

## LETTER

# A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought

Brandon T. Bestelmeyer,<sup>1\*</sup> Michael C. Duniway,<sup>1,2</sup> Darren K. James,<sup>1</sup> Laura M. Burkett<sup>1</sup> and Kris M. Havstad<sup>1</sup>

<sup>1</sup>USDA-ARS Jornada Experimental Range and Jornada Basin LTER, Box 30003, MSC 3JER, New Mexico State University, Las Cruces, NM, 88003, USA

<sup>2</sup>U.S. Geological Survey, Southwest Biological Science Center, 2290 SW Resource Blvd, Moab, UT, 84532, USA

\*Correspondence: E-mail: bbestelm@nmsu.edu

### Abstract

Theoretical models predict that drylands can cross critical thresholds, but experimental manipulations to evaluate them are non-existent. We used a long-term (13-year) pulse-perturbation experiment featuring heavy grazing and shrub removal to determine if critical thresholds and their determinants can be demonstrated in Chihuahuan Desert grasslands. We asked if cover values or patch-size metrics could predict vegetation recovery, supporting their use as early-warning indicators. We found that season of grazing, but not the presence of competing shrubs, mediated the severity of grazing impacts on dominant grasses. Recovery occurred at the same rate irrespective of grazing history, suggesting that critical thresholds were not crossed, even at low cover levels. Grass cover, but not patch size metrics, predicted variation in recovery rates. Some transition-prone ecosystems are surprisingly resilient; management of grazing impacts and simple cover measurements can be used to avert undesired transitions and initiate restoration.

### Keywords

Desertification, early warning, grazing, long-term experiment, patch size, regime shift, resilience, state-transition model.

*Ecology Letters* (2013) 16: 339–345

## INTRODUCTION

State transitions, also known as regime shifts or critical transitions, refer to the rapid and unexpected formation of alternative states that can only be reversed slowly, if at all (Scheffer & Carpenter 2003; Scheffer 2009). In semi-arid drylands, transitions from more to less productive states often involve the loss of herbaceous vegetation and its replacement by woody plant or bare ground cover that is reinforced by a series of feedback mechanisms (Bestelmeyer *et al.* 2011; reviewed in D'Odorico *et al.* 2012). There is great interest in developing tools and policies to prevent state transitions in drylands due to their profound societal costs (Reynolds *et al.* 2007; Stafford-Smith *et al.* 2007).

Two ideas dominate proposed management approaches for state transitions. The first is to develop a mechanistic understanding of threshold dynamics so that the environmental conditions resulting in state change can be avoided via resilience-based management (Suding & Hobbs 2009; Chapin *et al.* 2010). In drylands, livestock grazing recommendations (Briske *et al.* 2008) and the application of fire or periodic shrub removal (Ansley & Castellano 2006) are common strategies to avoid vulnerable conditions. The second idea is to develop early-warning indicators of imminent state transitions, serving as a backstop for when resilience-based approaches fail (Carpenter & Brock 2006; Scheffer 2009). Monitoring of plant cover has long served this role in drylands (Herrick *et al.* 2005). On theoretical grounds, it has been proposed that a suite of vegetation spatial patterns might provide superior early-warning indicators (Rietkerk *et al.* 2004; Dakos *et al.* 2011). A subgroup of indicators based on facilitation and vegetation–environment feedback mechanisms suggests that the frequency of large vegetated patches declines and the connectedness of open ground increases preceding state transitions

(Kéfi *et al.* 2007, 2011; see also Ludwig *et al.* 2007). It is unclear whether such indicators provide information that is not already captured in simple metrics such as vegetation cover (Maestre & Escudero 2009, 2010).

Direct observational or experimental evidence of threshold dynamics is rare (e.g. Petraitis *et al.* 2009; Carpenter *et al.* 2011; Dai *et al.* 2012). A recent review did not point to any empirical data on state transitions over time in terrestrial vegetation (Scheffer 2009). Such limitations have been used to call into question the applicability of threshold models (Schröder *et al.* 2005; Groffman *et al.* 2006; Petraitis *et al.* 2009).

We conducted a long-term pulse-perturbation experiment to test threshold dynamics in a Chihuahuan Desert grassland (Bender *et al.* 1984). This grassland type is known to have undergone transitions to shrubland under control of heavy grazing pressure coupled to native shrub invasion (Fig. S1; Schlesinger *et al.* 1990; Bestelmeyer *et al.* 2011). Two types of models are proposed to explain threshold dynamics in the Chihuahuan Desert: the driver and feedback control models. The driver control model hypothesises that dominant grasses are driven to low levels or to extinction under direct control of an external driver (grazing), mediated by other environmental conditions (season of impact, shrub density). Following this model, grasses would decline with a heavy grazing perturbation, but once the driver was reduced (no grazing), grasses would eventually recover from seeds or remnant plants, unless a severe magnitude of the driver directly causes widespread extinction. Without extinction, this model is similar to the driver threshold, linear tracking or non-catastrophic threshold models (Scheffer & Carpenter 2003; Andersen *et al.* 2009; Bestelmeyer *et al.* 2011). In the feedback control model, grass cover would be driven below a critical threshold, prior to extinction, and altered vegetation–environment feedbacks would

continue to reduce cover even after the driver magnitude is reduced. As the threshold is approached and crossed, the loss of large vegetated patches and increasing size of open-ground patches lead to increasingly harsh environmental conditions that accelerate the demise of remaining grasses while favouring shrub dominance, even without additional grazing pressure (D'Odorico *et al.* 2012). Because the size of vegetated and non-vegetated patches is related to facilitation and soil erosion feedbacks (Kéfi *et al.* 2007, 2011; Ludwig *et al.* 2007), patch size-based indicators should be related to grass recovery rates (Dakos *et al.* 2011). The feedback control model is similar to hysteresis (Scheffer & Carpenter 2003) and bistability models, especially those described by Rietkerk *et al.* (2004).

We evaluated evidence for the driver and feedback control models using acute defoliation of perennial grasses by cattle grazing within a shrub-invaded grassland that represents a precarious condition between grassland and eroding shrubland states (Bestelmeyer *et al.* 2004). We expected that grazing effects would be most severe in paddocks grazed in the summer growing season (by interfering with grass reproduction) and where competing shrubs were left intact. The driver control model would be indicated if recovery from remnant plants in grazing treatments was similar to that observed in the no-grazing treatment, suggesting a lack of strong hysteresis (Suding & Hobbs 2009).

Alternatively, the grazing perturbation could cause grass cover to cross a critical threshold after which it would remain low or continue to decline following the feedback control model (e.g. Dai *et al.* 2012; Veraart *et al.* 2012). A relationship between grass recovery following the perturbation and patch size would provide evidence for the spatial control of feedbacks and the potential use of patch size as an early-warning indicator. While our experiment precludes us from observing generic early-warning signals (*sensu* Dakos *et al.* 2012) during a gradual approach to a critical threshold, we evaluated the ability of two readily assessed patch-size metrics (the occurrence of vegetation in large patches and the cover of large non-vegetated patches) to predict variation in recovery rates, potentially spanning samples in pre- and post-threshold conditions. Following from the observation of Kéfi *et al.* (2011) that the loss of large plant patches signals increased stress and proximity to transition, we expected that paddocks with a sufficiently low dominance of large grass patches after the perturbation would not recover or recover more slowly (cf. critical slowing down, Dakos *et al.* 2011) than those with a greater dominance of large patches. We also expected that a comparatively high cover of non-vegetated patches would have similar effects due to increased resource loss and limitations to grass growth and reproduction (Bautista *et al.* 2007; Ludwig *et al.* 2007). We posit that if these measurements can be used to predict recovery rates, they might serve as useful early-warning indicators of the relative risk of transition in management settings.

Because changes in cover lead to changes in the frequency of patch sizes in randomly structured landscapes (Gardner *et al.* 1987), we used simulations to remove patchiness that would be expected based on cover alone. This approach allowed us to test if the non-random component of patch size made a significant contribution to explaining grass recovery rates compared to cover alone. Collectively, these results allow us to evaluate 1) evidence for threshold models in Chihuahuan Desert grasslands, 2) the effects of environment and management conditions on those thresholds and 3) the potential utility of cover values or patch-size metrics as early-warning indicators.

## METHODS

### Study site

The experiment was conducted on the USDA Agricultural Research Service Jornada Experimental Range near Las Cruces, New Mexico, USA (<http://jornada.nmsu.edu/>). Climate is arid to semi-arid, with long-term (90-year) mean annual temperature of 15 °C and mean annual precipitation of 250 mm, over half of which occurs in summer (July–September). This study spanned a period of unusually variable precipitation (Fig. S2). Annual rainfall in 2003 was about half of the long-term average, while that in 2006 was near record highs.

The study was conducted in an upland grassland type dominated by the perennial C4 grass black grama (*Bouteloua eriopoda* Torr.). This grassland type has undergone transitions to C3 shrublands dominated by honey mesquite shrubs (*Prosopis glandulosa* Torr.) and eroding bare ground (Gibbens *et al.* 2005; Bestelmeyer *et al.* 2011) and is the classic case of feedback-driven desertification presented in Schlesinger *et al.* (1990). See Appendix S1 for a detailed description of the study area and transition mechanisms.

### Experimental design

In 1995, eighteen 0.5-ha (70 × 70-m) grazing paddocks were established following the design in Fig. S3 including three blocks and six paddocks per block. The centre of this area is at 32°35'21.20" N, 106°51'03.00" W at an elevation of 1332 m, and aerial or satellite images of the experiment can be seen in Google Earth (inserting those coordinates) to as early as October 1996. Each paddock in each block was assigned one of three grazing treatments (summer grazed, winter grazed and non-grazed) and a shrub-removal treatment (intact or removed), resulting in six treatment combinations per block. Beginning in late spring 1996, all *P. glandulosa* shrubs in 'removed' treatments were clipped at the ground level, the vegetation removed and the stumps painted with glyphosate (360 g/L) to prevent resprouting. Removal of new plants or resprouts from underground was maintained each year until 2000. Beginning in August 1996, grazing was conducted in either August (summer) or February (winter) such that 65–80% removal of aboveground perennial grass biomass was achieved in all parts of the paddock over a 24- to 36-h period, resulting in a stubble height of < 5 cm. This level of biomass removal is over twice that typically recommended, and is known to harm *B. eriopoda* plants (Canfield 1939). Furthermore, this treatment was applied yearly from 1996 to 2000 such that each grazed paddock was defoliated four times in either summer or winter, effectively compounding the damage. No grazing had occurred in the paddocks since spring 2000.

Pre-manipulation measurements of vegetation were gathered in spring 1996. Post-manipulation measurements were gathered in fall 2002 (measuring the effects of the grazing perturbation) and again in fall 2009 (measuring the effects of the response). Line-point intercept (following Herrick *et al.* 2005) was used to estimate basal and foliar cover for each plant species in each paddock. Measurements were gathered on seven, 70-m transects spaced 10 m apart with 10-cm spacing between intercept points (4900 points per paddock).

### Data analysis

We used repeated-measures linear-mixed effects models (PROC MIXED; SAS V9.2; SAS Institute, Cary, NC, USA) to model the

effects of treatments and their interactions on the foliar cover of dominant perennial plant species (*B. eriopoda* and *Sporobolus* spp.). Grazing and shrub-removal treatments were fixed effects, block was a random effect and year (2002 and 2009) was a repeated effect with paddock as the subject. We used the cover of the grasses in 1996 as a covariate to adjust for pre-manipulation differences among paddocks. We used an unstructured temporal covariance for both models determined via the minimum small-sample Akaike's Information Criterion ( $AIC_c$ ). The Kenward–Roger method was used for computing denominator degrees of freedom for fixed effects. We tested for several specific effects of the perturbation (2002) and response (2009) using pre-planned contrasts.

We then asked how well *B. eriopoda* foliar cover and/or patch-size metrics observed in 2002 predicted change in *B. eriopoda* cover from 2002 to 2009. We examined only the grazed treatments in this analysis to focus on potential threshold dynamics due to our manipulations. We used model selection approaches of Burnham & Anderson (2002) to compare a series of linear models that included percentage cover and patch-size metrics obtained from the sequences of foliar and ground cover hits in line-point intercept data. We considered six potential patch-size metrics, including the percentage of *B. eriopoda* hits occurring in patches  $\geq 50$  cm and  $\geq 100$  cm that would not be expected by chance (dominance of large *B. eriopoda* patches; the degree to which *B. eriopoda* occurred in large patches), the percentage cover of patches  $\geq 50$  cm and  $\geq 100$  cm not containing *B. eriopoda* that would not be expected by chance (dominance of large non-*B. eriopoda* patches; the dominance of large patches not occupied by *B. eriopoda*) and the percentage cover of open patches  $\geq 50$  cm and  $\geq 100$  cm not containing any perennial plants that would not be expected by chance (dominance of large open patches; the dominance of large patches not occupied by perennial plants). See Appendix S2 for the calculation of patch-size metrics including adjustments based on randomised sequences of foliar and ground cover hits. Most metrics emphasise the dominant grass species because state transitions in Chihuahuan Desert ecosystems result in the eventual replacement of the dominant grass with shrubs (Peters *et al.* 2012).

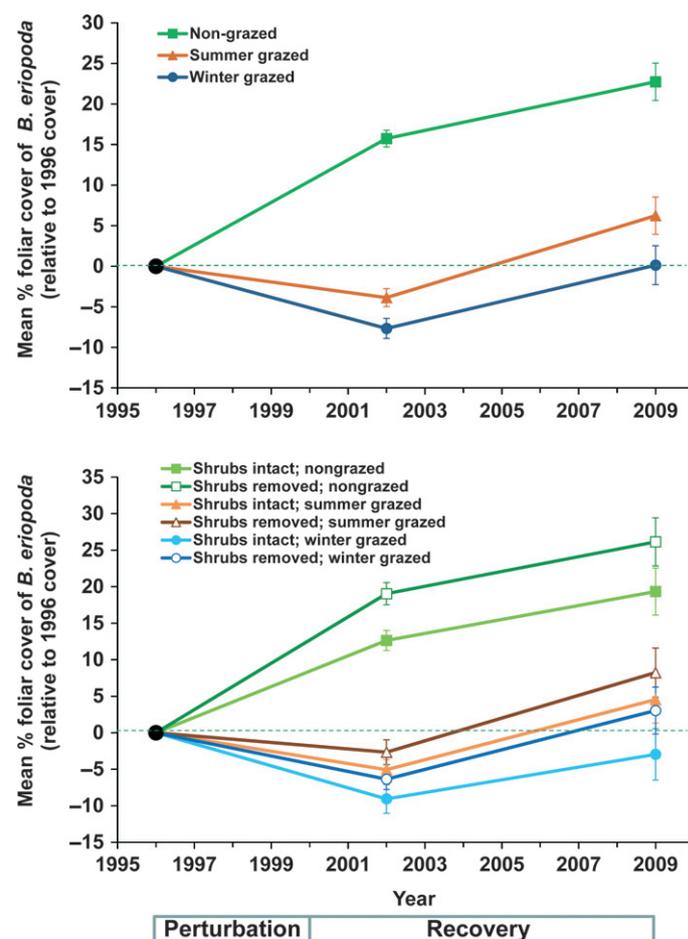
In selecting candidate models, we excluded patch-size metrics that were highly correlated ( $> 0.80$ ) with foliar cover and with one another, or that were in calculable in some paddocks. Of the six patch-size metrics considered, some paddocks did not exhibit *B. eriopoda* patches  $\geq 100$  cm and non-*B. eriopoda* and open patches  $\geq 50$  cm exhibited little variation among paddocks, so we excluded these variables. Of the remaining three variables, dominance of non-*B. eriopoda* patches  $\geq 100$  cm was highly correlated with foliar cover ( $r = 0.96$ ) and was excluded (Table S1). Dominance of *B. eriopoda* patches  $\geq 50$  cm and open patches  $\geq 100$  cm had low correlations with foliar cover ( $r = 0.43$  and  $0.13$  respectively) and with one another ( $r = 0.35$ ) and so were included in models. Unadjusted (observed) metrics all exhibited higher correlations with foliar cover than adjusted metrics. We used the  $AIC_c$  to rank models containing all combinations of foliar cover and the selected patch-size metrics, where the best models have the smallest  $AIC_c$  values and superior individual models have relatively large model probabilities (Akaike weight;  $W_i$ ).

## RESULTS

*B. eriopoda* was dominant in the experimental plots prior to the manipulations (1996) – at 10–12% foliar cover it accounted for 72–

79% of the total vegetation cover across the grazing treatments. By 2002, *B. eriopoda* cover increased dramatically in the non-grazed treatment (Fig. 1a) as a consequence of grazing rest and several good rainfall years (Fig. S2). This increase was constrained in the shrubs-intact vs. shrubs-removed treatments ( $-6.38 \pm 2.03$ ; d.f. = 8.7;  $t = -3.14$ ;  $P = 0.01$ ; Fig. 1b). Contrary to our expectations, *B. eriopoda* decreased less in the summer than in the winter-grazed treatments ( $3.83 \pm 1.77$ ; d.f. = 10.7;  $t = 2.16$ ;  $P = 0.054$ ). Decreases in *B. eriopoda* in the grazed plots were not different between shrubs-intact and shrubs-removed treatments ( $-5.09 \pm 3.57$ ; d.f. = 10.8;  $t = -1.43$ ;  $P = 0.18$ ; Fig. 1b).

Between 2002 and 2009, with no further grazing, *B. eriopoda* increased across all three grazing treatments (Fig. 1a). The amount of cover increase did not differ significantly among grazing treatments (summer vs. winter:  $2.47 \pm 2.29$ ; d.f. = 12;  $t = 1.08$ ;  $P = 0.30$ ; summer vs. non-grazed:  $3.34 \pm 2.29$ ; d.f. = 12;  $t = 1.46$ ;  $P = 0.16$ ; winter vs. non-grazed:  $0.87 \pm 2.29$ ; d.f. = 12;  $t = 0.38$ ;  $P = 0.70$ ) or between the shrub treatments ( $1.65 \pm 1.87$ ; d.f. = 12;  $t = 0.89$ ;  $P = 0.39$ ; Fig. 1b). Shrub recolonisation of the shrub-control plots was minimal ( $> 1\%$  cover). *Sporobolus* spp. grasses, a



**Figure 1** Least-squares mean estimates ( $\pm 1$  SE,  $n = 3$ ) of *B. eriopoda* foliar cover from the mixed-model analyses for (top) grazing treatments and (bottom) grazing treatment\*shrub treatment interactions. Values are relativised to the overall mean *B. eriopoda* cover in 1996 (black dot = 11.56%). The time periods of perturbation and recovery are noted at the bottom.

subdominant perennial group that tends to establish during high rainfall years and is rare in drought, established at slightly higher rate in shrub-intact treatments than in the shrub-removed treatments ( $1.33 \pm 0.45$ ; d.f. = 12;  $t = 2.95$ ;  $P = 0.01$ ). *Sporobolus* establishment did not differ across grazing treatments ( $F = 1.03$ ; d.f. = 2,11.3;  $P = 0.38$ ).

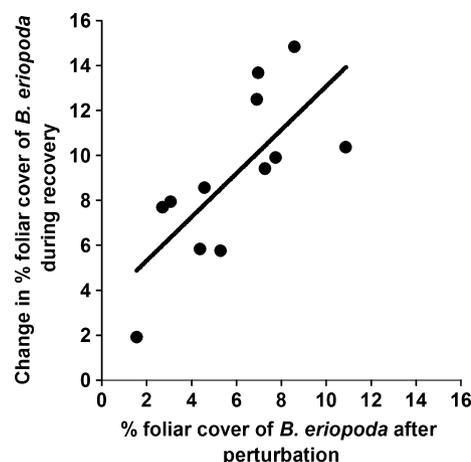
In spite of minor differences among treatments, we observed considerable variation in the response of *B. eriopoda* (2002–2009) among paddocks; some low-cover grazed paddocks exhibited little recovery, suggesting a weakening of feedbacks promoting *B. eriopoda* growth and an imminent threshold (Fig. S4). This variation served as a basis for evaluating the ability of cover and patch-size metrics in 2002 to predict future changes in cover. Model comparisons indicated that the best model included cover alone (Table 1; Fig. 2; parameter estimate [mean  $\pm$  1 SE] =  $0.97 \pm 0.27$ ). Other models had little to no support. We also examined models including patch-size metrics highly correlated with cover (including unadjusted values) and none were better than cover alone.

## DISCUSSION

### Perturbation effects and resilience-based management

*B. eriopoda* cover was reduced for several years due to intense grazing, in some paddocks to very low levels (Figs 2 and S4) that rivaled the conditions observed historically (Fig. S1) and that were similar to the worst conditions recently observed in landscapes outside of the study site (Fig. S5). Contrary to expectations, winter grazing had a slightly greater impact on *B. eriopoda* compared with summer grazing. High levels of defoliation in winter can expose soil and plant parts to dry spring winds that create a harsh environment for subsequent growth (Okin et al. 2009). While winter grazing is a common recommendation for *B. eriopoda* grasslands (Holechek & Herbel 1982), our data suggest that intense winter grazing may decrease grassland resilience.

*P. glandulosa* presence slowed recovery in the non-grazed treatment, but did not exacerbate grass-cover reductions in the grazed treatments. While efforts to control *P. glandulosa* populations may be warranted to prevent encroachment and competition with grasses (Ansley & Castellano 2006), our data suggest such efforts may be less important than grazing management. Shrub control is not likely to mitigate the effects of inappropriate grazing management as a long-term resilience-based strategy.



**Figure 2** The change in *B. eriopoda* foliar cover (2002–2009) as a linear function of *B. eriopoda* foliar cover recorded after the pulse perturbation (2002).

### Threshold models and indicators

The lack of differences among grazing or shrub-removal treatments in the recovery of *B. eriopoda* cover after the perturbation indicates that *B. eriopoda* recovery mechanisms were, on average, not demonstrably impaired by the grazing treatments nor limited by the presence of *P. glandulosa*. Furthermore, the amount of *B. eriopoda* cover gained during the recovery period tended to exceed the post-perturbation (2002) cover (Fig. 2). These patterns support the general applicability of the driver control model in our study; *B. eriopoda* was not driven below a critical threshold such that continued declines in cover were evident.

At the level of individual grazed paddocks, however, we found considerable variation in recovery rates (Figs 2 and S4). While many plots had cover values exceeding their pre-manipulation values, the lowest cover paddock in 2002 had not yet recovered to its pre-manipulation value. This observation is consistent with critical slowing down (Dakos et al. 2011), suggesting that feedback processes promoting *B. eriopoda* growth might be weakened by grazing in some instances and that a critical threshold may have been approached, even if not crossed.

We found that initial cover best predicted variation in recovery and that our patch-size metrics did not improve predictability. This result supports the contention of Maestre & Escudero (2009) that cover values might serve as early-warning indicators in some

**Table 1** Model selection results for predicting change in *B. eriopoda* cover (2002–2009) using cover and selected patch-size metrics in 2002 (see text), for paddocks in which grazing treatments occurred ( $n = 12$ ), ordered according to model probabilities ( $W_i$ ). Each column represents a different predictor variable (black, cover; dark grey, dominance of *B. eriopoda* patches  $\geq 50$  cm; and light grey, dominance of open patches  $\geq 100$  cm). AICc measures the relative goodness of fit of a given model;  $\Delta$ AICc is the difference in AICc of each model and that of the best model; and  $W_i$  is a measure of the strength of evidence of a model relative to the other models.

Cover	Dominance of <i>B. eriopoda</i> patches $\geq 50$ cm	Dominance of open patches $\geq 100$ cm	Adjusted $R^2$	AICc	$\Delta$ AICc	$W_i$
			0.47	63.95	0	0.804
			0.43	68.51	4.56	0.082
			0.42	68.55	4.6	0.080
			0.05	71.12	7.17	0.022
			-0.07	72.57	8.62	0.011
			0.38	74.43	10.48	0.004

threshold-prone drylands by providing easily measured benchmark values for evaluating the risk of state transitions (e.g. Samhouri *et al.* 2010).

### Why were threshold dynamics not observed?

The fact that we did not induce a state transition should not be viewed as evidence that state transitions do not occur in our study system. We have clear evidence from nearby historical observations that they can occur (Fig. S1). Historical transitions are likely to have been partly a consequence of weather patterns coinciding with heavy grazing (i.e. multiple causality; Scheffer & Carpenter 2003; Allen 2007). The weather patterns during our study, while including a severe drought year following the perturbation (Fig. S2), were not as severe as the sequences of drought years observed during periods when state transitions were noted at our study site (Yao *et al.* 2006). Furthermore, historical documents point to unique conditions of prolonged drought and high wind in particular time periods as triggers of state transitions (Appendix S3).

Had our experiment been conducted during a multiyear drought, and perhaps with experimental units of broader spatial extent and additional years of defoliation, we might have caused the transitions described in historical documents. The circumstances described suggest a third threshold model that we were not able to test: a *feedback-trigger control* model. In this model, the coincidence of low grass cover with a multiyear drought and high wind 'triggers' (*sensu* Suding & Hobbs 2009) could exacerbate the effects of changing feedbacks to drive grass extinct very rapidly. Such sequences of triggers and feedbacks are typically surprising, as expressed in the historical record (Appendix S3) and other cases (Stafford Smith *et al.* 2007). The long-term management that constituted 'protective effort' in the early 20<sup>th</sup> century had not been evaluated in the context of a trigger such as the 1950s' drought. Stocking rate recommendations are now even more conservative as a consequence (Holechek *et al.* 1999).

### Managing thresholds and using early-warning indicators

Dryland ecosystems may behave according to both the driver and feedback control models depending on the magnitude of management drivers and coincident environmental conditions. That our manipulations reduced grass cover to extremely low levels yet did not elicit a threshold response challenges the idea that our study system (Schlesinger *et al.* 1990; Bestelmeyer *et al.* 2004; Peters *et al.* 2006) and potentially other threshold-prone aridlands (Scheffer & Carpenter 2003; Bailey 2011) deterministically undergo transitions below a critical, but moderate, level of cover or patch fragmentation. The management implication is that transition-prone grasslands with even very low levels of remaining cover are potentially restorable with grazing rest (see also Valone *et al.* 2002). Strict belief in the feedback control threshold model might induce managers to abandon controversial management efforts in areas believed to be below a critical threshold, whereas the driver control model places increased value on ecosystems where even small populations of target species persist (Bestelmeyer 2006).

Nevertheless, the fact that surprising transitions have occurred within our study system suggests that the feedback control model may operate under certain circumstances, for example during peri-

ods when water resources are highly limited and when lateral resource and sediment transport processes are strong (Okin *et al.* 2009). Thus, even though low-cover grasslands can be restored, they represent an increased risk of catastrophic transition depending on the magnitude of other drivers that can be difficult to predict and impossible to control. Under such circumstances, specifying proximity to a threshold using snapshot measurements may not be possible.

Our results suggest that in certain dryland ecosystems, pattern-based early-warning indicators may provide little additional information relative to simple cover measurements as a means to anticipate transitions and potential for recovery. The utility of information about spatial pattern might be limited in comparatively resilient drylands or those in which transitions are caused by the sudden confluence of multiple drivers. Furthermore, spatial indicators might be highly correlated with cover in dryland ecosystems. In future studies, it would be worthwhile to separate the effects of cover from spatial pattern in evaluating indicators, thereby identifying the circumstances in which particular indicators are valuable (Dakos *et al.* 2011; Kéfi *et al.* 2011).

Given that low-cover conditions are associated with transitions in the historical record, we propose an early-warning rule of thumb that foliar cover of *B. eriopoda* should not be driven below *c.* 3%. Paddocks with greater values experienced significant recovery, and the paddock below this value had limited recovery. As noted above, however, ecosystems subject to exogenous processes that rapidly alter state variables or the strength of feedbacks may limit the utility of indicators aimed at maximising resource extraction without crossing thresholds (see also Scheffer *et al.* 2012). In spite of this limitation, development of simple, conservative and empirically justified rules of thumb may provide for rapidly implemented early-warning systems that are acceptable to managers.

### CONCLUSIONS

Experimental evaluations of critical thresholds in drylands are sorely needed to clarify the application of threshold concepts and indicators. Drylands may be more resilient than is implied by critical threshold models and historical observations. Thus, it may also be less technically demanding to avoid thresholds than some models and theoretical studies suggest. Minimum safe cover values can serve as early-warning indicators that are easily measured and understood; therefore, we suggest that the inadequacy of cover indicators should be demonstrated before seeking more demanding approaches. Furthermore, given the wide variation in grassland recovery rates that we observed given the same grazing pressure, in addition to the unpredictability of interacting climatic drivers, it may be foolish to use indicators to seek to approach thresholds without crossing them (c.f. steady-state resource management; Chapin *et al.* 2010) or to condemn systems as unrecoverable. Avoidance of potentially precarious cover values can be achieved by focusing resilience management on the principal drivers (e.g. avoidance of heavy defoliation during sensitive time periods rather than shrub control) and monitoring. Given the expanse and spatial heterogeneity of dryland rangelands, the greatest challenge for monitoring is to achieve sufficient spatial coverage and interpret the effects of background heterogeneity (e.g. via state-and-transition models for particular soil types). Empirical studies guided by theory, training in resilience-based management and financial investments in

ground-based and remotely sensed monitoring strategies based on simple indicators and rule sets may be effective for preventing dryland degradation.

## ACKNOWLEDGEMENTS

Thanks to those who helped establish and collected data on this experiment over the years, including Dawn Browning, Erica Courtwright, Amrita de Soyza, Don Devine, Rob Dunlap, Eddie Garcia, Bob Gibbens, Jim Lenz, Connie Maxwell, Kirsten Romig, Scott Shrader, Amy Slaughter, David Thatcher, Justin Van Zee, Walt Whitford, Jeb Williamson and Craig Winters. Reviews by Fernando Maestre, two other referees and Katie Suding improved the presentation. This research was supported by appropriated funds to the USDA-ARS Jornada Experimental Range, NSF Long-Term Ecological Research program (DEB0080412) and by the USDA NRCS Conservation Effects Assessment Program. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government. This work is dedicated to the memory of Eddie Garcia.

## STATEMENT OF AUTHORSHIP

BTB, KMH and MCD wrote the manuscript; MCD performed simulations with input from BTB; DKJ and LMB managed the data; LMB led data collection; BTB and DKJ performed data analysis; KMH conceived and initiated the study.

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Editor, Katharine Suding

Manuscript received 7 June 2012

First decision made 13 July 2012

Second decision made 18 September 2012

Manuscript accepted 4 November 2012