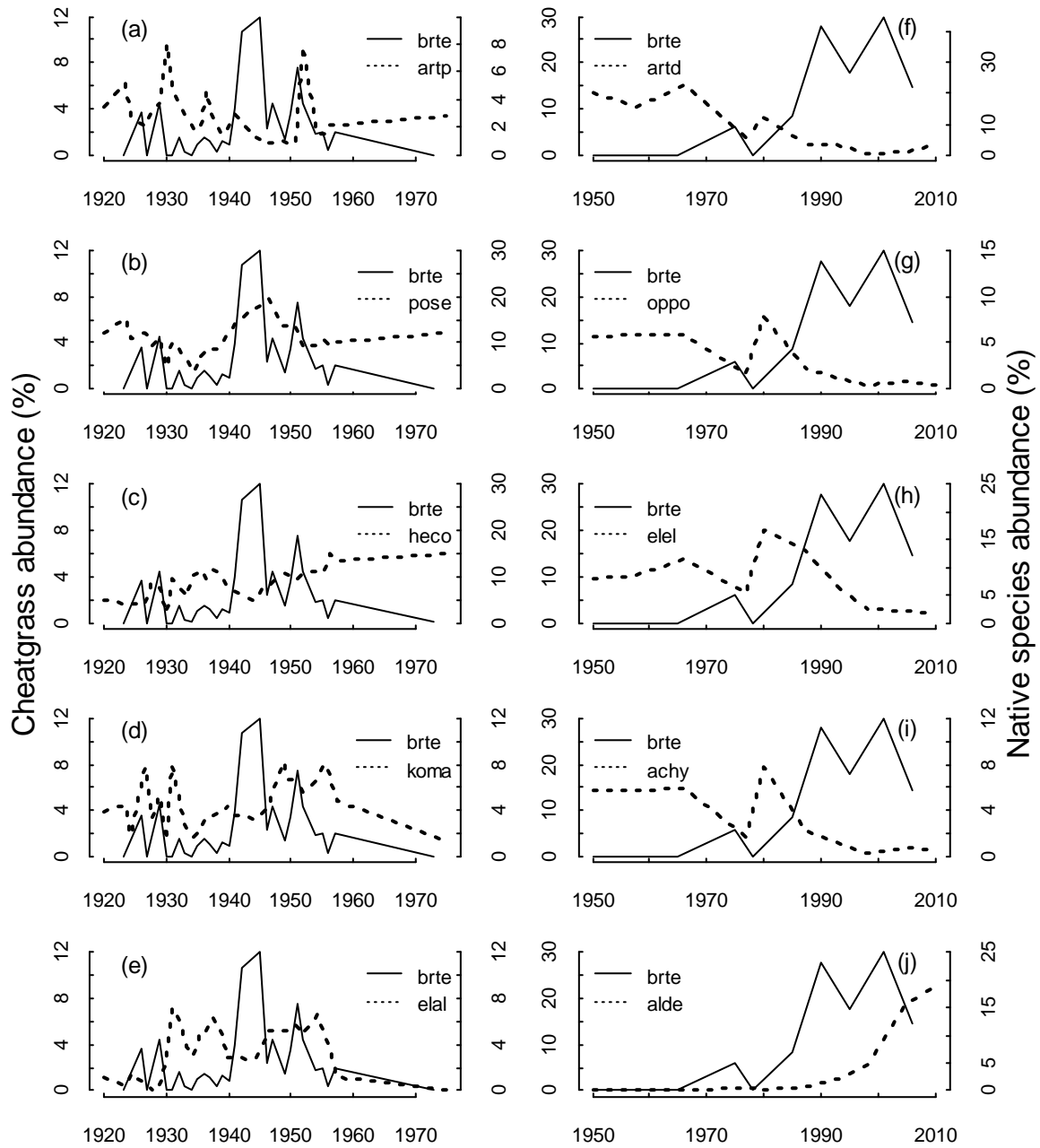
12 c) INEEL



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1 Fig. 2



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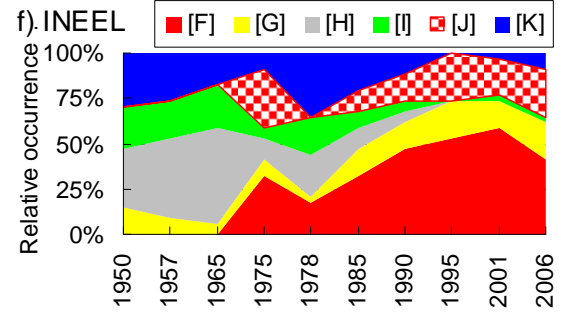
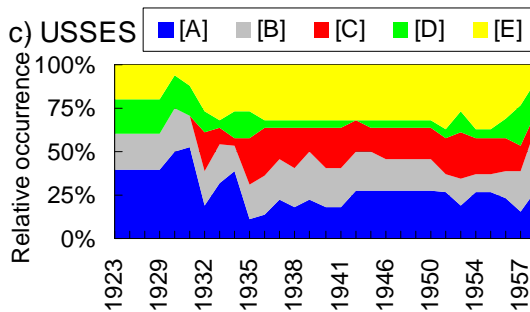
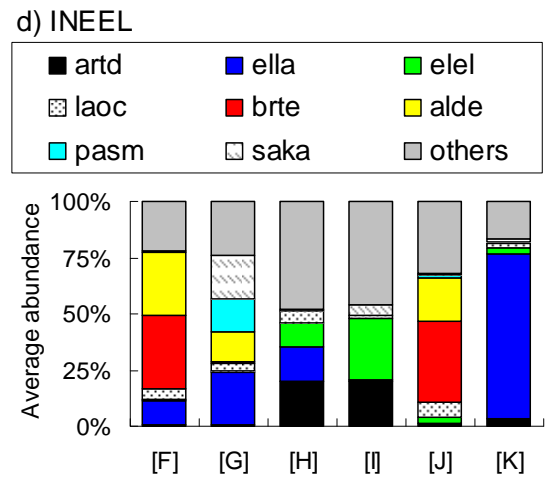
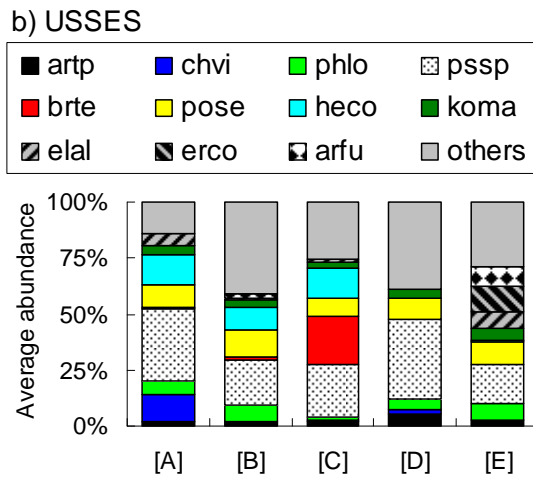
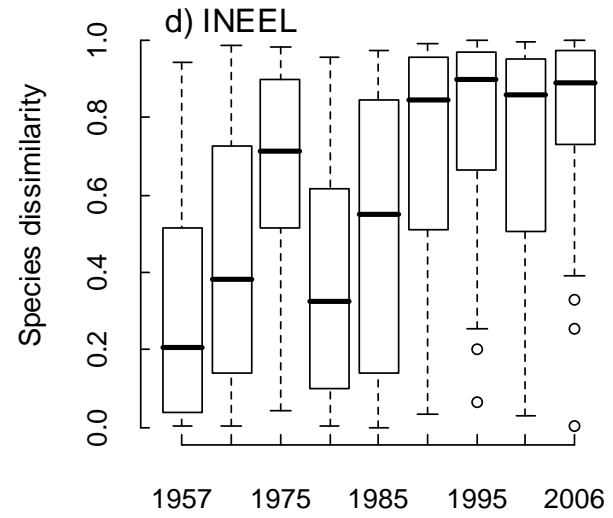
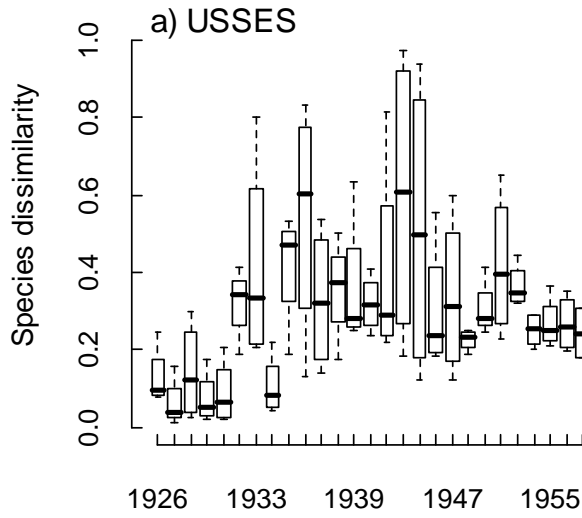
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1 Fig. 3



1 Fig. 4.

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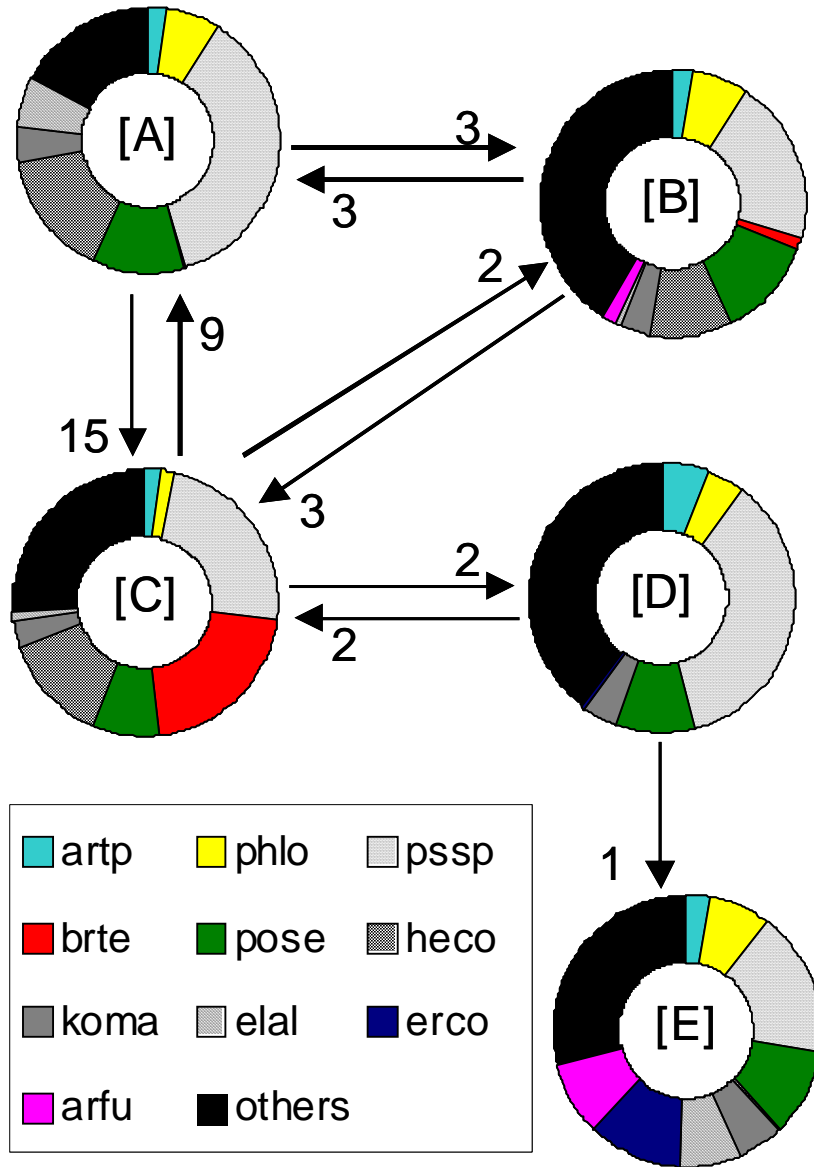
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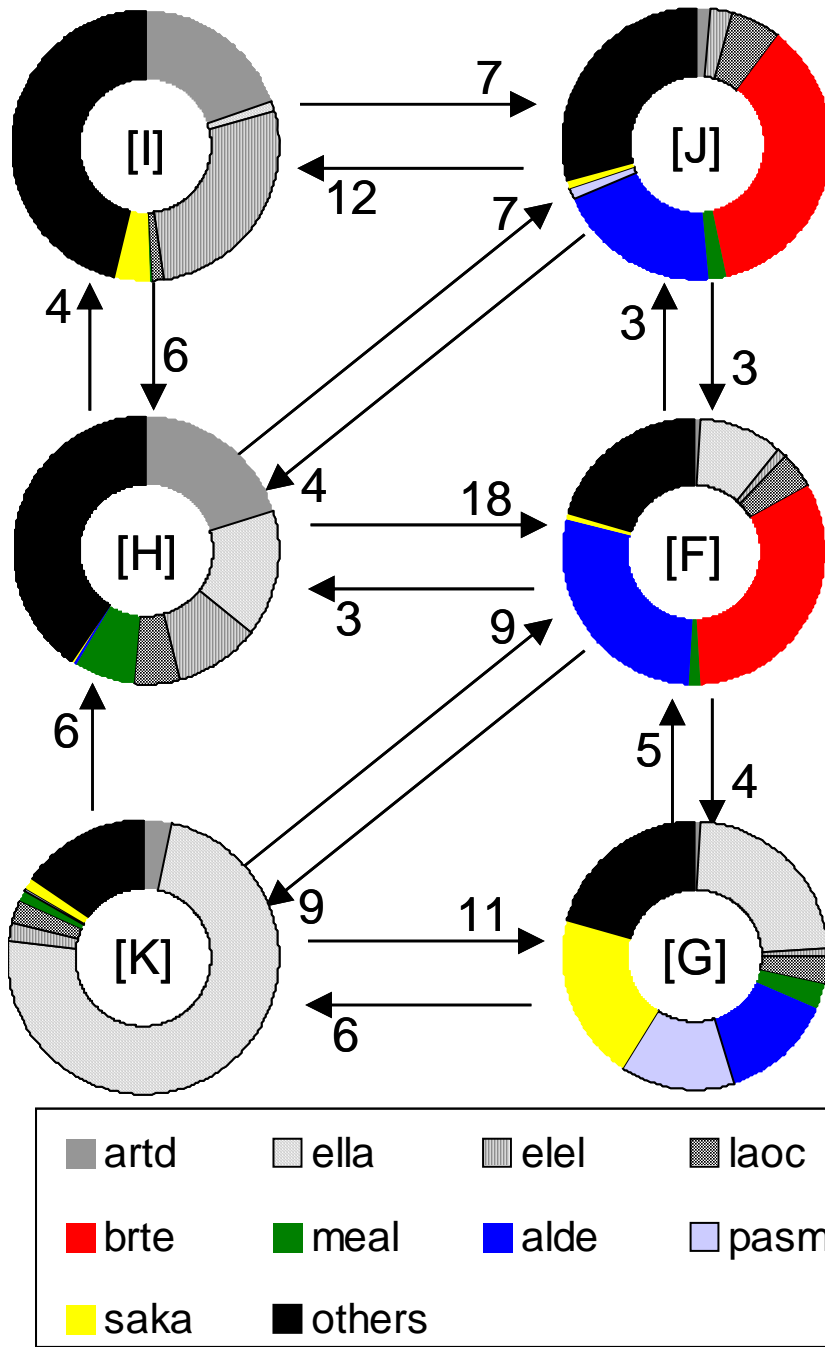
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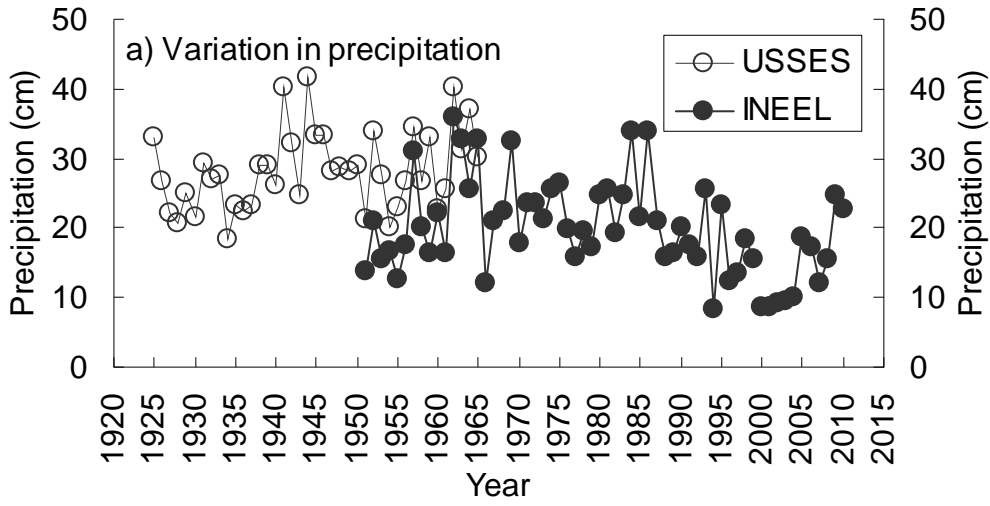


1 Fig. 5.

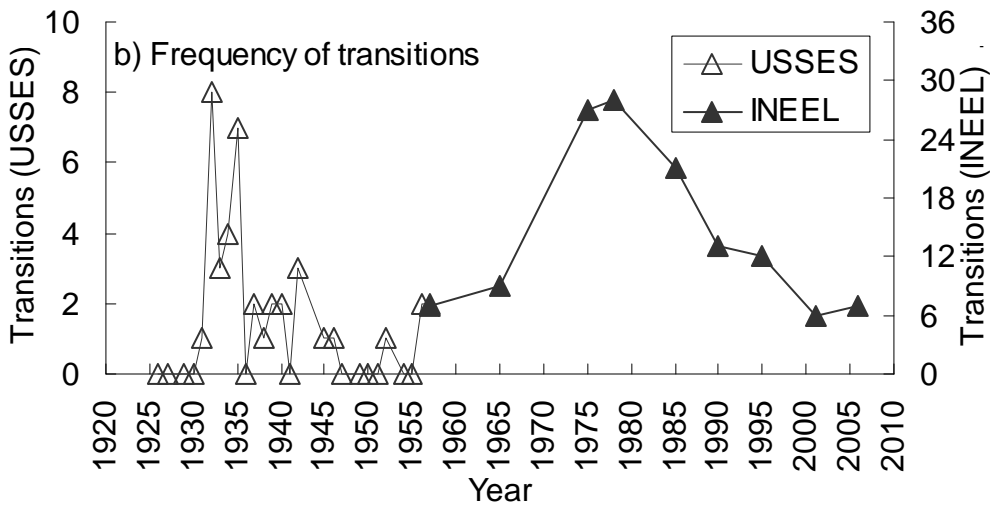
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1 Fig. 6.



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