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Vegetation in a Post-Ecological Threshold State May Not Recover after Short-Term Livestock Exclusion in Mongolian Rangelands

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In the present study, we tested the potential irreversibility of vegetation dynamics in Mongolian rangelands using well-studied plant communities that exist along grazing gradients, in which ecological thresholds (defined as the points or zones at which disturbance should be limited to prevent drastic changes in ecological conditions) exist in terms of the compositional changes along these gradients. To accomplish this, we removed livestock grazing impacts by establishing exclosures along a grazing gradient at two study sites located in Mandalgobi and Bulgan, Mongolia. Each exclosure was established in the summer of 2004 at a location with either a post-ecological threshold state or a pre-ecological threshold state. We examined general patterns of temporal change in vegetation for the permanent plots inside and outside each exclosure at each site between 2005 and 2010. The trajectories of floristic composition in the permanent plots outside and inside each exclosure were similar from 2005 to 2010, indicating that the trajectories were mainly associated with annual rainfall and annual phenological changes in the plant communities. Post-threshold states at both sites did not reach their respective target community for restoration, indicating the lack of restorability despite livestock exclusion. Moreover, ordination separated the trajectories of floristic composition for the permanent plots inside exclosure in the post-threshold state from those in the pre-threshold state. Thus, our results suggest that vegetation in a post-threshold state may not recover after short-term livestock exclusion in Mongolian rangelands.

Keywords alternative stable states, arid and semi-arid rangelands, ecological threshold, rangeland management, resilience

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Arid and semi-arid rangelands are particularly vulnerable ecosystems (Rietkerk & van de Koppel, 1997; van de Koppel et al., 1997; Scheffer et al., 2001). Loss of ecological resilience makes these systems even more fragile, and their original ecological state can shift rapidly into alternative stable states (Rietkerk & van de Koppel, 1997; van de Koppel et al., 1997; Scheffer et al., 2001; Folke et al., 2004; Gao et al., 2011). Land areas that are forced into an alternative stable state by human impacts cannot easily be restored, even when adequate restoration efforts are provided (Cao et al., 2010; Gao et al., 2011). Therefore, the existence of potentially irreversible shifts in real ecosystems must be recognized because it has important implications for providing management guidelines (Suding & Hobbs, 2009).

In our previous work (Sasaki, Okayasu, Jamsran, et al., 2008), we defined an ecological threshold as the points or zones at which disturbance should be limited to prevent drastic changes in ecological conditions. Such an ecological threshold can be readily translated into practical management guidelines (Radford et al., 2005; Bestelmeyer, 2006). Sasaki, Okayasu, Jamsran, et al. (2008) provided strong evidence for the existence of ecological thresholds based on the vegetation changes along a grazing gradient in Mongolian rangelands. This evidence can imply the existence of alternative stable states (Scheffer & Carpenter, 2003).

Yet, we know little about the irreversibility of change of vegetation state across an ecological threshold. In principle, a full demonstration of the existence of alternative stable states would require two testing processes: the first would be an empirical demonstration of the existence of nonlinearities of ecological responses to a prevailing disturbance, and the second would be a test of whether these nonlinear responses can be reversed after cessation of the disturbance (Scheffer & Carpenter, 2003).

In the present study, we tested the potential irreversibility of vegetation dynamics in Mongolian rangelands using well-studied plant communities that exist along grazing gradients (Sasaki, Okayasu, Jamsran, et al., 2008; Sasaki, Okubo, et al., 2009). Based on our previous knowledge (Sasaki, Okayasu, Jamsran, et al., 2008; Sasaki et al., 2011), we defined vegetation state after an ecological threshold has been crossed as a post-ecological threshold state, and the opposite as a pre-ecological threshold state. We removed the impact of livestock grazing by establishing several exclosures along each grazing gradient, with each exclosure therefore situated in either a post-ecological threshold state or a pre-ecological threshold state. We predicted that vegetation in a post-threshold state would be unable to recover after short-term livestock exclusion. This study will aid local management practice by providing the knowledge as to whether grazing exclusion is valuable option for restoring severely degraded areas.

Methods

Study Sites

The study was conducted from 2005 to 2010 at two study sites in the Mandalgobi (45°46′N, 106°16′E; 1510–1530 m a.s.l) and Bulgan (44°05′N, 103°32′E; 1660–1690 m a.s.l) areas of Mongolia's Dundgobi and South Gobi provinces, respectively. Hereafter, we refer to these as the Mandalgobi and Bulgan study sites (Sasaki, Okayasu, Jamsran, et al., 2008; Sasaki, Okubo, et al., 2009; Sasaki et al., 2011). The region's climate is arid and cold, with a short summer. Both sites have a long evolutionary history of grazing by domestic livestock under nomadic or semi-nomadic patterns of land use, and their landscape positions are hill and upper-pediment, respectively. The slope is generally less than 1.5° at both sites. The soil textures (0.0–5.0 cm) are sand and sandy clay loam, respectively (Sasaki, Okayasu, Jamsran, et al., 2008; Sasaki, Okayasu, Shirato, et al., 2008). The vegetation types are shrubland and grassland, and total vegetation cover at the plot where grazing impacts are considered minimal is approximately 15 and 10%, respectively. The main types of livestock are sheep, goats, and cattle (approximately 500 head in total) at Mandalgobi and sheep, goats, and camels (approximately 1000 head in total) at Bulgan. Based on meteorological data provided by the National Climatic Data Center, annual rainfall between 2000 and 2010 averaged around 120 mm (coefficient of variation = 47%) at Mandalgobi and 115 mm (40%) at Bulgan. In both areas, peak rainfall occurred in July. Summer and winter temperatures averaged around 19 and −14°C, respectively, at Mandalgobi and 21 and −11°C at Bulgan. Both areas sustained strong fluctuations in annual rainfall between 2005 and 2010 (Table 1).

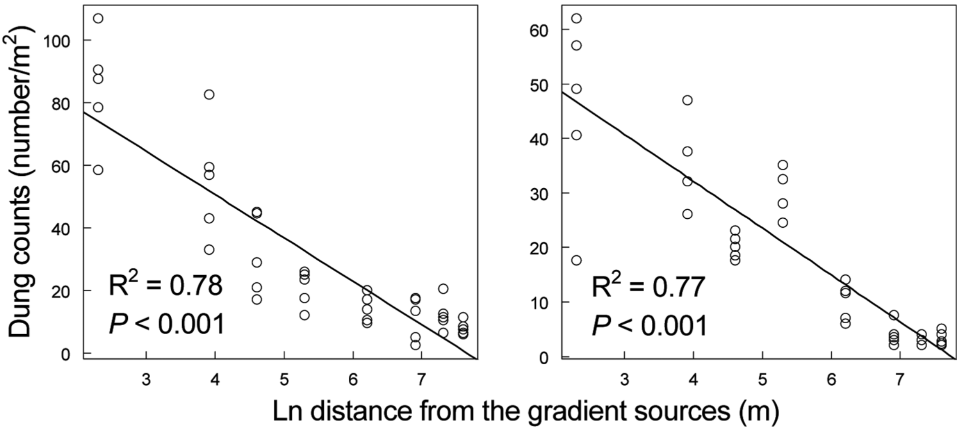
Ecological Thresholds along the Grazing Gradients

At each site, a grazing gradient had been established by years of grazing. At Mandalgobi, the gradient began at a livestock camp; at Bulgan, it began at a source of water. The two gradients represent a spatial gradient in the accumulated impact of long-term exposure to livestock (Sasaki, Okayasu, Jamsran, et al., 2008; Sasaki, Okubo, et al., 2009; Sasaki et al., 2011). Dung counts (number/m^2) decreased exponentially over 2000 m from the source of grazing gradient at each site (Figure 1). Sasaki and colleagues (Sasaki, Okayasu, Jamsran, et al., 2008; Sasaki et al., 2011) used piecewise regression models (Toms & Lesperance, 2003) fitted to relationships between the floristic composition data (the scores on the first axis of detrended correspondence analysis, DCA; Legendre & Legendre, 1998) and the distance from the gradient. The form of model is [Score of DCA axis $1 = a + b \times$ Distance, if Distance $\leq D$; Score of DCA axis $1 = a + b \times$ Distance $+ c \times$ (Distance − D), if Distance$>D$], where D is the breakpoint representing ecological threshold distance (Table 2). Since dung counts decreased exponentially as a function of distance from the gradient source (Figure 1), we also fitted a piecewise regression model to the relationship between floristic composition data and ln-transformed distance at each site. Another transformation of distance from the gradient source has been proposed in the literature (reciprocal transformation; Manthey & Peper, 2010), ln-transformed distance explained more of the variation in dung counts than reciprocal distance at both sites ($R^2 = 0.78$ and 0.77 for ln-transformed distance at the Mandalgobi and Bulgan sites, respectively; $R^2 = 0.72$ and 0.48 for reciprocal distance) and was therefore used. This analysis yielded a similar result for ecological threshold distance at each site

Table 1. Annual rainfall between 2005 and 2010

	2005	2006	2007	2008	2009	2010	2000–2010 mean
Mandalgobi	70.9	93.5	64.3	106.4	81.0	101.9	121.0
Bulgan	42.9	83.8	171.2	132.3	45.7	182.6	115.6

Note: Means are based on the data from 2000 to 2010. The data were provided by the National Climatic Data Center.



(a) (b)

Figure 1. Changes in dung counts along the grazing gradient at the (a) Mandalgobi and (b) Bulgan sites. The distance from the source of grazing gradient was ln-transformed. Dung counts decreased exponentially as a function of distance from the gradient source.

(Table 2). There was an ecological threshold with a single breakpoint for changes in floristic composition at Mandalgobi, whereas the response pattern indicated threshold changes with two breakpoints at Bulgan. At Bulgan, abrupt changes in floristic composition occurred relatively far from the gradient sources (i.e., the first breakpoint), possibly because of the large number of livestock at this site, and if the concentrated grazing impacts exceeded the threshold level (i.e., the second breakpoint), the vegetation could change into a contrasting state (Sasaki, Okayasu, Jamsran, et al., 2008). The threshold responses of vegetation to grazing reflect rapid

Table 2. Distances at which the exclosures were located from a livestock camp (Mandalgobi) or source of water (Bulgan), and the ecological threshold distance at each site

	Exclosure (Ex) distance (m)				Ecological threshold (m)*	Ecological threshold when exponential distribution of grazing intensity is considered (m)†
	Ex 1	Ex 2	Ex 3	Ex 4		
Mandalgobi	75.0	150.0	550.0	—	444.1	359.2
Bulgan	50.0	650.0	900.0	1500.0	484.1, 906.0‡	470.6, 1176.2

*Source of the data: Sasaki, Okayasu, Jamsran, et al. (2008). In searching for the ecological threshold, Sasaki, Okayasu, Jamsran, et al. (2008) used a piecewise regression model fitted to the floristic composition data for each transect, and simplified separately for each site by means of ordination.

†We also fitted a piecewise regression model to the scatterplot of the relationship between floristic composition data and ln-transformed distance at each site. We presented the back-transformed values for ecological threshold.

‡Sasaki, Okayasu, Jamsran, et al. (2008) identified two breakpoints in the compositional changes along the grazing gradient at this site.

and nonlinear replacement or decrease in plant cover at each site (Sasaki, Okayasu, Jamsran, et al., 2008): a rapid and nonlinear decrease in the shrub cover at the Mandalgobi site; and a rapid and nonlinear replacement between perennial grasses and weedy forbs at the Bulgan site.

Livestock Exclusion

We removed the impact of livestock grazing by establishing exclosures along the grazing gradient at each site in the summer of 2004 (Table 2). At Mandalgobi, we established three exclosures at set distances from the camp to the center of each exclosure: 75 m (Ex 1), 150 m (Ex 2), and 550 m (Ex 3). At Bulgan, four exclosures were established at set distances from the source of water to the center of each exclosure: 50 m (Ex 1), 650 m (Ex 2), 900 m (Ex 3), and 1500 m (Ex 4). Consequently, Ex 1 and 2 at Mandalgobi and Ex 1, 2, and 3 at Bulgan are in a post-threshold state. The study design thus allowed us to test the potential irreversibility of changes in vegetation dynamics caused by grazing in these Mongolian rangelands. The fenced-in areas were 15 × 25 m, 20 × 40 m, and 50 × 100 m, respectively, at Mandalgobi and 10 × 20 m, 30 × 30 m, 30 × 30 m, and 30 × 30 m, respectively, at Bulgan. Because larger fences near the livestock camp or source of water would have inconvenienced local herders, we established smaller fences. It would have also inconvenienced local herders if we had established the exclosures at set distances along several replicates of the gradient that ran in different directions. Hence, we decided to use a single gradient at each site and established a single exclosure at each distance along that gradient.

Vegetation Sampling

We sampled vegetation annually at the end of July at Mandalgobi and at the beginning of August at Bulgan, as these were the times of peak aboveground biomass between 2005 and 2010. We systematically established 10 pairs of 1 × 1 m permanent plots at each of the exclosures at the two sites, with one member of each pair inside the exclosure and the other member outside, for a total of 20 pairs of permanent plots. The pairs of plots on opposite sides of the exclosure were located at intervals of at least 2 m. Because the exclosure itself may influence results through edge effects such as differences in the degrees of livestock trampling and seed dispersal across the exclosure, we placed both plots in the pair at a distance of at least 3 m from the exclosure fence. We recorded the cover (%) of all plant species present within each plot. We also sampled vegetation annually from 2006 to 2010 in five 1 × 1 m permanent plots set at 2000 m from the gradient source, where livestock impacts were considered minimal (only very small amounts of dung could be found; Figure 1). Despite the lack of replication, we believe that the sampling effort (with large number of quadrats monitored over six consecutive years) is adequate to allow the detection of any general patterns in vegetation recovery after the exclusion of livestock grazing. Taxonomic nomenclature follows Grubov (1982).

Data Analysis

To assess the temporal patterns of changes in floristic composition for each permanent plot inside and outside each exclosure at each site between 2005 and 2010, we used detrended correspondence analysis (DCA) based on the cover value for each species. In this analysis, we included the floristic composition data from 2006 to 2010 in each permanent plot set at 2000 m from the gradient source where livestock impacts were considered minimal, to indicate a target community for restoration in an ordination space. We performed a multi-response permutation procedure (MRPP) over the first two DCA axes (using Euclidean distances with 10000 permutations) to examine the difference between the trends in floristic composition for the permanent plots inside exclosure in a post-threshold state and those in a pre-threshold state at each site. All statistical analyses were performed with version 2.10.1 of the R software (R Development Core Team, 2009).

Results

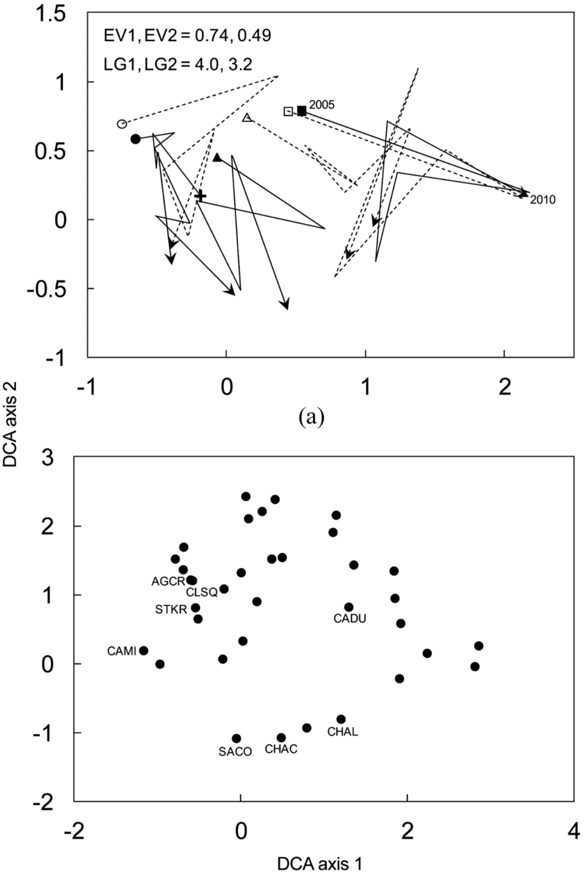
At both sites, changes in the floristic composition along the grazing gradient appeared along axis 1 of the DCA ordination across all years (Figures 2a and 3a). The floristic composition of the permanent plots varied to a greater or lesser extent in the ordination space from 2005 to 2010 at both sites. However, the permanent plots outside and inside each exclosure followed similar trajectories from 2005 to 2010.

The ordination for Mandalgobi showed a separation between the trajectories of Ex 1 and 2, which were in a post-threshold state, and that of Ex 3, which was in a pre-threshold state (MRPP, $P < 0.001$)(Figure 2a). The trajectories of Ex 1 and 2 had never reached the target community at 2000 m from the gradient source. *Caragana microphylla* Lam. (the dominant shrub at the site) and grasses such as *Agropyron cristatum* L., *Cleistogenes squarrosa* (Trin.) Keng, and *Stipa krylovii* Roshev. were arrayed to the left of axis 1 (Figure 2b).

At the Bulgan site, there was also separation between the trajectories of Ex 1, 2, and 3, which were in a post-threshold state, and that of Ex 4, which was in a pre-threshold state (MRPP, $P < 0.001$)(Figure 3a). Furthermore, there was a separation between the trajectories of Ex 1 and those of Ex 2 and 3 (MRPP, $P < 0.001$). The trajectories of Ex 1, 2, and 3 had never reached the target community at 2000 m from the gradient source. *Stipa gobica* Roshev. (the dominant grass at the site) was arrayed to the left of axis 1 (Figure 3b). *Peganum nigellastrum* Bunge (weedy perennial forb) and *Chenopodium album* L. (weedy annual forb) were arrayed to the right.

Discussion

Although we detected temporal variations in the floristic composition of the permanent plots, the trajectories of the paired permanent plots outside and inside each exclosure were similar from 2005 to 2010 (Figures 2a and 3a). We suggest that these trajectories did not reflect a vegetation restoration pathway after livestock exclusion, but might be instead mostly associated with yearly changes in rainfall (Table 1) and with annual phenological changes in the plant communities. Post-threshold states at both sites did not reach their respective target community for restoration, indicating the lack of restorability despite livestock exclusion. In addition, there is a boundary between the trajectories in floristic composition for the permanent plots inside exclosure in the post-threshold state and those in the pre-threshold state at both sites (Figures 2a and 3a). An additional separation among vegetation in a post-threshold state at Bulgan (i.e., Ex 1 vs. Ex 2 and 3; Figure 3a), which probably reflected the existence of two breakpoints in the compositional changes along the grazing gradient



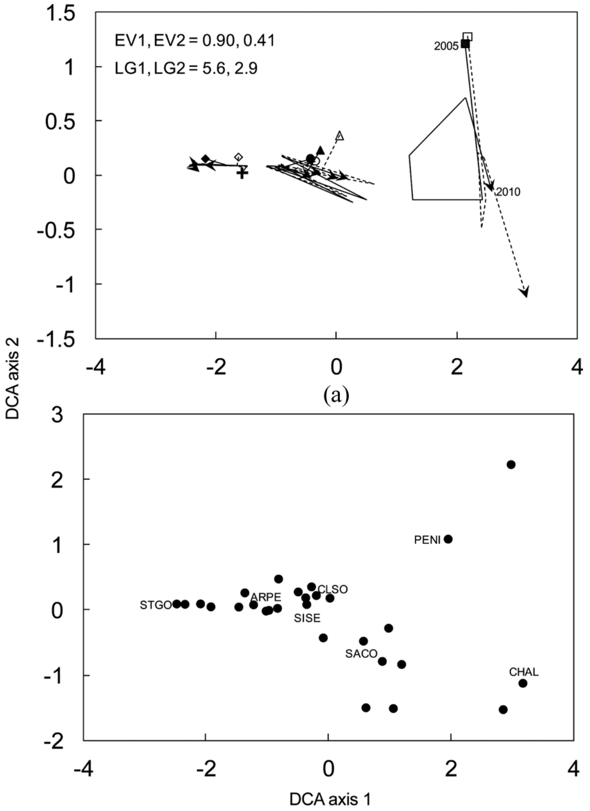
(a)

(b)

Figure 2. DCA ordination of the floristic composition data at the Mandalgobi site. (a) Trends in floristic composition from 2005 to 2010 (indicated by arrows). The centroids of all permanent plots outside (Op) and inside (Ex) each exclosure are shown: Op 1 (□), Ex 1 (■), Op 2 (△), Ex 2 (▲), Op 3 (○), and Ex 3(●). The centroid of all permanent plots set at 2000 m from the gradient source (where the impacts of grazing considered minimal) is represented by + to indicate a target community for restoration. The first and second axes eigenvalue (EV1, EV2) and length of gradient (LG1, LG2) are also shown. The MRPP revealed the difference between the trends in floristic composition for the permanent plots inside exclosure in a post-threshold state (Ex 1 and 2) and those in a pre-threshold state (Ex 3)($P < 0.001$). (b) Ordination of species; species codes for the common species only: AGCR, *Agropyron cristatum* L.; CADU, *Carex duriuscula* C. A. Mey.; CAMI, *Caragana microphylla* Lam.; CHAC, *Chenopodium acuminatum* Willd.; CHAL, *Chenopodium album* L.; CLSQ, *Cleistogenes squarrosa* (Trin.) Keng; SACO, *Salsola collina* Pall.; STKR, *Stipa krylovii* Roshev.

(Table 2). This evidence suggested that a contrasting state is maintained even after livestock exclusion and that vegetation changes beyond ecological thresholds may be irreversible in the studied systems (Suding & Hobbs, 2009).

When biotic structures and interactions are modified by grazing impacts, they are assumed to reveal the presence of an ecological threshold (Briske et al., 2006). Sasaki, Okayasu, Jamsran, et al. (2008) suggested that the ecological threshold in



(b)

Figure 3. DCA ordination of the floristic composition data at the Bulgan site. (a) Trends in floristic composition from 2005 to 2010 (indicated by arrows). The centroids of all permanent plots outside (Op) and inside (Ex) each exclosure are shown: Op 1 (□), Ex 1 (■), Op 2 (△), Ex 2 (▲), Op 3 (○), Ex 3(●), Op 4 (◇) and Ex 4 (◆). The centroid of all plots set at 2000 m from the gradient source (where the impacts of grazing considered minimal) is represented by + to indicate a target community for restoration. The first and second axes eigenvalue (EV1, EV2) and length of gradient (LG1, LG2) are also shown. The MRPP revealed the difference between the trends in floristic composition for the permanent plots inside exclosure in a post-threshold state (Ex 1, 2, and 3) and those in a pre-threshold state (Ex 4)($P < 0.001$). (b) Ordination of species; species codes for the common species only: ARPE, *Artemisia pectinata* Pall.; CHAL, *Chenopodium album* L.; CLSO, *Cleistogenes songorica* Roshev.; PENI, *Peganum nigellastrum* Bunge.; SACO, *Salsola collina* Pall.; SISE, *Sibbaldianthe sericea* Grub.; STGO, *Stipa gobica* Roshev.

vegetation change reflected a rapid and nonlinear decrease in the shrub cover at the Mandalgobi site. Recovery of the post-threshold state may possibly be retarded by positive feedback between decreasing the shrub cover and increasing wind erosion (Sasaki, Okayasu, Shirato, et al., 2008). At the Bulgan site, Sasaki, Okayasu, Jamsran, et al. (2008) suggested that the ecological threshold reflected a nonlinear and rapid replacement of perennial grasses by weedy perennial and annual forbs. Dominance of weedy perennial and annual forbs in the post-threshold state may possibly constrain recovery through establishment limitation of perennial grasses

(Coomes et al., 2003). Although theory suggests that some interactions or positive feedbacks among system elements could contribute to the existence of alternative stable states (van de Koppel et al., 1997), field experiments that include manipulation of biotic structures, abiotic environments, or both, and theoretical predictions based on these manipulations, will be required to provide a definitive examination of potential interactions or positive feedbacks.

Thus, our study generally demonstrated that vegetation in a post-ecological threshold state may not recover after short-term livestock exclusion in the study areas. This suggests that the plant communities may perhaps cross a critical threshold and shift into an alternative stable state as a result of severe livestock grazing.

Implications for Restoration

In real ecosystems, an explicit determination of thresholds representing boundaries between alternative stable states as defined in ecological theory remains a considerable methodological challenge (Radford et al., 2005; Bestelmeyer, 2006). The present study cannot exclude the possibility that long-term restoration would eventually lead to recovery of the post-threshold states to their respective target community. Nonetheless, our results may represent a change of vegetation state across ecological thresholds is irreversible within a realistic management time frame (Friedel, 1991); land managers often do not have the luxury of waiting for eventual recovery that may perhaps take more than decades. In our previous work (Sasaki, Okayasu, Jamsran, et al., 2008), we demonstrated that an ecological threshold corresponding to abrupt changes in ecological responses will more readily translate into management guidelines. Moreover, Sasaki, Okayasu, et al. (2009) suggested that high rainfall variability in arid and semi-arid rangelands may modify the effects of long-term exclosure on vegetation. In the context of seeking the most cost-effective management options in such highly stochastic systems, local management practice should therefore include alternative management options such as preventive management based on the concept of ecological thresholds (Sasaki, Okayasu, Jamsran, et al., 2008). It remains a future task to provide options for the restoration of the post-threshold states such as fertilization or planting of shrubs (e.g., Cao et al., 2009; Li et al., 2009). An essential part of the decision-making process involves evaluating the evidence for, and the uncertainty of, threshold behavior in a given management situation (Suding & Hobbs, 2009). Thus, our study complements the importance of ecological indicators (i.e., the cover of certain plant functional groups) of approaching an ecological threshold (Sasaki et al., 2011). In addition, utilizing such indicators as information sources can help managers to recognize that adverse changes in vegetation state beyond the ecological threshold might essentially be irreversible.

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