Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2016, **53,** 1013–1022 doi: 10.1111/1365-2664.12630

Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change

Lauren M. Porensky[1]*, Kevin E. Mueller[1], David J. Augustine[1] and Justin D. Derner[2]

[1]Rangeland Resources Research Unit, USDA-ARS, 1701 Centre Ave, Fort Collins, CO 80526, USA; and [2]Rangeland Resources Research Unit, USDA-ARS, 8408 Hildreth Road, Cheyenne, WY 82009, USA

Summary

1. Temporal changes in semi-arid ecosystems can include transitions between alternative stable states, involving thresholds and multiple domains of attraction, but can also include relatively continuous, symmetric and reversible shifts within a single stable state. Conceptual state-and-transition models (STMs) describe both types of ecosystem dynamics by including state transitions (plant community changes difficult-to-reverse without substantial input or effort) and phase shifts (easily reversible community changes) as consequences of management practices and environmental variability. Grazing management is purported to be the primary driver of state transitions in current STMs for North American grasslands, but there is limited empirical evidence from these grasslands showing that grazing can cause difficult-to-reverse transitions between alternate stable states.

2. In a northern mixed-grass prairie in Wyoming, USA, we examined plant community responses to (i) long-term (33-year) grazing intensity treatments (none, light, moderate and heavy stocking rates) and (ii) 8 years of light or no grazing in pastures that were grazed heavily for the previous 25 years.

3. Long-term grazing treatments were associated with distinct, but not stable, plant communities. From year 22 to 33, heavier stocking rates decreased cover of dominant C_3 grasses and increased cover of the dominant C_4 grass *Bouteloua gracilis*.

4. Reversing stocking rates from heavy to light or no grazing resulted in reversal of changes induced by prior heavy stocking for dominant C_3 grasses, but not for *B. gracilis*. For both groups, rates of change following grazing treatment reversals were consistent with rates of change during the initial years of the experiment (1982–1990).

5. *Synthesis and applications*. In a semi-arid rangeland with a long evolutionary history of grazing, different long-term grazing intensity treatments caused slow, continuous and directional changes with important management implications, but did not appear to induce alternative stable states. For this and similar ecosystems, quantifying the time-scales and compositional gradients associated with key phase shifts may be more important than identifying thresholds between alternative stable states.

Key-words: alternative stable states, blue grama, cool-season grasses, grazing intensity, *Hesperostipa comata*, non-equilibrium dynamics, *Pascopyrum smithii*, rangeland, state-and-transition models, stocking rates

Introduction

Rangeland ecosystems can exhibit both continuous (single stable state) and threshold-dominated (multiple stable states) vegetation dynamics in response to grazing and other forms of disturbance (Briske, Fuhlendorf & Smeins 2003). Optimizing ecosystem goods and services and avoiding undesirable threshold shifts necessitates an understanding of how temporal and spatial scales, management practices, landscape characteristics and other drivers interactively influence ecosystem dynamics (e.g.

---

*Correspondence author. E-mail: lauren.porensky@ars.usda.gov

Fuhlendorf, Briske & Smeins 2001; Bestelmeyer *et al.* 2003). Moreover, this complexity needs to be accurately represented in conceptual frameworks that inform management decisions.

State-and-transition models (STMs) are conceptual models that embrace the potential for (i) *phase shifts*, defined as continuous and reversible vegetation changes in which similar rates and mechanisms of change are observed during deviations away from and back towards a starting point, and (ii) *state transitions*, defined as difficult-to-reverse and often sudden changes between alternative stable states (Westoby, Walker & Noy-Meir 1989; Laycock 1991; Bestelmeyer *et al.* 2003). STMs are being developed for ecosystems around the world (Wong, Morgan & Dorrough 2010) and underlie one of the world's largest formal land management frameworks (Twidwell, Allred & Fuhlendorf 2013). An important challenge in developing STMs is identifying those conditions, processes and ecological interactions that result in phase shifts versus state transitions. This distinction is critical because the ecological mechanisms and management implications of a state transition generally differ dramatically from those of a phase shift. While considerable attention has been devoted to understanding the theoretical underpinnings of state transitions in rangelands (van de Koppel, Rietkerk & Weissing 1997; Briske, Fuhlendorf & Smeins 2003, 2005) and identifying thresholds at which such transitions can occur (Bagchi *et al.* 2013; Kachergis, Rocca & Fernández-Giménez 2014), few studies have evaluated long-term vegetation dynamics associated with experimentally sustained and reversed management treatments (Milchunas 2011).

Livestock grazing is implicated as the primary driver of state transitions and phase shifts in STMs developed for North American rangelands (Twidwell, Allred & Fuhlendorf 2013). In some cases, empirical evidence supports the idea that grazing induces transitions to alternative states (Courtois, Perryman & Hussein 2004; Briske, Fuhlendorf & Smeins 2005; Miller *et al.* 2011). However, studies from several different rangelands have emphasized that grazing-induced vegetation changes can occur gradually over time-scales of decades or longer, and are frequently reversible at those time-scales (Fuhlendorf, Briske & Smeins 2001; Valone *et al.* 2002; Milchunas 2011; Bestelmeyer *et al.* 2013). Differences in plant community responses to grazing are likely related to evolutionary history of grazing (Milchunas, Sala & Lauenroth 1988), landscape and management context, and the spatial and temporal scales of different studies. Long-term studies that evaluate the time-scales and reversibility of grazing-induced vegetation changes are clearly needed, both to advance the development of quantitative STMs (Fuhlendorf, Briske & Smeins 2001; Bagchi *et al.* 2013) and to determine the relative importance of reversible phase shifts versus difficult-to-reverse state transitions in rangelands.

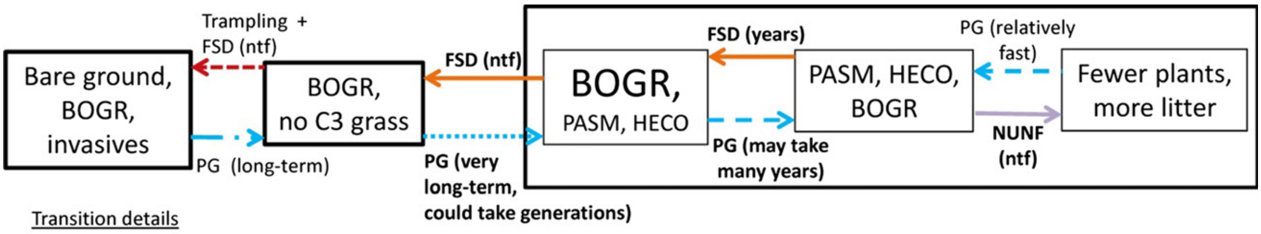
We studied plant community responses to grazing treatments implemented for 33 years in a northern mixed-grass prairie. Previously, Manley *et al.* (1997) reported that during the first 13 years of the experiment, heavy stocking increased the cover of C_4 grasses and reduced the cover and biomass of C_3 graminoids. Treatments began to differ significantly in C_3 graminoid cover only in year 8, and shifts in C_4 grass cover took even longer to become significant (Manley *et al.* 1997). Here, we focus on years 22–33 of the experiment. We also evaluate temporal plant community dynamics in a second experiment, where a subset of heavily stocked pastures were switched after 25 years to either light or no grazing treatments, which were then maintained for the next 8 years. An existing STM for our study area posits that long-term heavy grazing will induce a transition from a mixed C_3/C_4 perennial graminoid state to a state lacking C_3 graminoids; the expected transition rate under heavy grazing (less than a decade) is much more rapid than the reverse transition following removal of heavy grazing (four or more decades, Fig. 1; USDA NRCS 2008). Asymmetry is also expected in rates of change among different community phases within a state (Fig. 1). According to the STM, asymmetric rates of change result from alterations in competitive dynamics, infiltration capacity and propagule availability (USDA NRCS 2008). Such asymmetry in rates of change associated with the application versus removal of heavy grazing is a widely held assumption in STMs for many North American rangelands (Twidwell, Allred & Fuhlendorf 2013).

Here, we empirically evaluate several of the thresholds and rates of change between alternative states and community phases detailed in this broadly representative (*sensu* Twidwell, Allred & Fuhlendorf 2013) STM. First, we examine whether long-term grazing treatments generated alternative stable states. Evidence for alternative stable states would include (i) plant communities that were different and stable over time during the third decade of this experiment and (ii) evidence that after reducing stocking rate from heavy (1982–2006) to light or no grazing (2007–2014), the plant community did not shift back towards the expected community composition for a lightly grazed or ungrazed state. Secondly, we used long-term experimental data to evaluate specific elements of the existing STM. In particular, we (i) quantify the magnitude and temporal dynamics of vegetation change associated with different grazing practices and (ii) determine whether long-term heavy grazing causes the extirpation of C_3 perennial grasses (Fig. 1).

Materials and methods

SITE DESCRIPTION

This experiment began in 1982 on northern mixed-grass prairie at the High Plains Grasslands Research Station, located ~7 km north-west of Cheyenne, Wyoming (41°11′ N 104°53′ W). The site had previously been lightly grazed by livestock and wildlife. Mean annual air temperature is 7·3 °C. Mean annual



Transition details

FSD = frequent, severe defoliation

PG = prescribed grazing

NUNF = no use, no fire

ntf = no time-frame specified

Fig. 1. Stylized version of the current state-and-transition model for the study system (BOGR: *Bouteloua gracilis*; PASM: *Pascopyrum smithii*; HECO: *Hesperostipa comata*). Available information on rates of change is included. Boxes with thin lines denote phases, and boxes with thick lines denote states. Transitions relevant to this study are bolded. For further information, see USDA NRCS (2008).

precipitation is 381 mm (132 mm year average) and peaks in May. Soils are coarse, well-drained loams and gravelly loams (Stevenson, Baumgartner & Schuman 1984). Vegetation is predominately grasses. Common perennial C_3 graminoids include *Pascopyrum smithii* [Rydb.] Á. Löve (western wheatgrass), *Hesperostipa comata* [Trin. & Rupr.] Barkworth (needle-and-thread) and *Carex duriuscula* C.A. Mey (needleleaf sedge). *Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths (blue grama) is the dominant perennial C_4 grass.

GRAZING TREATMENTS

Season-long (early June–early October) continuous grazing treatments were initiated in 1982 on two replicate pastures (one north-facing and one south-facing) per treatment and have continued each year to present: light (15·7 ± 2·8 animal unit days per hectare [AUD ha^{-1}]; mean ± SD; or 4 steers per 20 ha), moderate (32·6 ± 5·5 AUD ha^{-1} or 4 steers per 12 ha) and heavy (43·4 ± 7·3 AUD ha^{-1} or 4 steers per 9 ha) stocking rates (Reeves *et al.* 2013). One AUD equals one 454 kg animal for 1 day. These stocking rates were established to be ~35% below, equal to and ~33% above stocking rates recommended by the USDA NRCS (Hart *et al.* 1988). The light stocking rate treatment was implemented in one large pasture that included north-facing and south-facing aspects (monitored separately), but the pasture was not formally divided (fenced) into two replicate pastures; results should be interpreted cautiously for this pseudo-replicated treatment. Two 0·5 ha fenced exclosures constructed in 1981 remained ungrazed throughout the experiment. The original experiment also included eight pastures (four north-facing and four south-facing) assigned to rotational grazing treatments (Hart *et al.* 1988). In 2007, four pastures that were heavily stocked with rotational grazing from 1982 to 2006 were switched to continuous light or no grazing (one north-facing and one south-facing pasture for each new treatment). Prior to the switch, plant community composition and production did not differ significantly among the six heavily stocked pastures, regardless of grazing system (Manley *et al.* 1997; Derner & Hart 2007; see also Fig. S1 in Supporting information). Thus, our analyses are based on two pasture-scale replications each of six grazing treatments: none, light (pseudo-replicated), moderate, heavy, heavy to light and heavy to none.

Yearling steers (castrated males of Hereford, Black Angus or crossed English breeds) were used as grazing animals. Grazing season length was constrained by weather and forage availability. Grazing seasons were skipped or shortened due to drought in 5 years (Derner & Hart 2007).

VEGETATION SAMPLING

To quantify changes in plant species composition, we sampled 25, 0·1 m^2 (0·2 × 0·5 m) permanent quadrats randomly located along each of two 50-m permanent transects per pasture. Quadrats were sampled annually in mid-July from 2003 to 2014. Plants within each quadrat were identified to species, except for two rare legumes with similar appearances. Basal and foliar cover of each species was visually estimated using modified Daubenmire (1959) cover categories of: 0–1%, 1–5%, 6–15%, 16–25%, 26–40%, 41–60% and >60%. To be consistent with earlier reports from this experiment, mid-points of cover classes were used in calculating abundance of each species (Hickman & Derner 2007), though this approach is known to be imperfect (Currall 1987). For each transect, data from the 25 quadrats were averaged to generate transect-scale cover by species. Transect-scale data were used for all statistical analyses. Plant community data were not collected from 1994 to 2002, precluding analysis of vegetation dynamics across the full 33-year experiment.

STATISTICAL ANALYSIS

To assess long-term impacts of stocking rate on plant community composition and identify which plant species were most responsive to the grazing treatments, we used a partial redundancy analysis (RDA) ordination with year included as a covariable (Lepš & Šmilauer 2003). Results included sample and species scores along a set of constrained RDA axes which related plant community composition to treatments and year × treatment interactions. Two sets of partial RDA analyses explored impacts of (i) long-term grazing treatments (exclosure, light, moderate and heavy stocking; timeframe = 2003–2014, hereafter referred to as the 'long-term' experiment) and (ii) long-term grazing treatments vs. grazing reversal treatments (exclosure, light, moderate and heavy stocking plus new exclosure and new light stocking; timeframe = 2007–2014, hereafter referred to as the 'grazing reversal' experiment). Prior to RDA analyses, we normalized species cover values to represent proportions of total vascular plant cover. We then excluded species that occurred in <5% of the samples (c.f. Harrison, Damschen & Grace 2010; Alday *et al.* 2013). We ran

RDA ordinations on this reduced data set and evaluated the overall significance of ordinations using the anova.cca function in vegan (Oksanen *et al.* 2013). We identified the number of constrained RDA axes that explained ≥90% of treatment-related sample variance, then extracted species and sample (transect × year combination) scores for these axes. Significance of each axis was tested using a permutation test after factoring out lower-level axes (Van den Brink & Ter Braak 1998). Data transformations that reduce the role of abundant species (e.g. Wisconsin square root) did not qualitatively affect our results, but reduced the percentage variance explained by RDA axes. Thus, we present results from ordinations on untransformed data. Results for foliar cover were very similar to results for basal cover. For brevity, we only report results for basal cover, which is less sensitive to variability in weather.

We used linear mixed models (LMMs) to understand relationships between grazing treatments and the sample scores along the first two RDA axes. This approach evaluates effects of grazing on overall community composition while accounting for spatial autocorrelation and the potentially confounding effects of weather. Random factors included pasture and transect nested within pasture. We used a compound symmetry covariance structure to address non-independence among repeated surveys along the same transect. Fixed effects included grazing treatment (discrete variable), year (continuous variable) and the grazing treatment × year interaction. Spring weather (April–June) can strongly impact primary and secondary production in this system (Derner & Hart 2007; Derner *et al.* 2008; Reeves *et al.* 2013), so we included total spring precipitation, average spring temperature and their interactions with grazing treatment as covariates in mixed models. Consequently, the year and year × grazing treatment terms can be interpreted as being independent of interannual variability in spring weather and should more accurately reflect the effects of experiment duration, the primary focus of this study. Weather covariate results are presented in Appendix S1. Using the same model structure, we ran LMMs on species that scored highly on RDA axes 1 and 2, including relative and absolute cover of *P. smithii*, *H. comata* and *B. gracilis*. To provide additional context, we ran parallel LMMs on total basal plant cover, bryophyte (lichen + moss) cover, bare ground and litter cover.

Analyses were conducted in R 2.12.2 using the VEGAN (Oksanen *et al.* 2013) and NLME packages (Pinheiro *et al.* 2013). Response values were transformed or variance-weighted when necessary to meet model assumptions. Reported results are untransformed means ± 1 SE.

Results

PLANT COMMUNITY

For both the long-term experiment and the grazing reversal experiment, partial RDA ordinations revealed significant variation among grazing treatments and years (anova.cca *P*-values < 0·0005). Grazing treatment, year and grazing × year interactions explained 64–66% of the total variance in plant community composition (Table S1). Of the variance explained by grazing and grazing × year, RDA Axis 1 accounted for 86–87% and RDA Axis 2 accounted for 5–6% (Table S1). Both axes were highly significant (Table S1). RDA Axis 1 was not affected by spring precipitation, spring temperature or weather × grazing interactions. Conversely, RDA Axis 2 models included significant main effects of spring precipitation and significant precipitation × grazing interactions (Appendix S1).

Long-term experiment

Long-term stocking rate treatments caused continued, directional shifts in plant community composition from 2003 to 2014 (years 22–33 of the experiment). RDA Axis 1 separated *B. gracilis* (negative loadings) from *P. smithii*, *H. comata*, other C_3 perennial graminoids and forbs (positive loadings; Fig. 2a). Higher stocking rates were associated with lower RDA scores, indicating increased cover of *B. gracilis* and reduced cover of *P. smithii*, *H. comata*, other C_3 graminoids and forbs (Fig. 3a; $F_{3,4} = 8{\cdot}72$, $P = 0{\cdot}03$). Moreover, plant communities subjected to different stocking rate treatments diverged from one another between 2003 and 2014 (Fig. 3a; $F_{3,164} = 16{\cdot}63$, $P < 0{\cdot}0001$).

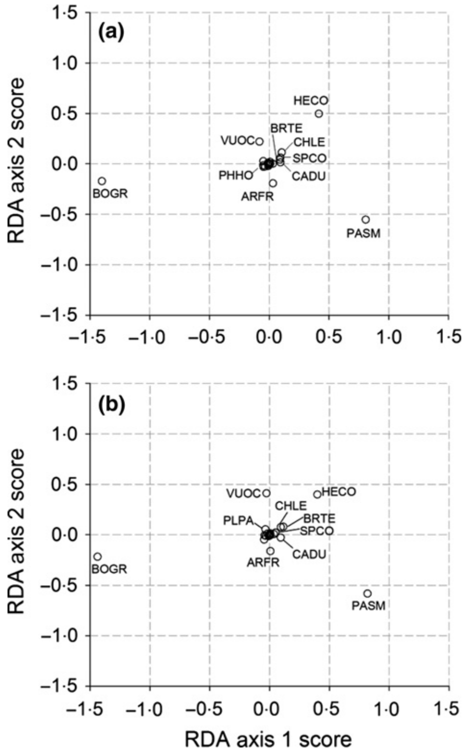


Fig. 2. Relationships between community-level results and individual species for (a) the long-term grazing study and (b) the grazing reversal study. Points represent species scores plotted against the first two RDA axes, based on constrained ordinations of basal cover. ARFR: *Artemisia frigida*, BOGR: *Bouteloua gracilis*, BRTE: *Bromus tectorum*, CADU: *Carex duriuscula*, CHLE: *Chenopodium leptophyllum*, HECO: *Hesperostipa comata*, PASM: *Pascopyrum smithii*, PHHO: *Phlox hoodii*, PLPA: *Plantago patagonica*, SPCO: *Sphaeralcea coccinea*, VUOC: *Vulpia octoflora*.

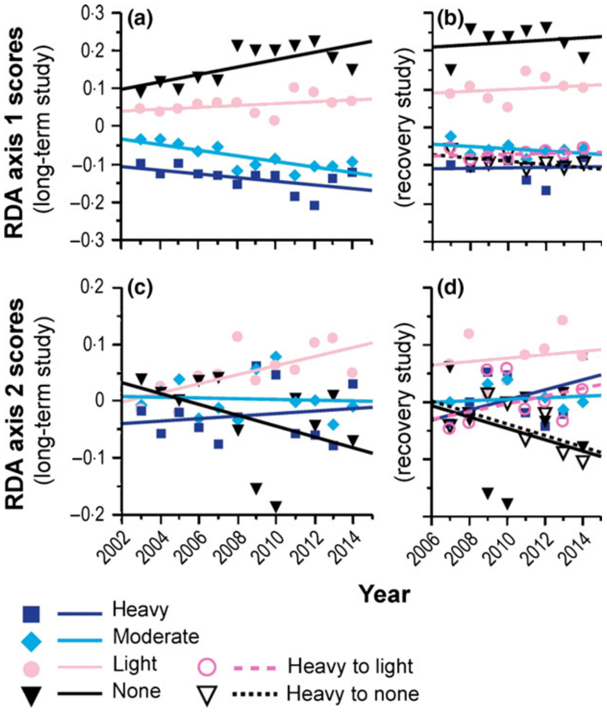


Fig. 3. RDA Axis 1 (a,b) and Axis 2 (c,d) scores for constrained plant community ordination of basal cover. The left panels (a,c) show results for the long-term grazing study, and the right panels (b,d) show results for the grazing reversal study. Points represent RDA scores averaged across 4 transects (2 transects × 2 replicate pastures). Lines show treatment-specific predictions using mean spring climate conditions during the observation period associated with each study. See Appendix S2 for estimates of variance.

RDA Axis 2 separated *P. smithii* (negative loadings) from *H. comata* (positive loadings; Fig. 2a). This axis also provided evidence of long-term community divergence among grazing treatments (Fig. 3c; grazing $F_{3,4}$ = 0·30, P = 0·86; grazing × year $F_{3,164}$ = 5·11, P = 0·002). From 2003 to 2014, RDA Axis 2 scores for exclosures decreased, indicating more cover of *P. smithii*, while scores for lightly grazed pastures increased, indicating more cover of *H. comata* (Fig. 3c). Moderately and heavily grazed pastures had low and stable scores on RDA Axis 2, reflecting low relative cover of both dominant C_3 grasses.

Analyses of three plant species which scored highly on RDA axes 1 and 2 (*P. smithii*, *H. comata* and *B. gracilis*, which together constitute 62% of total plant basal cover) complemented the community-level results. Patterns and statistical tests for relative and absolute cover were very similar (Fig. 4; Appendix S1), so we present relative cover here. For the summed cover of the two most dominant C_3 perennial graminoids (*P. smithii* and *H. comata*), relative cover was initially similar for the exclosure and lightly stocked treatments (41% and 38% in 2003) and lower in the moderately and heavily stocked treatments (27% and 16%; Fig. 4a; $F_{3,4}$ = 4·99, P = 0·08). Over time, combined cover of *P. smithii* and *H. comata* increased sharply in exclosures, remained stable in lightly stocked pastures and decreased in moderately and heavily stocked pastures (Fig. 4a; $F_{3,163}$ = 23·2, P < 0·0001). This resulted in magnified differences between pastures with no to light grazing and pastures with moderate-to-heavy grazing. For *P. smithii* alone, relative cover in exclosures was initially 2·5 times higher than in heavily stocked pastures (Fig. 4c; $F_{3,4}$ = 7·01, P = 0·05), and treatments diverged over time, with cover in exclosures increasing by 63% while cover in heavily grazed pastures declined by 47% ($F_{3,163}$ = 17·1, P < 0·0001). For *H. comata* alone, cover in heavily stocked pastures decreased by 62%, while cover in exclosures showed no directional trend (Fig. 4e; grazing $F_{3,4}$ = 0·78, P = 0·6, grazing × year $F_{3,163}$ = 2·95, P = 0·03).

Bouteloua gracilis comprised 99% of C_4 perennial grass basal cover. For *B. gracilis* in 2003, relative cover in heavily stocked pastures was 314% higher than in exclosures and 105% higher than in lightly stocked pastures (Fig. 4g; $F_{3,4}$ = 6·99, P = 0·05). *B. gracilis* cover increased strongly over time under heavy and moderate stocking, but remained stable in lightly stocked pastures and exclosures (Fig. 4g; $F_{3,164}$ = 4·61, P = 0·004). By 2014, cover of *B. gracilis* in heavily stocked pastures was 353% higher than in exclosures and 153% higher than in lightly stocked pastures.

Grazing reversal experiment

Similar to the long-term experiment, variation along RDA Axis 1 was driven by differences between *B. gracilis* (negative loadings) and C_3 perennial graminoids and forbs (positive loadings; Fig. 2b). Higher stocking rates were associated with lower RDA scores (Fig. 3b; $F_{5,6}$ = 11·4, P = 0·005). Grazing reversal treatments did not differ from the long-term heavy stocking treatment (Fig. 3b), and all of these treatments had significantly lower RDA scores than long-term light stocking and exclosure treatments. Grazing treatments did not have different temporal trajectories along Axis 1 (Fig. 3b; $F_{5,150}$ = 0·66, P = 0·7).

Along RDA Axis 2, which separated *H. comata* and *Vulpia octoflora* (Walt.) Rydb. (positive loadings) from *P. smithii* (negative loadings; Fig. 2b), different grazing treatments displayed different temporal trajectories (Fig. 3d; grazing treatment: $F_{5,6}$ = 0·86, P = 0·6, grazing × year: $F_{5,150}$ = 3·68, P = 0·004). New exclosures became increasingly different from long-term heavily and moderately grazed pastures, indicating increased relative cover of *P. smithii* in the new exclosures (Fig. 3d).

Following reversal to light stocking or no grazing, responses varied among the three dominant plant species. Again, patterns and statistics for absolute cover were similar to those for relative cover (Fig. 4; Appendix S1). From 2007 to 2014, the combined relative cover of *P. smithii* and *H. comata* increased in the grazing reversal and long-term exclosure treatments, while it continued to decrease slightly in the long-term moderate and heavy stocking treatments (Fig. 4a; $F_{5,148}$ = 4·29, P = 0·001). By 2014, dominant C_3 perennial grass cover in grazing reversal pastures was similar to cover in long-term moderately stocked pastures, 74%

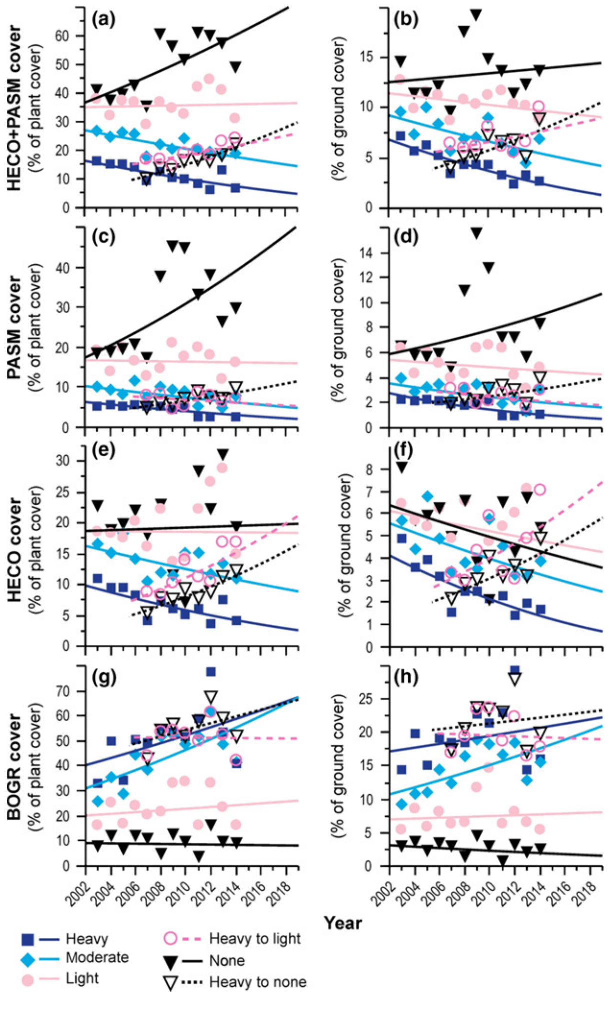


Fig. 4. Temporal patterns in the basal cover of (a,b) the sum of the two most dominant perennial C_3 graminoids (PASM + HECO: *Pascopyrum smithii* and *Hesperostipa comata*), (c,d) *P. smithii*, (e,f) *H. comata* and (g,h) the dominant perennial C4 grass (BOGR: *Bouteloua gracilis*) across different grazing treatments. Points represent mean relative (a,c,e,g) and absolute (b,d,f,h) basal cover based on 4 transects (2 transects × 2 replicate pastures). Lines show treatment-specific predictions of basal cover (see Fig. 3 for details), extended slightly to show potential temporal trajectories based on the modelled impact of experimental duration. See Appendix S2 for estimates of variance.

of cover in long-term lightly stocked pastures and 47% of cover in long-term exclosures (Fig. 4a; $F_{5,6} = 6{\cdot}06$, $P = 0{\cdot}03$). Individual species displayed patterns that supported their grouped response. For *P. smithii*, relative cover increased in new exclosures but did not increase in new lightly grazed, long-term moderately grazed or long-term heavily grazed pastures (Fig. 4c; grazing $F_{5,6} = 10{\cdot}3$, $P = 0{\cdot}008$; grazing × year $F_{5,149} = 2{\cdot}56$, $P = 0{\cdot}03$). For *H. comata*, relative cover increased strongly in both grazing reversal treatments (Fig. 4e; grazing $F_{5,6} = 0{\cdot}79$, $P = 0{\cdot}6$; grazing × year $F_{5,149} = 2{\cdot}00$, $P = 0{\cdot}08$). By 2014, *H. comata* cover in grazing reversal pastures was similar to cover in long-term lightly grazed pastures.

Basal cover of *B. gracilis* did not respond strongly to grazing reversal treatments during the first 8 years after implementation of grazing reversal treatments. Relative cover values did not differ among long-term heavily stocked pastures, new lightly stocked pastures and new exclosures (55%, 51% and 55% of total basal plant cover, respectively, on average from 2007 to 2013). All three treatments had significantly higher cover of *B. gracilis* than long-term light or no stocking treatments (25% and 10% of total basal plant cover, respectively; Fig. 4g; $F_{5,6} = 10{\cdot}4$, $P = 0{\cdot}008$). Temporal trends for *B. gracilis* basal cover did not differ among stocking rate treatments from 2007 to 2014 (Fig. 4g; $F_{5,149} = 0{\cdot}94$, $P = 0{\cdot}5$).

ADDITIONAL PROPERTIES

Long-term experiment

Between 2003 and 2014, stocking rate treatments diverged from one another for total vascular plant basal cover and bryophyte cover. Initially, plant cover and bryophyte cover were 1·2 and 2·7 times greater in heavily grazed pastures compared to exclosures, respectively (Fig. 5a,b; total cover $F_{3,4} = 9{\cdot}44$, $P = 0{\cdot}03$; bryophyte $F_{3,4} = 17{\cdot}0$, $P = 0{\cdot}009$). Plant cover declined over time, and declines were strongest in exclosures (Fig. 5a; $F_{3,164} = 2{\cdot}98$, $P = 0{\cdot}03$). Bryophyte cover also declined over time, but decreases were stronger in moderate and heavily grazed pastures (Fig. 5b; $F_{3,162} = 3{\cdot}69$, $P = 0{\cdot}01$). Litter cover was higher in pastures with lower stocking rates (Fig. 5d; $F_{3,4} = 11{\cdot}6$, $P = 0{\cdot}02$), but treatments did not display significantly different temporal trends ($F_{3,163} = 1$, $P = 0{\cdot}4$). Grazing treatments did not significantly affect bare ground, although there was a consistent tendency for more bare ground in the moderately and heavily grazed pastures (Fig. 5c; *P*-values > 0·14).

Grazing reversal experiment

From 2007 to 2014, bryophyte cover in grazing reversal pastures became more similar to pastures with a long-term history of light to no grazing and less similar to pastures with a long-term history of heavy grazing. Bryophyte cover declined over time, and decreases were strongest for grazing reversal treatments (Fig. 5b; bryophyte $F_{5,150} = 3{\cdot}55$, $P = 0{\cdot}005$). For total plant cover, litter cover and bare ground, temporal trends did not differ significantly among grazing treatments during the grazing reversal timeframe (Fig. 5a,c,d; grazing × year interaction *P*-values > 0·4), though bare ground showed a non-significant decline in grazing reversal pastures.

Discussion

EVIDENCE FOR ALTERNATIVE STABLE STATES

Based on existing conceptual frameworks for this (Fig. 1) and many similar semi-arid rangelands (Twidwell, Allred & Fuhlendorf 2013), we expected that heavy grazing

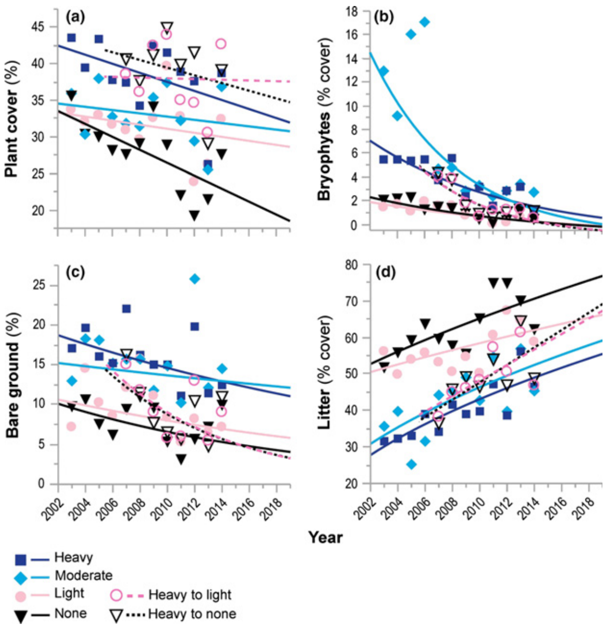


Fig. 5. (a) Total basal plant cover, (b) bryophyte cover, (c) bare soil and (d) litter across different grazing treatments. Points represent mean values based on 4 transects (2 transects × 2 replicate pastures). Lines show treatment-specific predictions (see Fig. 3 for more details). See Appendix S2 for estimates of variance.

applied for 33 years would push the ecosystem into an alternative stable state (Suding & Hobbs 2009). Although our study cannot eliminate the possibility of alternative stable states in this ecosystem, our results are most consistent with a temporal gradient model in which grazing induces slow, continuous and reversible changes in plant species abundance. During the third decade of this experiment, plant communities associated with different grazing intensities had not reached apparent, alternate stable equilibria, but instead were continuing to steadily diverge. These results concur with an earlier report from this experiment (Manley *et al.* 1997), which emphasized the slow and steady nature of plant community change in this ecosystem.

It is possible that a state shift occurred but was not marked by sudden changes or subsequent stabilization of vegetation composition (Kachergis, Rocca & Fernández-Giménez 2014). The grazing reversal study allowed us to determine whether, after the removal of heavy grazing, plant community components began shifting back towards levels characteristic of a lightly grazed state (indicating that a threshold had not been crossed) or continued to remain at levels characteristic of a heavily grazed state (indicating that the system could be in a new, alternative stable state). In particular, we tested whether rates of change following imposition of heavy grazing (in 1982) were more rapid than rates of change following removal of heavy grazing (in 2007). For pastures converted from heavy stocking to light or no grazing, we saw strong evidence of reversibility and symmetry in rates of change for the two most dominant C_3 perennial grasses. These two species have substantial ecological and economic value in the region (Derner *et al.* 2009; Dunn *et al.* 2010) and, in years with sufficient spring moisture, are taller and substantially more productive than the co-occurring C_4 shortgrasses (Milchunas, Forwood & Lauenroth 1994). Under long-term heavy grazing, cover of these C_3 grasses declined by 0·32% annually, while following removal of heavy grazing they increased by 0·35% annually (Fig. 6). This evidence for symmetric rates of change contrasts with the current STM's predictions (Fig. 1). Release from heavy grazing did not induce significant changes in basal cover of the dominant C_4 shortgrass (Fig. 4); this finding is consistent with expected rates of change for *B. gracilis*, which took more than 8 years to begin responding to experimental grazing treatments imposed in 1982 (Hart *et al.* 1988; Manley *et al.* 1997). We hypothesize that this species displays time-lagged above-ground responses to management changes because it is disturbance tolerant, has ample below-ground reserves and, due to differing phenology, has relatively weak interaction strength with the C_3 species most affected by grazing management (Monson, Littlejohn & Williams 1983; Milchunas, Sala & Lauenroth 1988). Future monitoring is necessary to determine whether plant communities continue to shift in grazing reversal pastures. However, given that our findings match extremely well with previously measured rates of change in this ecosystem (Hart *et al.* 1988; Manley *et al.* 1997), it seems likely that evidence of reversal will continue to become stronger in the next few years. Several studies in other rangelands have also observed grazing-related changes that are reversible, but only over relatively long (e.g. decadal) time-scales (Fuhlendorf, Briske & Smeins 2001; Valone *et al.* 2002; Milchunas 2011).

It is possible that we did not detect a state transition that would have occurred if stocking rates were maintained at a level higher than this study's heavy stocking rate (targeted for 60% utilization). However, even if a state transition is possible (e.g. with very high stocking rates sustained over a long time), this possibility has little relevance for management because sustained high stocking rates substantially reduce annual forage production (Derner & Hart 2007), livestock performance per animal (Derner *et al.* 2008) and ranch-level drought tolerance (Kachergis *et al.* 2014). For a wide range of livestock prices and weather conditions, the economically optimum stocking rate ranges from below our moderate rate to a level intermediate between our moderate and heavy rates (Manley *et al.* 1997; Dunn *et al.* 2010). Although ranching operations may occasionally implement very high stocking rates, particularly in years of favourable prices, sustained stocking at levels above our heavy rate is unlikely (Fang *et al.* 2014).

It is also possible that heavy grazing could induce a state transition in parts of the northern mixed-grass prairie that occupy different soil types (as compared to our study), experience different climatic conditions or modify grazing differently in response to weather variability. However, our site is representative of the northern mixed-grass prairie

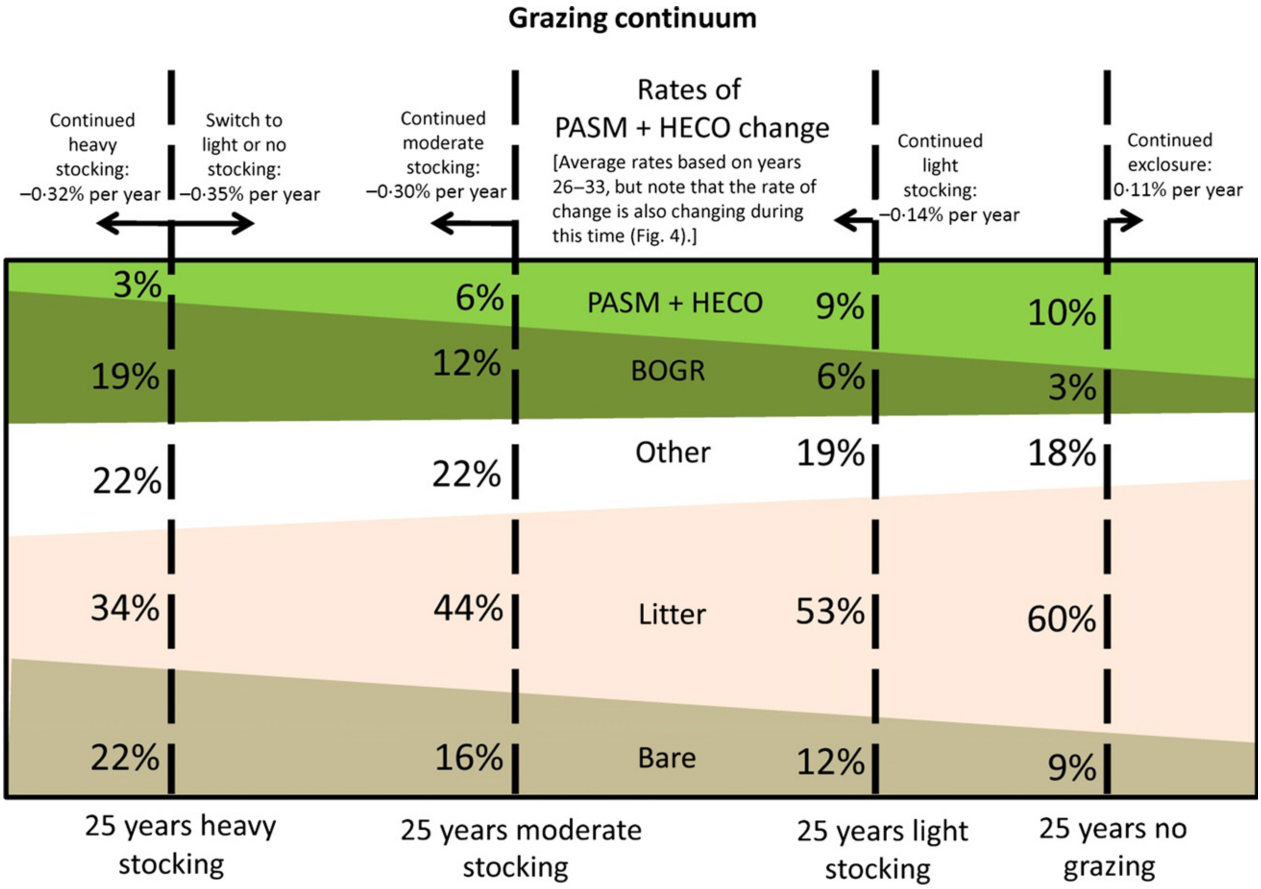


Fig. 6. Gradient-based structure for describing continuous plant community change (phases) within a given state. Includes percentage of basal cover of key groups within plant communities exposed to stocking rate treatments for 25 consecutive years (BOGR: *Bouteloua gracilis*; PASM: *Pascopyrum smithii*; HECO: *Hesperostipa comata*). Also includes rates of PASM + HECO change (absolute basal cover) during years 26–33 of the experiment, based on predictions from models corrected for weather variability.

region in terms of climate, geology, plant community composition (Singh *et al*. 1983; Coupland 1992) and grazing management practices (Roche *et al*. 2015). Thus, existing literature suggests that our results should be applicable across a relatively broad geographic region.

Although the scope of our inferences could be limited because there were only two spatial replicates of each grazing treatment, there are two reasons for confidence in our estimates of grazing impacts. First, the relative abundance of key plant types was similar across treatments initially and during the first several years of the experiment (Hart *et al*. 1988; Manley *et al*. 1997), suggesting that differences among treatments in subsequent years were not caused by pre-existing site differences (e.g. due to soil type or landscape position). Secondly, our results are well-aligned with previous work on plant community responses to grazing in northern mixed-grass prairie and neighbouring shortgrass steppe ecosystems (Coupland 1992; Milchunas, Forwood & Lauenroth 1994).

IMPLICATIONS FOR STMS

In contrast with expectations based on the STM for our study site (Fig. 1; USDA NRCS 2008) and existing STMs for many other semi-arid rangelands in North America (Twidwell, Allred & Fuhlendorf 2013), our long-term experiment shows that the elimination of C_3 perennial grasses did not occur after >30 years of heavy grazing. This calls into question whether, under realistic conditions, grazing or even grazing–drought interactions can induce changes in this ecosystem that prevent C_3 perennial grass recovery when heavy grazing pressure is removed. However, as stated above, our results cannot eliminate the possibility of such a threshold shift in other locations, or in situations where grazing pressure is even more intense.

Although our findings do not support a threshold shift to *B. gracilis* sod lacking C_3 perennial grasses, they do provide general support for the sequence of community phases within the current STM's reference state. Our results suggest that these phases do not exist as discrete units (as represented in the existing STM, Fig. 1) but instead comprise a broad, continuous gradient. Many STMs emphasize state transitions, thresholds and discrete phases within states, while downplaying or lacking quantitative data on dynamics associated with slow, continuous changes in plant composition (Bagchi *et al*. 2013). Box-and-arrow diagrams in STMs are an ineffective visual tool for describing continuous, gradient-like changes. Moreover, rates of change, which have key management consequences, are often not quantified in STMs, and this omission is a recognized weakness (Knapp *et al.* 2011; Bagchi *et al.* 2013). Using our findings, we present a first step towards embracing quantitative rates of change and compositional gradients within states (rather than discrete phases) in STMs (Fig. 6). Including explicit rates of change may help resolve questions surrounding an effective way to represent plant community changes that are reversible, but only over ‘longer’ time-scales (Wong, Morgan & Dorrough 2010). One approach to dealing with slow reversibility has been to differentiate states from phases based (at least in part) on the time-scale of transition reversibility (Bestelmeyer *et al.* 2003). However, this approach can create confusion by confounding slow rates of change with alternative feedback processes (Bestelmeyer *et al.* 2010). Moreover, definitions of ‘long-term’ and ‘slow’ are subjective. We suggest that, especially in rangelands where reversible dynamics are likely, STMs will be more useful for management decision-making if they embrace a more flexible conceptual model structure (Fig. 6) that explicitly quantifies rates of plant community change in response to grazing and other management practices.

IMPLICATIONS FOR GRAZING MANAGEMENT

In our long-term experiment, the greatest divergence in plant community composition occurred between lightly and moderately stocked pastures. Moderately stocked pastures were fairly similar to heavily stocked pastures and both treatments became increasingly dominated by *B. gracilis* at the expense of C_3 grasses (Fig. 4). In contrast, the cover of C_3 grasses was high and stable in lightly stocked pastures (Figs 2 and 3). For managers attempting to increase or maintain the dominance of C_3 grasses, our results suggest that season-long grazing at the NRCS-recommended moderate stocking rate may be too intense. Compositional stability under the light stocking rate with continuous, season-long grazing is likely related to the ability of dominant C_3 perennial grasses to tolerate low rates of tiller defoliation, coupled with a loss of competitive ability under greater frequency and intensity of defoliation (especially grazing during critical growth periods for consecutive years; Mullahey, Waller & Moser 1990; Hart, Clapp & Test 1993).

In pastures grazed heavily for 25 years and then reversed to light or no grazing, C_3 perennial graminoid cover increased substantially after 8 years of grazing reversal, at the expense of bryophytes and bare ground (Fig. 5b,c). The capacity for C_3 graminoids to recover in less than a decade to levels observed in moderately grazed pastures, and to do so even in the absence of a large decline in C_4 grasses, is an important finding of our study. Such resilience may reflect the long evolutionary history of large herbivore grazing in this region (Milchunas, Sala & Lauenroth 1988), which likely selected for plant traits conferring tolerance to grazing. At the same time, the recovery rates we measured indicate that in pastures that have experienced multiple decades of heavy grazing, more than a decade of light grazing may be needed to achieve C_3 graminoid cover values similar to those in lightly grazed pastures (Fig. 4). For other ecosystem components, recovery rates were even slower or null (Figs 3–5). Light stocking for multiple decades is not economically feasible for most managers, though it may be practical for a protected area or in conjunction with payments for ecosystem services. In pastures that have been heavily grazed for multiple decades, avoiding further losses of C_3 perennial grass cover may be a more realistic goal.

In summary, our results suggest that STMs for our study system and other, similar rangelands might misrepresent the resilience of such ecosystems to grazing by (i) overemphasizing the role of non-reversible transitions and (ii) overstating the potential for asymmetry in rates of change associated with shifts in grazing intensity. When using or developing STMs in resilient ecosystems, it may be more important to understand the time-scales and compositional gradients associated with key phase shifts than to focus on the possibility of threshold shifts between alternative stable states.

Acknowledgements

Thanks to Dr. Richard Hart for initiating this study and to the University of Wyoming and 8A Hay and Cattle Company for providing steers. Funding was from USDA-ARS. Matt Mortenson ably maintained the infrastructure. Matt, Jeff Thomas, Mary Ashby and others conducted vegetation sampling.

Data accessibility

Raw basal cover data are available online in the Dryad Digital Repository doi:10.5061/dryad.3m8p1 (Porensky *et al.* 2016).

References

Alday, J.G., Cox, E.S., Pakeman, R.J., Harris, M.P., LeDuc, M.G. & Marrs, R.H. (2013) Overcoming resistance and resilience of an invaded community is necessary for effective restoration: a multi-site bracken control study. *Journal of Applied Ecology*, **50**, 156–167.

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

Bestelmeyer, B.T., Brown, J.R., Havstad, K.M., Alexander, R., Chavez, G. & Herrick, J.E. (2003) Development and use of state-and-transition models for rangelands. *Journal of Range Management*, **56**, 114–126.

Bestelmeyer, B.T., Moseley, K., Shaver, P.L., Sanchez, H., Briske, D.D. & Fernandez-Gimenez, M.E. (2010) Practical guidance for developing state-and-transition models. *Rangelands*, **32**, 23–30.

Bestelmeyer, B.T., Duniway, M.C., James, D.K., Burkett, L.M. & Havstad, K.M. (2013) A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecology Letters*, **16**, 339–345.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2003) Vegetation dynamics on rangelands: a critique of the current paradigms. *Journal of Applied Ecology*, **40**, 601–614.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2005) State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management*, **58**, 1–10.

Coupland, R.T. (1992) Mixed prairie. *Ecosystems of the World 8A: Natural Grasslands, Introduction and Western Hemisphere*, pp. 151–182. Elsevier, New York.

Courtois, D.R., Perryman, B.L. & Hussein, H.S. (2004) Vegetation change after 65 years of grazing and grazing exclusion. *Journal of Range Management*, **57**, 574–582.

Currall, J.E.P. (1987) A transformation of the Domin scale. *Vegetatio*, **72**, 81–87.

Daubenmire, R.F. (1959) Canopy coverage method of vegetation analysis. *Northwest Science*, **33**, 43–64.

Derner, J.D. & Hart, R.H. (2007) Grazing-induced modifications to peak standing crop in northern mixed-grass prairie. *Rangeland Ecology and Management*, **60**, 270–276.

Derner, J.D., Hart, R.H., Smith, M.A. & Waggoner, J.W. Jr (2008) Long-term cattle gain responses to stocking rate and grazing systems in northern mixed-grass prairie. *Livestock Science*, **117**, 60–69.

Derner, J.D., Lauenroth, W.K., Stapp, P. & Augustine, D.J. (2009) Livestock as ecosystem engineers for grassland bird habitat in the Western Great Plains of North America. *Rangeland Ecology and Management*, **62**, 111–118.

Dunn, B.H., Smart, A.J., Gates, R.N., Johnson, P.S., Beutler, M.K., Diersen, M.A. & Janssen, L.L. (2010) Long-term production and profitability from grazing cattle in the northern mixed grass prairie. *Rangeland Ecology and Management*, **63**, 233–242.

Fang, Q.X., Andales, A.A., Derner, J.D., Ahuja, L.R., Ma, L., Bartling, P.N.S., Reeves, J.L. & Qi, Z. (2014) Modeling weather and stocking rate effects on forage and steer production in northern mixed-grass prairie. *Agricultural Systems*, **129**, 103–114.

Fuhlendorf, S.D., Briske, D.D. & Smeins, F.E. (2001) Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. *Applied Vegetation Science*, **4**, 177–188.

Harrison, S., Damschen, E.I. & Grace, J.B. (2010) Ecological contingency in the effects of climatic warming on forest herb communities. *Proceedings of the National Academy of Sciences*, **107**, 19362–19367.

Hart, R.H., Clapp, S. & Test, P.S. (1993) Grazing strategies, stocking rates, and frequency and intensity of grazing on western wheatgrass and blue grama. *Journal of Range Management*, **46**, 122–126.

Hart, R.H., Samuel, M.J., Test, P.S. & Smith, M.A. (1988) Cattle, vegetation, and economic responses to grazing systems and grazing pressure. *Journal of Range Management*, **41**, 282–286.

Hickman, K.R. & Derner, J.D. (2007) Blackland tallgrass prairie vegetation dynamics following cessation of herbicide application. *Rangeland Ecology and Management*, **60**, 186–190.

Kachergis, E., Rocca, M.E. & Fernández-Giménez, M.E. (2014) Long-term vegetation change provides evidence for alternate states in silver sagebrush. *Rangeland Ecology and Management*, **67**, 183–194.

Kachergis, E., Derner, J.D., Cutts, B.B., Roche, L.M., Eviner, V.T., Lubell, M.N. & Tate, K.W. (2014) Increasing flexibility in rangeland management during drought. *Ecosphere*, **5**, Article 77.

Knapp, C.N., Fernandez-Gimenez, M.E., Briske, D.D., Bestelmeyer, B.T. & Wu, X.B. (2011) An assessment of state-and-transition models: perceptions following two decades of development and implementation. *Rangeland Ecology and Management*, **64**, 598–606.

van de Koppel, J., Rietkerk, M. & Weissing, F.J. (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology & Evolution*, **12**, 352–356.

Laycock, W.A. (1991) Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management*, **44**, 427–433.

Lepš, J. & Šmilauer, P. (2003) Advanced use of ordination. *Multivariate Analysis of Ecological Data Using CANOCO*. pp. 60–75. Cambridge University Press, New York.

Manley, W.A., Hart, R.H., Samuel, M.J., Smith, M.A., Waggoner, J.W. Jr & Manley, J.T. (1997) Vegetation, cattle, and economic responses to grazing strategies and pressures. *Journal of Range Management*, **50**, 638–646.

Milchunas, D.G. (2011) Plant community dynamics in shortgrass steppe with grazing relaxation and imposition by large and small herbivores. *Israel Journal of Ecology and Evolution*, **57**, 23–41.

Milchunas, D.G., Forwood, J.R. & Lauenroth, W.K. (1994) Productivity of long-term grazing treatments in response to seasonal precipitation. *Journal of Range Management*, **47**, 133–139.

Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, **132**, 87–106.

Miller, M.E., Belote, R.T., Bowker, M.A. & Garman, S.L. (2011) Alternative states of a semiarid grassland ecosystem: implications for ecosystem services. *Ecosphere*, **2**, 1–18.

Monson, R.K., Littlejohn, R.O. Jr & Williams, G.J. III (1983) Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. *Oecologia*, **58**, 43–51.

Mullahey, J.J., Waller, S.S. & Moser, L.E. (1990) Defoliation effects on production and morphological development of little bluestem. *Journal of Range Management*, **43**, 497–500.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* (2013) vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package = vegan.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. & the R Development Core Team (2013) nlme: Linear and Nonlinear Mixed Effects Models. *R package version 3*.

Porensky, L.M., Mueller, K.E., Augustine, D.J. & Derner, J.D. (2016) Data from: Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.3m8p1.

Reeves, J.L., Derner, J.D., Sanderson, M.A., Petersen, M.K., Vermeire, L.T., Hendrickson, J.R. & Kronberg, S.L. (2013) Temperature and precipitation affect steer weight gains differentially by stocking rate in northern mixed-grass prairie. *Rangeland Ecology and Management*, **66**, 438–444.

Roche, L.M., Cutts, B.B., Derner, J.D., Lubell, M.N. & Tate, K.W. (2015) On-Ranch grazing strategies: context for the rotational grazing dilemma. *Rangeland Ecology and Management*, **68**, 248–256.

Singh, J.S., Lauenroth, W.K., Heitschmidt, R.K. & Dodd, J.L. (1983) Structural and functional attributes of the vegetation of northern mixed prairie of North America. *The Botanical Review*, **49**, 117–149.

Stevenson, A., Baumgartner, R.E. & Schuman, G.E. (1984) *High Plains Grasslands Research Station, Detailed Soil Survey*. USDA Publication 1–84/1C/3.62, Laramie, WY, USA.

Suding, K.N. & Hobbs, R.J. (2009) Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution*, **24**, 271–279.

Twidwell, D., Allred, B.W. & Fuhlendorf, S.D. (2013) National-scale assessment of ecological content in the world's largest land management framework. *Ecosphere*, doi: 10.1890/ES13-00124.1.

USDA NRCS (2008) Ecological Site Description R067AY122WY, Available Online: https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?approved = yes&repType = regular&id = R067AY122WY.

Valone, T.J., Meyer, M., Brown, J.H. & Chew, R.M. (2002) Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. *Conservation Biology*, **16**, 995–1002.

Van den Brink, P.J. & Ter Braak, C.J.F. (1998) Multivariate analysis of stress in experimental ecosystems by Principal Response Curves and similarity analysis. *Aquatic Ecology*, **32**, 163–178.

Westoby, M., Walker, B. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266–274.

Wong, N.K., Morgan, J.W. & Dorrough, J. (2010) A conceptual model of plant community changes following cessation of cultivation in semi-arid grassland. *Applied Vegetation Science*, **13**, 389–402.

Received 17 July 2015; accepted 15 February 2016
Handling Editor: Joslin Moore

Supporting Information

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

Fig. S1 Relative cover of dominant plant species in different heavily grazed treatments from 2003 to 2006.

Table S1 Percentage of variance in plant community composition explained by grazing treatments, time, and the first three RDA axes.

Appendix S1 Parameter estimates and ANOVA tables for all statistical models.

Appendix S2 Spatial and temporal variance details.